Ecosystem functioning in streams under pressure

Understanding the roles of biotic, abiotic and spatial drivers

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Ecosystem functioning in streams under pressure - Understanding the roles of biotic, abiotic and spatial drivers.

Abstract

What will happen if human populations are not able to rely on Earth's ecosystems to deliver fundamental benefits in a near future? Stream ecosystems provide several essential services to human civilizations, but are currently under threat from multiple anthropogenic pressures. These pressures give rise to stressors that impact biodiversity, ecosystem functioning, and ultimately ecosystem service delivery from streams. Based on a novel synthesis of the literature, I developed a framework integrating the roles that communities, environment and spatial drivers play in regulating ecosystem processes, further applied in field studies and an experiment.

In field studies, I assessed the variation in community structure of four taxonomic groups, and several ecosystem processes, along gradients of increasing pressure from agriculture, river regulation and forestry management. Ecosystem processes frequently varied along the pressure gradients, but the form of response typically contrasted, reflecting the complex interactions of abiotic and biotic factors that are into play. Environmental variables were shown to impact ecosystem processes either directly or indirectly through community-mediated responses. Changes in communities along a gradient depended on the associated stressors, the organism groups and the spatial scale at which they operate, and species traits were sometimes more responsive than species composition. Finally, my results from both the field and experimental studies highlight the importance of local and regional spatial scales for regulating the composition of communities and the processes they regulate, in particular for microorganisms.

Although policy frameworks mention the importance of ecosystem functioning in maintaining ecosystem services, the use of abiotic and taxonomic variables as indicators of human impacts on ecosystems remain the most common approach. My results reveal that community structure and specific aspects of ecosystem functioning might not always be strongly correlated, highlighting the importance of incorporating quantification of ecosystem processes in biomonitoring. Additionally, my results point towards the need to develop more spatially explicit biomonitoring schemes, able to account for position of sampling sites in the landscape.

Keywords: Abiotic factors, Anthropogenic stressors, Community ecology, Ecosystem functioning, Habitat patchiness, Pressure gradient, Recovery, Spatial connectivity, Species traits

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Ekosystemfunktioner under stress – att förstå påverkan från biotiska, abiotiska och rumsliga faktorer

Sammanfattning

Vilka blir konsekvenserna för mänskligheten om vi inte längre kan tillgodogöra oss jordens ekosystemtjänster? Vattendragens ekosystem bidrar med flera grundläggande tjänster som gynnar jordens befolkning, men som just nu är hotade av flera antropogena påfrestningar. Dessa påfrestningar ger upphov till stress som påverkar både biodiversitet, ekosystemfunktioner, och i slutändan även leveransen av ekosystemtjänster från vattendrag. Baserad på en litteratursyntes utvecklade jag ett ramverk som bedömer hur biologiska samhällen, miljön och rumsliga faktorer påverkar ekosystemprocesser, som vidare blev tillämpad i fältstudier och experiment.

I mina fältstudier har jag bedömt variationen i samhällsstruktur inom fyra taxonomiska grupper, och flera ekosystemprocesser längs en gradient av ökande påverkan från jordbruk, vattendragsreglering och skogsbruk. Ekosystemprocesser varierade frekvent längs gradienten för påverkan, men typen av respons kontrasterade ofta, något som återspeglar de komplexa sambanden mellan abiotiska och biotiska faktorer.

Miljövariablerna visade sig påverka ekosystemprocesser antingen direkt eller indirekt genom respons medförd av förändringar i samhällsstrukturerna. Ändringar i samhällen längs en gradient beror på den associerade stressen, organismgrupperna och rumsliga faktorer i vilka de verkar. Arternas egenskaper var ibland mer lättpåverkade än artssammansättningen. Slutligen, så visar mina resultat från både fält- och experimentstudier betydelsen av lokal och regional rumslig faktor för att reglera sammansättningen av samhällen och de processer som de reglerar, speciellt för mikroorganismer.

Även om policydokument nämner betydelsen av ekosystemfunktioner för att tillvarata ekosystemtjänster, kvarstår fortfarande bruken av abiotiska och taxonomiska variabler som indikatorer för mänsklig påverkan på ekosystem som det vanligaste tillvägagångssättet. Mina resultat avslöjar att samhällsstruktur och specifika aspekter av ekosystemfunktioner inte alltid är starkt korrelerade, vilket lyfter vikten av att inkludera kvantifiering av ekosystemprocesser i biologisk miljöövervakning. Vidare så pekar mina resultat mot ett behov av att utveckla mer rumsligt explicita övervakningsplaner för biologisk miljöövervakning, som tar hänsyn till positionen för provlokalerna i landskapet.

Nyckelord: Abitotiska faktorer, Antropogen påverkan, Artegenskaper, Ekosystemfunktioner, Fragmenterade habitat, Påverkansgradient, Rumsliga samband, Samhällsekologi, Återhämtning

Fonctionnement des écosystèmes fluviaux – Roles des facteurs abiotiques, de la biodiversité et des échelles spatiales.

Résumé

Que se passera-t-il lorsque les Hommes ne pourront plus tirer profit des écosystèmes que la planète offre? Les écosystèmes aquatiques fournissent différents services aux civilisations humaines, mais sont actuellement menacés par leurs nombreuses activités. Ces activités engendrent des perturbations affectant la biodiversité, le fonctionnement des écosystèmes et par conséquent, les services écosystémiques qui en découlent. En rédigeant une synthèse de la littérature existante, j'ai pu délimiter un cadre théorique novateur qui prend en compte les effets des communautés, de l'environnement et des échelles spatiales sur les processus écosystémiques, cadre que j'ai ensuite appliqué à mes expériences sur le terrain et en mésocosme.

Les expériences menées sur le terrain m'ont permise d'évaluer les changements de structure de quatre communautés et des processus écosystémiques associés, le long de gradients croissant de perturbations environnementales, à savoir, l'agriculture, les barrages hydroélectriques et la gestion forestière. Le plus souvent, les processus écosystémiques variaient le long des gradients mais le type de réponse contrastait en fonction du processus étudié, reflétant les interactions complexes qui se jouent entre facteurs abiotiques et biotiques. En effet, les facteurs environnementaux ont un impact sur les processus écosystémiques soit directement ou soit indirectement, en affectant tout d'abord les communautés. Les changements au sein des communautés en réponse aux gradients dépendent des facteurs de stress associés aux-dits gradients, des organismes vivants eux-mêmes et de l'échelle spatiale qu'ils exploitent. Les traits fonctionnels des espèces ont parfois répondu de manière plus significative le long des gradients que la composition en espèces des communautés. Pour finir, les résultats tirés des expériences de terrain et en mésocosme soulignent l'importance des échelles locale et régionale pour la composition en espèces des communautés et des processus écosystémiques associés, en particulier pour les micro-organismes.

Bien que la politique environnementale européenne mentionne l'importance du bon fonctionnement des écosystèmes pour le maintien des services qu'ils fournissent, l'utilisation des facteurs abiotiques et des données taxonomiques afin d'évaluer les impacts anthropogéniques reste la norme. Mes résultats mettent en avant le fait que la structure des communautés et certains aspects des processus écosystémiques ne sont pas toujours corrélés, d'où l'importance d'inclure les processus écosystémiques dans les programmes de suivi environnementaux. Enfin, mes résultats montrent la nécessité de développer des programmes qui prennent en compte la position géographique de la rivière étudiée.

Mots-clés: Connectivité spatiale, Ecologie des communautés, Facteurs abiotiques, Fonctionnement des écosystèmes, Fragmentation de l'habitat, Perturbations environnementales, Rétablissement des écosystèmes, Stress anthropique, Traits écologiques

Dedication

To my children,
I hope to raise you with the same respect and love towards nature as my grand-parents and my parents did.

Les rivières ne se précipitent pas plus vite dans la mer que les hommes dans l'erreur.

Voltaire

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Truchy, A., Angeler, D. G., Sponseller, R. A., Johnson, R. K. & McKie, B. G.* (2015). Linking biodiversity, ecosystem functioning and services, and ecological resilience: Towards an integrative framework for improved management. *Advances in Ecological Research*, 53, pp. 55-96.

II Truchy A., Angeler, D. G., Sponseller, R. A., Ecke, F., Kahlert, M., Bundschuh, M., Johnson, R. K. & McKie, B. G. Responses of multiple structural and functional indicators along three contrasting disturbance gradients. (*Manuscript*).

III Truchy A.*, Göthe, E., Angeler, D. G., Ecke, F., Sponseller, R. A., Bundschuh, M., Johnson, R. K. & McKie, B. G. Partitioning spatial, environmental and community drivers of ecosystem functioning. (*Submitted manuscript*).

IV Truchy, A., Sarremejane, R., Muotka, T. Angeler, D. G., Mykrä, H., Huusko, A., Johnson, R. K., Sponseller, R. A. & McKie, B. G. Ecological connectivity and effects of drought on community structure and ecosystem function in a stream channel mesocosm. (*Manuscript*).

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The contribution of Amélie Truchy to the papers included in this thesis was as follows:

I Planned the study with co-authors. Had the main responsibility for compiling and synthesising the literature, and took the lead on writing the majority of sections.

II Planned the study with co-authors. Carried out field work sampling. Had the main responsibility for laboratory work, data handling, data analyses, interpretation and writing.

III Planned the study with co-authors. Carried out field work sampling. Had the main responsibility for laboratory work, data handling, data analyses, interpretation and writing.

IV Planned the study with co-authors. Carried out field work and experiments. Had the main responsibility for laboratory work, data handling, data analyses, interpretation and writing.

Additional papers

In addition to the papers included in this thesis, the author has contributed to the following papers:

I Ecke, F.*, Levanoni, O., Audet, J., Carlson, P. E., Eklöf, K. Hartman, G., McKie, B. G., Ledesma, J. L. J., Segersten, J., Truchy, A., Futter, M. N. (2017). Meta-analysis of environmental effects of beaver in relation to artificial dams. *Environmental Research Letters*, 12, pp. 113002.

* Corresponding author.

Abbreviations

AFDM	Ash free dry mass
B-EF	Biodiversity-ecosystem functioning
B-ES	Biodiversity-ecosystem services
BLAST	Basic local alignment search tool
CWM	Community weighted mean
DHRAM	Dundee hydrological regime assessment method
DNA	Deoxyribonucleic acid
DOC	Dissolved organic carbon
FPOM	Fine particulate organic matter
GIS	Geographical information system
MEM	Mixed-effect model
OTU	Operational taxonomic unit
PERMANOVA	Permutational multivariate analyses of variance
TOC	Total organic carbon
TP	Total phosphorus
VP	Variance partitioning
WFD	Water Framework Directive

1 Introduction

Water covers 71% of Earth's surface but freshwater environments only comprise a small portion of the hydrosphere (about 2.5%) and an even smaller proportion of the water is contained in rivers and streams (0.006%; Malmqvist & Rundle (2002)). These figures do not accurately reflect the true significance of freshwaters for the biosphere. Besides sheltering as much as 2 600 aquatic plants and 30% of the world vertebrates (Dudgeon et al., 2006), freshwater ecosystems provide multiple key ecosystem services, such as drinking water, mitigation of pollutants, recreational values and food (UNEP, 2005), sustaining human civilizations and life in general at the same time (Duffy, 2009).

Ecosystem services are defined as "the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life" (Daily, 1997). The concept was further refined in The Millennium Ecosystem Assessment (MEA) that divided ecosystem services into four categories. The first three of these categories encompass "final" ecosystem services that directly benefit humanity, namely provisioning, regulating, and cultural services. The fourth category includes "supporting" ecosystem services, corresponding to various ecosystem-level processes (UNEP, 2005) that underpin ecosystem functioning and delivery of final services.

The very services provided by streams also contribute to the attractiveness of running waters as magnets for human settlement and exploitation. Consequently, running waters are among the most highly exploited ecosystems in the world. Land-use modifications, water extraction for agricultural and industrial purposes, hydropower, transport and leisure activities are just a few of many human pressures affecting stream ecosystems (Malmqvist & Rundle, 2002, Vörösmarty et al., 2010). These anthropogenic pressures result in abiotic and biotic stressors (e.g. organic and inorganic pollution, altered flow regimes and spread of invasive species) that impact biodiversity, ecosystem stability and services (Craig et al., 2017, Vörösmarty et al., 2010). As a consequence, stream ecosystems are frequently highly degraded, and often unable to provide either supporting or final services at the same level as undisturbed systems.

The scale of threat posed by human activities to both diversity and ecosystem service delivery from stream ecosystems has motivated a recent research effort focussed on understanding the drivers underlying ecosystem functioning of streams and rivers. Ecosystem functioning is defined as “the joint effects of all processes [fluxes of energy and matter] that sustain an ecosystem” over time and space through biological activities (Naeem et al., 1999, Naeem & Wright, 2003, Reiss et al., 2009). Examples of ecosystem processes include the biomass production of primary producers, the biomass accumulation of the consumers (so-called secondary production), rates of nutrient cycling or rates of resource consumption, including decomposition of organic matter. Although the EU’s Water Framework Directive (WFD) mentions the importance of ecosystem functioning for understanding an ecosystem capacity to deliver ecosystem services, the WFD and other similar policy frameworks are still largely based on the use of abiotic or taxonomic variables as indicators of human impacts on ecosystem health (Feld et al., 2009, WFD, 2000).

Abiotic variables, such as nutrient concentrations, temperature, pH and sediment loads strongly regulate ecosystem processes such as litter decomposition (Hooper et al., 2005, Woodward et al., 2012). However, abiotic drivers often interact with each other in a synergistic (e.g. combined positive effects of nutrients and temperature on algal productivity) or antagonistic (e.g. counteracting effects of nutrients and deposition of fine sediments on algal productivity) fashion when influencing a given ecosystem process rate (Ferreira & Chauvet, 2011, Folt et al., 1999, Piggott et al., 2015). This can result in non-monotonic relationships between ecosystem functioning and environmental changes (Woodward et al., 2012). Moreover, these abiotic stressors can act at different scales: for instance, streams are affected by a range of local, regional and catchment-wide stressors such as alteration of flow regime, degradation of their hydromorphology, changes in sediment loads, accumulation of organic and inorganic pollutants and invasion by non-native species (Malmqvist & Rundle, 2002, Tockner et al., 2010, Young & Collier, 2009). Crucially, quantification of these abiotic factors can give direct insight into changes in the physico-chemical status of the water and stream environment (Fölster et al., 2014, Friberg et al., 2011), but not necessarily into whether these changes are having an effect on community structure or ecosystem function (McKie & Malmqvist, 2009, Townsend et al., 2008).

Despite the prominence given to ecosystem functioning in e.g. the WFD, most biomonitoring continues to focus on quantification of community structure and diversity along broad environmental gradients (Bunn & Davies, 2000). Partly, this is based on an expectation that community composition changes faster than ecosystem processes and presumably reflect the ecological integrity of their environments (Cranston et al., 1996, Friberg et al., 2005, Palmer et al., 2005). For instance, algae have been extensively used to assess nutrient pollution, while macroinvertebrates have been used to evaluate many types of impacts (Friberg et al., 2003, Heckmann & Friberg, 2005, Hering et al., 2006). However, metrics based on community structure and diversity of these groups (i.e. species richness, indices of species sensitivities to specific impacts) do not necessarily capture dynamics of ecosystem nutrient and energy cycling and transformation, or biological productivity, i.e. its performance with respect to ecosystem functioning and service delivery (Palmer & Febria, 2012). Therefore, approaches are needed to assess relationships between these processes and their underlying abiotic, biotic and spatial drivers, in order to clarify changes in ecosystem functioning along anthropogenic gradients.

Historically, an assumption underpinning ecological monitoring and assessment has been that changes in communities would be at least partly correlated with changes in ecosystem functioning (Cranston et al., 1996). Supporting this, biodiversity-ecosystem functioning (B-EF) research has often found a positive relationship between species richness and diversity and, ecosystem functioning (Balvanera et al., 2006, Hooper et al., 2005, McKie et al., 2008), albeit in often simplified experiments (but see Frainer et al., 2014). One explanation for this is that diverse communities are more productive because they contain key species that have a large influence on ecosystem productivity (e.g. plant biomass, Tilman et al. (1997)). Alternatively, diversity may enhance ecosystem functioning when the organisms regulating an ecosystem process are complementary to one another in their functional attributes (i.e. species traits) and patterns of resource use (Díaz & Cabido, 2001, Gessner et al., 2010, Loreau & Hector, 2001).

Biodiversity can also enhance the stability of functioning. For example, a greater biodiversity is more likely to encompass species belonging to the same functional group (comprising species that are functionally redundant, sharing similar functional traits), but responding differently to disturbances (Angeler et al., 2014, Yachi & Loreau, 1999). At larger (i.e. landscape scale) spatial scales and with greater temporal variability, a more heterogeneous environment increases opportunities for species to exploit more niches, disperse and colonise new ecosystems (Loreau et al., 2003). In this landscape context, diversity supports ecosystem stability and resilience by maintaining ecosystem functioning in the face of human disturbances (Elmqvist et al., 2003, Nystrom & Folke, 2001) because sensitive species can be replaced by functionally redundant species (Loreau et al., 2002, Naeem & Li, 1997, Yachi & Loreau, 1999).

My research has focused on understanding the roles that abiotic, biotic and spatial drivers play in influencing ecosystem functioning in stream ecosystems affected by human pressures. Through a novel synthesis of the literature and, field and experimental studies, I aimed at combining for the most part hitherto disparate lines of research related to B-EF, meta-ecosystem and resilience. As part of this, I investigated the effects of multiple human pressures (agriculture, river regulation, forestry management and drought) on community structure and ecosystem function. Increasingly, community structure and ecosystem function are studied together (Fernandez et al., 2016, Frainer & McKie, 2015), but my work builds on this by considering responses of multiple organism groups and ecosystem processes together, from small to large spatial scales, to multiple types of human pressure.

2 Objectives

In this thesis, I aimed at assessing the **drivers of ecosystem functioning in streams under anthropogenic pressures**, with a particular focus on studying the relationships between communities, ecosystem functioning and spatial processes, based on **experimental and correlative research, and a novel synthesis of the literature**.

To achieve this goal, I addressed the following questions:

- How do anthropogenic stressors, such as drought (**paper IV**), agricultural land use, forest management and river regulation associated with hydropower dams (**papers II & III**), affect stream communities and functioning? In particular, do metrics of community structure and function respond concordantly to anthropogenic disturbance, or does one type of metric respond more than others (papers **II & IV**)?

- What is the relative importance of different abiotic and biotic drivers for ecosystem functioning (**all papers**)? In particular, do they impact different ecosystem processes (**papers II, III & IV**) to a similar extent?

- What is the importance of spatial drivers in shaping stream ecosystem functioning, in relation to abiotic and biotic drivers (**papers I, III & IV**)? At what scale do spatial drivers operate (**papers III & IV**), and does greater spatial connectivity enhance the resilience of an ecosystem after a disturbance (**paper IV**)?

- Are species traits more responsive to disturbance than species composition (**papers I, II & III**)?

3 Methods

This thesis is based on a novel synthesis of the literature (**paper I**), a field study (**papers II & III**), covering 36 different streams, and an experimental study (**paper IV**). Throughout, I focussed on stream ecosystem processes that are linked to different organism groups, as summarised in Figure 1.

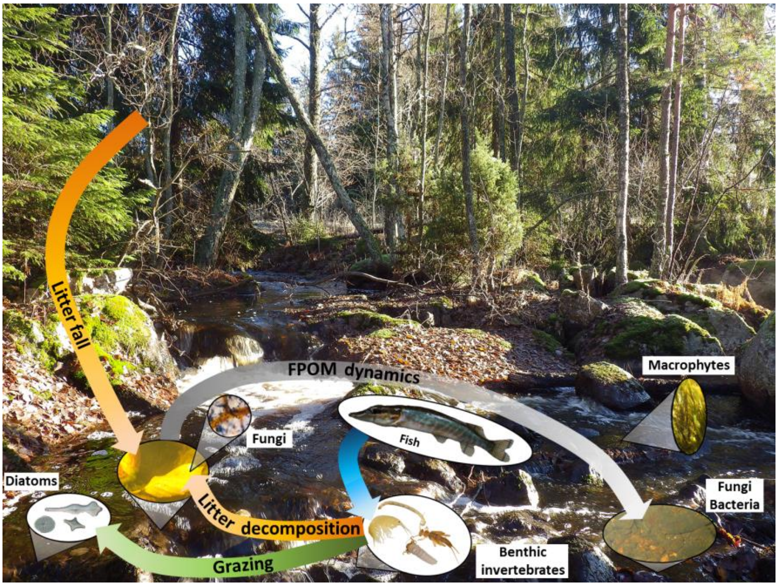

Figure 1. Diagram showing how the ecosystem processes I measured are linked to the organism groups sampled in my thesis. These organism groups also interact with each other and reflect a typical stream food web. Litter decomposition is a key ecosystem process that links terrestrial and aquatic ecosystems.

The literature synthesis (**paper I**) was based on a thorough review of literature relating to biodiversity, ecosystem functioning and services, and focussed on streams but encompassed all ecosystem types. This constitutes the framework within which my empirical work was conducted. The field studies investigated the relationships between environment, space, species composition and ecosystem functioning in situ along three pressure gradients (i.e. agricultural land use, river regulation and forestry management). The experiment was conducted to investigate how spatial arrangement of habitat and an enhanced connectivity with a regional species pool mediated the effects of a drought disturbance on community structure and/or ecosystem processes associated with heterotrophic and autotrophic pathways.

As the literature synthesis has no specific empirical methodology, the focus of my methods summary here is on the approaches used in my field and experimental studies.

3.1 Study sites & sampling design

3.1.1 Field study (papers II & III)

My field sites were located in three distinct regions in Sweden, to ensure coverage of strong anthropogenic pressure gradients (Figure 2). Within each region, I focussed either on agricultural land use (southern Sweden), river regulation (mid-Sweden) and forest management (northern Sweden), reflecting where these pressures are intense regionally, though all pressures commonly occur throughout the country. On each stream, I established a single sampling site which constituted the unit of replication, although some functional measurements were replicated within each sampling site.

All sites were characterised according to catchment land use, tree volume and stand age, and mapping of ditching networks extracted from GIS layers. In addition, I collected information on hydrological modifications (22 variables from GIS layers or modelled with DHRAM). For the river regulation gradient, I additionally obtained information on channelization and in-stream habitat simplification. I also measured local environmental variables, including water temperature, velocity and depth, stream width and slope, canopy cover, TOC and DOC, nutrient concentrations, pH, dissolved oxygen, alkalinity, turbidity and conductivity.

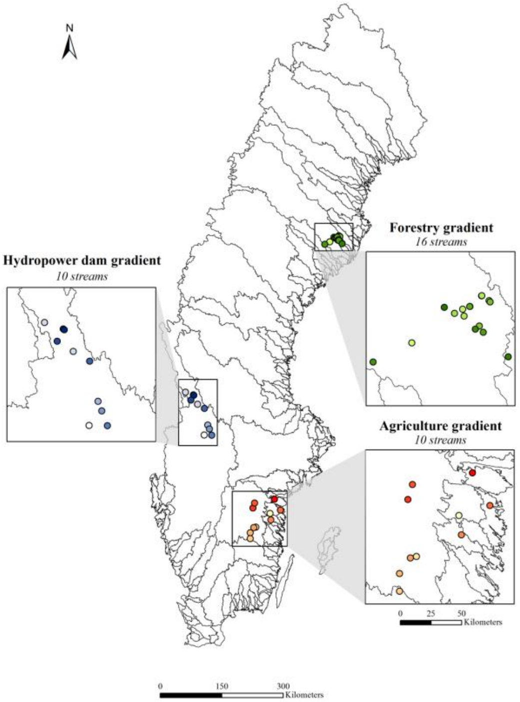

Figure 2. Location of my sampling sites across Sweden representing the three anthropogenic pressure gradients of interest. The forestry gradient comprised 16 streams in the province of Västerbotten (green circles), while the hydropower dam and agricultural gradients each consisted of 10 streams sampled in the provinces of Värmland (blue circles) and Östergötland (orange circles), respectively. Along each gradient, a colour ramp indicates the strength of impact with the less impacted streams being represented by light-coloured symbols, while the most heavily impacted sites are dark coloured. Along both the forestry and hydropower gradients, some sites were geographically so close to each other that their symbols overlap on the map.

3.1.2 Experiment study (paper IV)

My experimental study comprised a mesocosm experiment, run for six weeks at the Kainuu Fisheries Research Station, Finland (64°24'13.4"N, 27°31'23.0"E). I manipulated flow, habitat patchiness and ecological connectivity in 24 outdoors flow-through artificial stream channels (Figure 3). The experimental channels are permanently fed with water from a nearby stream channel, ensuring natural colonisation by invertebrates, algae and microorganisms.

I measured flow velocity in the channels (to calculate mean discharge), water depth, pH, conductivity, turbidity and dissolved oxygen. Temperatures were also recorded continuously during the study period using data loggers.

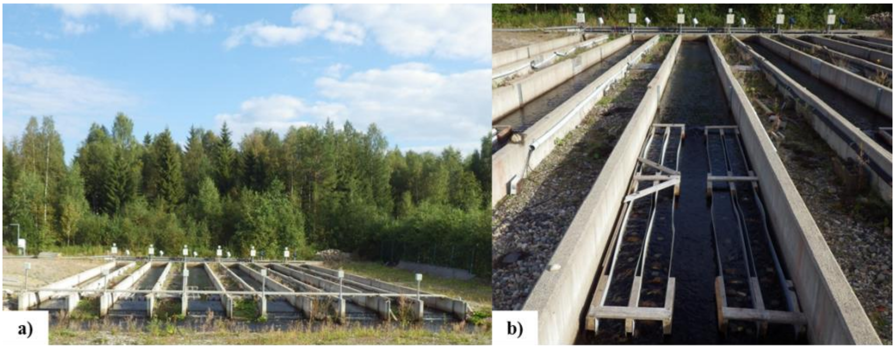

Figure 3. **a**) The stream mesocosms at the Kainuu Fisheries Research Station in Finland. **b**) Six main channels were divided into four sub-units. Each main channel had a valve system that allowed me to control discharge. In each of the 24 experimental channels, I manipulated habitat patchiness, flow and connectivity to a regional species pool.

Channel experiment design

In the experiment, I used a 2x2x2 factorial design: two levels of habitat patchiness (aggregated vs. evenly spaced), two levels of flow (constant flow vs. drought), and two levels of connectivity to a regional species pool (without vs. with enhanced connectivity).

For the habitat patchiness treatment, I manipulated the spatial arrangement of heterotrophic resources, comprising leaf litter and cotton strips that serve as both habitat and detrital resource for invertebrates and fungal decomposers. In the aggregated habitat treatment, ten litterbags were aggregated into two groups of five each, at the beginning and end of each channel. Five cotton strips were buried in the sediments under each litterbag aggregation. For the even distribution treatment, litterbags and cotton strips were spaced at regular 50 cm intervals.

Flow levels were kept similar between the 24 channels for the first 2.5 weeks of the experiment. I then reduced the discharge in 12 channels to mimic a low flow event that could arise as a result of drought, water abstraction, or river regulation associated with hydropower. After eight days of drought, discharge in the low-flow channels was returned to the same levels as the control channels, and no further flow manipulation occurred.

Just after the drought treatment concluded, benthic invertebrates were added to 12 of the subchannels to simulate enhanced connectivity with a regional species pool. These invertebrates were obtained from an adjacent stream and homogeneously distributed along the upper half of each channel, to simulate a dispersal event.

3.2 Ecosystem functioning

In both the field and channel experiments, I quantified several **different indicators of stream ecosystem functioning** (Figures 1 & 4). Some of these were direct measures of ecosystem processes (e.g. algal biomass accrual and litter decomposition), whilst others were variables from which strong inferences about functioning could be drawn (e.g. FPOM dynamics).

I measured **algal biomass accrual** as a measure of algal production, in **papers II, III & IV**. I used ceramic tiles anchored at the stream bottom and allowed algae to colonise and grow for about 30 days (Figure 4a). In **papers II and III**, the edges of four tiles were coated with petroleum jelly preventing access of grazing invertebrates to the algal resources. A benthotorch was used to measure the fluorescence of chlorophyll *a*, a proxy for algal biomass (Kahlert & McKie, 2014).

In **papers II, III & IV**, I used **leaf litter** enclosed in mesh bags (litterbags, Figure 4b) to assess how detritivore invertebrates and heterotrophic microbes influenced **organic matter decomposition** under anthropogenic disturbance. Birch leaves (*Betula* spp.) were collected at abscission and air-dried for two weeks. Litterbags were either constructed from coarse mesh (10 mm) or from fine mesh (0.5 mm, **papers II & III**; 0.25 mm, **paper IV**). These two different mesh sizes allowed the quantification of the microbial-mediated (fine bags) and microbial- + invertebrate-mediated (coarse bags) components of litter decomposition. I enclosed 5.0 ± 0.1g of air-dried leaves in both mesh-types of litterbags in **papers II & III**. In **paper IV**, I only used 3.0 ± 0.1g of air-dried leaves in coarse bags and 0.02 ± 0.001g in fine bags. In both the field and experimental studies, I aimed at reaching a 40-50% rate of decomposition, which reduces confounding effects related to decomposition stages (Frainer et al., 2017). After retrieval, leaves were rinsed under tap water, with invertebrates washed from the coarse bags picked and stored in 70% ethanol for later identification. 10-mm diameter leaf discs were cut from both coarse and fine (**paper II & III**) or only coarse bags (**paper IV**) for fungal biomass quantification (**papers II, III & IV**), and extraction of fungal DNA for characterisation of fungal communities based on next generation sequencing (**paper IV**). All remaining leaf material was subsequently oven-dried for 48 hours at 110°C and weighed to the nearest 0.001g. To correct for the confounding effects related to fine mineral sediments trapped on the leaves, the dried litter was then ashed at 550°C for four hours to obtain ash free dry mass (AFDM). Leaf decomposition rates *k* were calculated for each litterbag using the negative exponential decay model (Benfield, 1996):

$$-k = \frac{\ln(dry\ mass_{end}) - \ln(dry\ mass_{initial})}{\sum_{days} daily\ average\ temperature\ above\ zero}$$

Fungal biomass was estimated as ergosterol concentration, a component present in fungi cell membranes (Gessner, 2005). Ergosterol was extracted from freeze-dried leaf discs using high-performance liquid chromatography (HPLC) (**papers II, III & IV**). In **papers II & III**, ergosterol concentrations were used as a proxy for **fungal biomass**. I then calculated **fungal biomass accrual** corrected for temperature and days of exposure, based on an assumption that no fungal colonisation occurred prior to immersion in stream water (Krauss et al., 2005).

As an additional measure of organic matter decomposition mediated by microbes, I measured the **decline in tensile strength of cotton strips** in **paper IV** (Tiegs et al., 2013). My strips (8×2.5cm) were cut from woven cotton artist canvas (Figure 4c) and leached under running tap water for 24h prior to the experiment to remove any residual chemicals from the canvas manufacturing process. After weighing, the cotton strips were either placed in coarse bags or embedded in the sediments of the experimental channels. On retrieval, microbial respiration was measured, following which the cotton strips were dried at 40°C for 48h, and then weighed to the nearest 0.01g. To measure tensile strength, cotton strips were placed within the grips of a tensiometer and pulled apart at a fixed speed of $2 cm.min^{-1}$. Tensile loss was expressed as percent of the initial tensile-strength lost per day (Tiegs et al., 2013).

In **paper IV, microbial respiration measurements** were performed both on leaves from the fine bags and on cotton strips from coarse bags and the sediments (Figure 4d). These measurements were conducted on two occasions (post-drought and post-recovery periods). Cotton strips or leaves were placed in 80 mL containers filled with unfiltered channel water of known oxygen concentration (near 100%). Each container was sealed with transparent Parafilm M® (Bemis) and incubated in the dark for 3h. Some containers were filled with only water to correct for background O_2 changes throughout the incubation period. Microbial respiration was then calculated as the difference in O_2 between start and finish, corrected for background O_2 consumed, and dry weight of leaves or cotton strip.

In **paper II**, I included two extra indicators of ecosystem functioning that represent additional food web compartments: **fine particulate organic matter (FPOM) dynamics** and the **biomass accrual of an aquatic moss** (*Fontinalis dalecarlica*). *F. dalecarlica* was collected from two reference sites situated outside of my sampling regions. The green tips of the moss were cut, enclosed in fine bags (6.0 ± 0.1g), and deployed in the streams (Figure 4e). After retrieval, samples were rinsed under tap water, weighed to the nearest 0.01g, oven-dried at 60°C for 48h and weighed again. Initial dry weights were back calculated using a linear regression made from extra samples. The biomass accrual of *F. dalecarlica* was then calculated as a dry weight difference corrected for temperature and exposure days.

Figure 4. Indicators of ecosystem functioning used in my thesis. **a)** Algal biomass accrual on ceramic tiles anchored to the bottom of the stream with metal poles. The tile at the top-left corner was coated with petroleum jelly on its edges. **b)** Litter decomposition using litterbags. The green litterbag (coarse mesh) allows invertebrates to feed on the leaves, while the fine litterbag only allows for microbial-mediated decomposition. **c)** Cotton strips buried in the channel substrate. This method allows for quantification of organic matter decomposition mediated by microbes, quantified as a decline in tensile strength of the strips. **d)** Measures of microbial respiration on cotton strips. **e)** Green tips of *Fontinalis dalecarlica* were enclosed in fine bags to quantify the biomass accrual of this common aquatic moss. **f)** Astroturf mats collecting FPOM that was deposited on the stream bottom. Sand and inorganic material were also trapped but separated from the organic fraction burnt in the muffle furnace.

Suspended FPOM was sampled by filling a 1L water bottle at the water surface. To assess short-term FPOM deposition rates, Astroturf mats (Wolters et al., 2004) were attached at the stream bottom for three days (Figure 4f). Both types of samples were rinsed and filtered through a 0.063 mm sieve. For both suspended and deposited FPOM, retained material was oven-dried for 24 h at 60°C, weighed to the nearest 0.01 mg and ashed at 550°C for 4 h in order to get AFDM. I could then calculate the ratio suspended vs. deposited FPOM.

3.3 Biotic communities

Species composition of four different communities i.e. **benthic diatoms, macrophytes, benthic invertebrates** and **fish** (Figure 1, **papers II & III**) were sampled according to European and Swedish standard methods.

Additionally, I identified the **invertebrate detritivores** of leaf litter (known as shredders) that colonised the coarse litterbags to the lowest taxonomic level possible (**papers II, III & IV**). I also measured the length of these invertebrates to the nearest mm, and converted the length to biomass, based on formulae from Baumgärtner & Rothhaupt (2003) and Meyer (1989).

In **paper IV**, I quantified **fungal community composition** from the leaf discs from coarse litterbags using next generation DNA sequencing techniques. Operational taxonomic units (OTUs) were based on DNA sequences and fungal taxa identified with basic local alignment search tool (BLAST) procedure. I chose to work with both approaches because the BLAST procedure only identifies fungi that are indexed in the database, thus omitting a large component of community composition due to unidentified fungi taxa.

For each of these six communities (i.e. benthic diatoms, macrophytes, benthic invertebrates, fish, shredders and fungi), I computed **indices of community structure**: abundance, richness (as number of species), Shannon diversity index and Pielou evenness index.

For the purpose of **paper III**, I also gathered information about **species traits** for both benthic invertebrates and fish. The trait information were retrieved from Tachet et al. (2010) and Freshwaterecology.info database (Schmidt-Kloiber & Hering, 2015). For both communities, I focussed on traits most likely to represent the effects of organisms on ecosystem processes (i.e. functional effect traits, Truchy et al. (2015)). I further computed Community Weighted Means (CWM) to take into account the mass-ratio hypothesis (Grime, 1998), stating that the functioning of an ecosystem is determined to a large extent by the traits of the dominant species.

3.4 Data analyses

I used a number of different statistical tools in analysing my data, but the three most important were **mixed effect models** (MEM), **permutational**

multivariate analyses of variance (PERMANOVA) and **variance partitioning** analysis (VP).

MEMs are used to quantify the variation in a response variable that is attributable to variation in a set of predictors (fixed factors) and the random variation due to sampling units, such as in a split-plot design (random factors). The random factors can also be nested within each other. MEMs were run using the R package lme4 (Bates et al., 2015) in **papers II & IV**.

A PERMANOVA is analogous to a multivariate analysis of variance (MANOVA) and tests for differences in means between different experimental groups. PERMANOVA was used in **papers II & IV** using the R package vegan (Oksanen et al., 2015).

VP was the main analysis used in **paper III**. This statistical analysis allows partitioning the variation attributable purely to single sets of explanatory variables from the shared variation of two or more sets of explanatory variables. I used the R package vegan (Oksanen et al., 2015).

4 Results and discussion

Underpinning framework: Synthesis of the literature

In my synthesis of the literature on biodiversity, ecosystem functioning and services, I identified and integrated key insights into the abiotic, biotic and spatial drivers regulating ecosystem functioning. I gathered literature from different branches of ecology which have not always been well-integrated, such as meta-ecosystem ecology, biodiversity-ecosystem functioning (B-EF) and biodiversity-ecosystem service (B-ES) relationships, and ecological resilience. I considered a trait-based framework as a unifying approach in the assessment of ecosystem functioning and services. I also identified a set of "resilience attributes" for characterising ecological resilience, accounting for community structure, ecosystem functioning and service delivery. With this review, I developed a framework suitable for addressing impacts of human disturbances on ecosystem processes and the services they support but raised the still-existing uncertainties when linking species traits and interactions with ecosystem functioning and services.

How do anthropogenic stressors, such as drought, agricultural land use, forest management and river regulation, affect stream communities and functioning?

The vast majority of environmental impact assessments focus on species composition rather than ecosystem processes, partly because structural based approaches are better developed at the present time, but also because species composition is presumed to respond more rapidly to environmental change. This assumption is based on the ability of stress-tolerant taxa to maintain ecosystem functioning in disturbed ecosystems (Vinebrooke et al., 2004). Indeed, under disturbance, species-rich assemblages should enhance ecosystem functioning (*sensu* the insurance hypothesis, Naeem & Li (1997), Yachi &

Loreau (1999)) because they are more likely to include functionally redundant taxa or tolerant species that are able to cope with the new environmental conditions, and therefore compensate for the loss of more sensitive species (Elmqvist et al., 2003, Loreau et al., 2002).

I found ample evidence that **the complexity of anthropogenic stressors impact both community structure and ecosystem functioning** (Table 1). Agriculture and river regulation were associated with the strongest overall impacts, related to changes in species composition in three to four of the five communities I studied (**paper II**). The importance of hydromorphological variation was also observed in my experiment, which showed that drought resulted in negative impacts on microbial communities and the ecosystem processes they mediate (**paper IV**). These observations are consistent with earlier studies supporting the idea that agricultural land use and river regulation are major causes of degradation in stream ecosystems (e.g. Colas et al., 2016, Dejalon & Sanchez, 1994, Johnson et al., 2017, Martínez et al., 2013, Matthaei et al., 2010, Piggott et al., 2012), leading to alterations in community composition, life cycles/histories, access to and availability of habitats, and drought stress (Bragg et al., 2005, Lake, 2003, Poff & Zimmerman, 2010, Riis & Biggs, 2003, Ulvi et al., 2007). These gradients were also associated with the most extensive effects on functioning, indicating the pressures having strong effects on community composition can also result in impairment of ecosystem processes (Elosegi et al., 2010, Johnson et al., 2009, Jonsson, 2006, O'Connor & Donohue, 2013). However, changes in ecosystem functioning were not always associated with the same variables within each gradient as changes in community structure (McKie et al., 2009), and the form of relationship often contrasted between functional and structural measurements (Table 1; see below).

Surprisingly, I **did not detect any effects of forest management on any of the variables** I measured (Table 1). Instead, I found that community structure and ecosystem functioning responded to natural variation in environmental variables (i.e. TOC, TP, pH and alkalinity, **paper II**). A number of earlier studies have also failed to show consistent patterns of changes in community structure (Herlihy et al., 2005, Jonsson et al., 2017) and ecosystem functioning (Benfield et al., 2001, Lecerf & Richardson, 2010, McKie & Malmqvist, 2009) associated with forestry. These inconsistent responses can be related to i) the short-lived effects (0-10 years at the very most) of logging on biological communities (Herlihy et al., 2005, Hutchens et al., 2004) and, ii) the extent with which the catchment is affected by clear-cutting (e.g. 30% threshold proposed by Palviainen et al. (2014)). Only one of my study sites met both conditions, as such the lack of impact of forestry on stream ecosystem observed in my study does not necessarily apply to landscapes with more extensive clear-cutting.

Community structure and ecosystem processes rarely varied concordantly along the anthropogenic pressure gradients studied (Table 1), or in the experiment. For instance, litter decomposition rates in coarse bags were lower under dry conditions, while leaf-shredding invertebrates were not affected by the disturbance (**paper IV**). This finding likely reflects the fundamental role played by fungi in mediating litter decomposition, through direct enzymatic decomposition rending the litter more palatable to invertebrate detritivores (Bärlocher, 1992, Suberkropp et al., 1983). Another example is the agricultural gradient along which litter decomposition rates in the coarse bags were asymptotic while shredder community composition remained unaffected.

Overall, **ecosystem functioning responded more frequently to human stressors than community structure**, with 2/3 of the functional metrics responding (vs. 1/3 of the community metrics; Table 1). Notably, this conclusion could be drawn from both the field and the experimental study. This decoupling between changes in community structure and ecosystem function has been reported in the literature. For instance, McKie & Malmqvist (2009) showed no effects of forest clear-cuts on species composition of benthic invertebrates, while they observed increased litter decomposition rates and detritivore biomass in streams affected by clear-cutting. Together, these results suggest that ecosystem processes may not be as resistant to or do not recover as fast as the organisms mediating them. Hence, monitoring programs only based on metrics of community structure are likely to miss important ecosystem-level impacts of human stressors.

Table 1. *Summary table of the effects of anthropogenic disturbance on communities*[1] *and ecosystem functioning. Positive relationships are represented by blue arrows while, negative relationships are represented by red arrows. When no change was observed along a given disturbance, it is indicated with a black arrow. Hump-shaped and U-shaped relationships are displayed with green arrows. "Yes" means that the community composition changed significantly along the anthropogenic pressure gradients. NS stands for "Not studied".*

	Response	Agriculture	River regulation	Forest management	Drought
Diatoms	Community composition	Yes	No	No	NS
	Abundance				
	Richness				
	Shannon diversity				
	Evenness	↗			
Fungi	Community composition	NS	NS	NS	Yes
	Biomass				→
	Richness				→
	Shannon diversity				→
	Eveness				→
Macrophytes	Community composition	Yes	Yes	No	NS
	Abundance	↗			
	Richness				
	Shannon diversity				
	Evenness				
Benthic invertebrates	Community composition	Yes	Yes	No	Yes
	Abundance				↘
	Richness				↘
	Shannon diversity				
	Evenness				
	Functional composition	NS	NS	NS	Yes
Fish	Community composition	Yes	Yes	No	NS
	Abundance				
	Richness				
	Shannon diversity	↘			
	Evenness		↗		
Ecosystem functioning	Algal biomass accrual	→	↘		↘
	Fungal biomass accrual	↗	→		→
	Litter decomposition	C: ↱ F: ∧	↗		↘
	Microbial respiration	NS	NS	NS	↗
Shredders	Community composition	No	No	No	No
	Abundance		↘		→
	Richness				→
	Shannon diversity				→
	Evenness				→
	Total biomass	∨			→

What is the relative importance of different abiotic and biotic drivers for ecosystem functioning?

By definition, an ecosystem process involves interactions between species within the food web and with their environment (**paper I**, Gessner & Chauvet (2002)). Accordingly, **abiotic factors that affect species are potential drivers**

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[1] The responses of benthic invertebrates to drought are not detailed in this thesis but are part of a paper by Sarremejane et al. (in prep) originating from the same mesocosm experiment.

of ecosystem functioning. The most important abiotic variables in stream ecosystems appear to be temperature, light, nutrients, sediment loading and hydrological regimes (**paper I**); variables that are known to play a crucial role in organisms' development (e.g. Bott, 2006, Brown et al., 2004, Burrows et al., 2015, Hauer & Hill, 2006, Jones et al., 2012) and activities (i.e. the ecosystem processes they mediate, e.g. Burrell et al. (2014), Hladyz et al. (2011), McKie & Malmqvist (2009), Stanley et al. (2010), Young & Huryn (1999)). Therefore, understanding variation in ecosystem functioning based only on abiotic factors would rarely be complete – the ways in which those variables alter biodiversity and the activities of species also need to be accounted for.

Supporting this statement, I found that **environmental variables explained relatively small fractions of variation in ecosystem functioning**, compared to the significant, unique variation in functioning attributed to community composition (**paper III**). **15% of the variation in overall ecosystem functioning was explained jointly by community composition and the environmental variables** describing the studied streams (**paper III**), suggesting that effects of abiotic variables on ecosystem functioning are often mediated through effects on community composition (Jonsson, 2006, O'Connor & Donohue, 2013, Törnroos et al., 2015). This implies that biotic interactions, behaviour and even trait expression are at least as important as direct impacts of abiotic variables on ecosystem functioning (Brose & Hillebrand, 2016, McKie et al., 2009).

Interestingly, **responses of individual ecosystem processes to anthropogenic stressors were often not concordant** (**paper III**) with contrasting functional responses (linear, quadratic, asymptotic) to the same environmental gradients. This finding is similar to some previous studies that have observed divergent responses of different functional indicators along gradients of disturbance (Frainer et al., 2017, Young and Collier, 2009). While some functional indicators responded to the agricultural gradient (e.g. fungal biomass accrual and litter decomposition in coarse bags), other indicators displayed unexpected patterns, such as the lack of response of algal biomass accrual and litter decomposition in fine bags (Table 1, **paper II**). Nutrient enrichment associated with agricultural practices is known to enhance microbial responses (Gulis & Suberkropp, 2003, Young & Huryn, 1999). Therefore, I expected an increase in both algal biomass and litter decomposition along the agricultural gradient, as has been reported previously (Bott, 2006, Gessner et al., 2010, Tank et al., 2010). Similarly, algal biomass accrual decreased and litter decomposition increased along my river regulation gradient, contrasting with the body of literature (Dewson et al., 2007, González et al., 2013, Mbaka & Schäfer, 2015, Ponsatí et al., 2015). Discrepancies between studies may reflect the complexity of interactions among various stressors (Crain et al., 2008, Folt et al., 1999, Jackson et al., 2016), and difficulties to predict stress-response interactions from single-stressor experiments (Matthaei et al., 2010, Townsend et al., 2008). For example, neither algal productivity nor fungal biomass accrual display the increase that is typically seen in response to nutrient enrichment along agricultural gradients (Bernot et al., 2010, Tank et al., 2010). I hypothesised that the high turbidity associated with some of the agricultural sites (i.e. high levels of suspended sediments) negatively affected aquatic communities and limited algal and fungal growth.

These results are also reflected in the VP analyses ran on ecosystem processes separately (**paper III**). The unique fraction of variation was significantly explained by community composition for algal biomass accrual only. However, the variance explained jointly by community composition and environment ranged from 1% (litter decomposition in fine bags and fungal biomass accrual in coarse bags) to 56% (algal biomass accrual), showing that much of the variation in functioning arises from interactions between species and their environments. In particular, litter decomposition in coarse bags and algal biomass accrual showed the greatest variation explained by both community composition and environmental descriptors (20% and 56%, respectively), corroborating the idea that these ecosystem processes responded most strongly to the contrasting effects of the multiple stressors usually associated with anthropogenic pressures.

Finally, the mesocosm experiment revealed that microbially-mediated processes are key to understanding the effects of a disturbance, such as a drought, on ecosystem functioning (**paper IV**). Drought had strong effects on processes mediated by hetero- and autotrophic microbes, however in agreement with the field study, **ecosystem processes mediated by microbes did not respond in concordant fashion** (Table 1). Algal biomass accrual and litter decomposition in coarse bags decreased following the drought, while microbial respiration in coarse bags increased. These results highlight the crucial roles played by microorganisms in stream ecosystems (e.g. fungi for litter decomposition, diatoms for biofilms etc.). The strong and persistent negative effect of drought on algal biomass accrual shows the sensitivity of this process to short dry spells occurring late in the season, limiting the period for recovery of ecosystem processes mediated by algae before autumn die-back. This low degree of engineering resilience could have larger effects on food web structure and secondary production (Ledger et al., 2013, Ledger et al., 2011).

What is the importance of spatial drivers in shaping stream ecosystem functioning, in relation to abiotic and biotic drivers? Does greater spatial connectivity enhance the stability of an ecosystem facing a disturbance?

To answer this question, I had to broaden my knowledge of metacommunity theory (**paper I**). Habitat patches, such as leaf litter, are connected with each other by flows of organisms and materials at a broader spatial scale (i.e. regional scale) that may strongly influence ecosystem functioning at the local scale (Figure 5). For instance, immigration and emigration of organisms among litter patches can strongly influence the composition and diversity of species, traits, and species interactions at the local scale, with consequences for ecosystem processes (Cardinale et al., 2004, Hagen et al., 2012, Loreau et al., 2003, Massol & Petit, 2013). Moreover, empirical studies have shown a positive relationship between local and regional diversities and ecosystem functioning when habitat patches are well-connected (Matthiessen & Hillebrand, 2006). Within this framework, local habitat patches can be seen as sources-sinks for species, contributing to the maintenance of ecosystem functioning at the regional scale (Loreau et al., 2003, Mouquet & Loreau, 2003), by extending the pool of functionally redundant species (Naeem & Li, 1997, Yachi & Loreau, 1999).

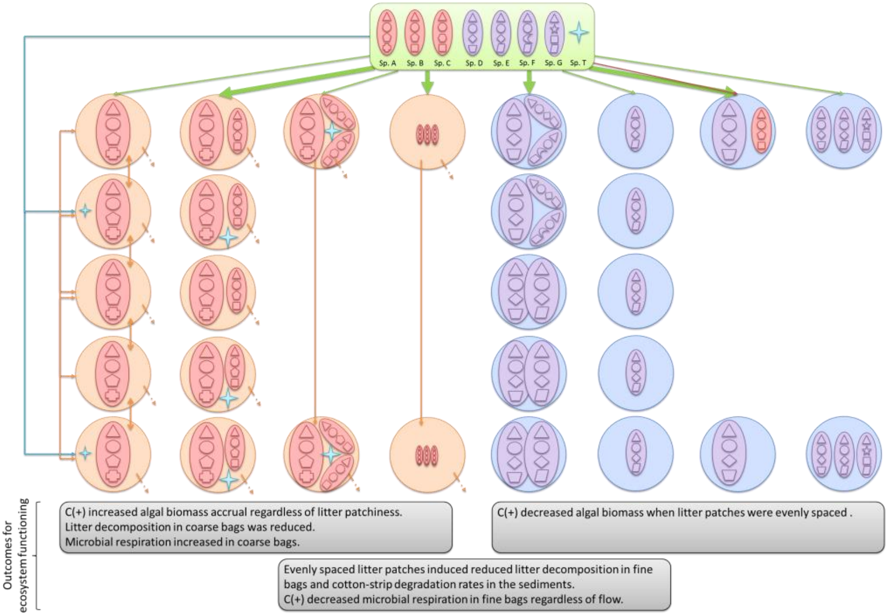
Applying this theoretical framework to my field study, I was only able to identify **spatial structuring of ecosystem functioning at the regional scale** (F = 11.62; $p<0.05$, **paper III**), suggesting stronger climatic and phenotypic influences on local ecosystem functioning. However, variation in ecosystem functioning was not only explained by environmental variables and community composition alone, but also by spatial location. **Space explained significant unique variation in ecosystem functioning that was often greater than the variation explained by environmental variables**. Moreover, combined, the three predictor matrices (i.e. spatial location, environmental variables and community composition) explained 53% ($p = 0.001$) of the total variation of stream ecosystem functioning, with sometimes **a highly significant joint variance component** (up to 56%). This points towards the importance of partitioning out the confounding spatial effects when working with large data sets to be able to assess “pure” environmental and community effects on ecosystem functioning.

The mesocosm study allowed me to experimentally assess how local and regional connectivity influenced the impacts of drought on stream communities and ecosystem functioning (**paper IV**). First, I was able to show that **both local and regional spatial scales are important for microorganisms and the ecosystem processes they mediate**. Indeed, litter patchiness affected both microbial communities and the ecosystem processes they mediate, such as organic matter decomposition (i.e. decomposition of leaf litter and cotton strips) (Figure 5). Litter patches close to each other were associated with higher fungal biomass but lower fungal richness and overall higher rates of organic matter decomposition in both surface waters and the stream substrate. These results contradict much of the literature suggesting that microbes are everywhere (Giller et al., 2004, Kivlin et al., 2014), due to many avenues of dispersal (Bärlocher, 1981, Bärlocher, 1992, Chauvet et al., 2016a). Three scenarios could explain the observed patterns: i) closeness between litter patches could favour retention of fungal spores and/or conidia at local scales, thus leading to an accumulation of potential colonising propagules, with a possible knock-on effect on litter decomposition (Gessner & Chauvet, 1994); ii) shredder invertebrates might first ingest fungal spores in one part of the litter patch, and then move to another part of the same patch. While feeding at the new location, invertebrates can excrete faecal pellets containing spores and hyphae (Bärlocher, 1981, Chauvet et al., 2016a), again boosting the local abundance of fungal spores, and enhancing litter decomposition (Jabiol et al., 2013); and iii) dispersal of fungi might be facilitated by the proximity of two litter patches. Fungi could disperse horizontally by extending their hyphae and transfer resources from nutrient-rich to nutrient-poor litter (Schimel & Hättenschwiler, 2007, Tiunov, 2009), or vertically towards the streambed enhancing organic matter decomposition embedded in the substrata (Bärlocher et al., 2006, Bärlocher et al., 2008, Chauvet et al., 2016a, Sudheep & Sridhar, 2012). These scenarios imply that contrasting fungal traits (e.g. enzymes associated with different fungal species) influence function over a given time period, whilst the second and third scenarios also involve potential nutrient subsidies (from faecal pellets or other detrital sources).

Enhanced connectivity with the regional species pool was associated with lower fungal biomass and lower respiration rates of microbes in the fine bags (Figure 5). These results corroborate the negative effects of regional connectivity on fungal biomass and diversity found in previous laboratory experiments (de Boer et al., 2014, Matthiessen et al., 2007, Matthiessen & Hillebrand, 2006). Two hypotheses can be formulated to explain these results: i) either the enhanced connectivity treatment introduced colonizing invertebrates that grazed more intensively on microbial biofilms, thereby reducing fungal biomass or, ii) the invertebrates were accompanied by other types of microorganisms (e.g. attached to their exoskeletons or in their guts) that altered the competitive balance within the established biofilms.

Additionally, I also detected significant two- and three-way interactions, indicating that **spatial distribution of habitat and level of ecological connectivity can moderate the response and recovery of communities to**

disturbance. Enhanced connectivity often led to a decrease in fungal biomass as well as diversity, but results depended on interactions with drought and litter patchiness (Figure 5). For instance, enhanced connectivity did not affect fungal biomass in dry channels when litter patches were aggregated; potentially indicating that drought affected the palatability of the litter for the colonising invertebrates. Further, enhanced connectivity, in combination with habitat



C(+) increased algal biomass accrual regardless of litter patchiness.
Litter decomposition in coarse bags was reduced.
Microbial respiration increased in coarse bags.

C(+) decreased algal biomass when litter patches were evenly spaced .

Evenly spaced litter patches induced reduced litter decomposition in fine bags and cotton-strip degradation rates in the sediments.
C(+) decreased microbial respiration in fine bags regardless of flow.

Figure 5. Applying the metacommunity framework to the design and outcomes of my mesocosm experiment. Orange patches represent litter patches subjected to drought conditions while blue patches are litter patches that are under constant flowing conditions. The trait characteristics of each species are represented by symbols overlaid onto the ovals (after Reiss et al., 2009) and species T is a terrestrial species. The biomass of the species is represented by the size of the oval (i.e. higher biomass, bigger oval). All species are represented in the regional species pool (green rectangle) and disperse to the local litter patches (green arrows). My enhanced connectivity treatment (i.e. addition of invertebrates to the experimental channels) is depicted with a bold green arrow. The distribution of species between drought and constant flowing conditions is in line with their environmental preferences and tolerance, reflecting the species-sorting paradigm (Leibold et al., 2004). Diversity in the litter patches is regulated by dispersal, with the arrows between patches representing dispersal pathways. Only arrows were drawn between litter patches in drought conditions for clarity. Dashed arrows from the litter patch represent dispersal pathways to the channel substrate. Species C persists in litter patches in constant flowing conditions as a steady flow of colonisers from the regional species pool maintains its presence under constant flow (red arrow), reflecting the mass-effect paradigm (Leibold et al., 2004). This source-sink dynamic enhances ecosystem functioning under constant flow despite the low fitness of species C in these environmental conditions and competition from more tolerant species (species D) to rapid flow. C(+) stands for enhanced colonisation (bold green arrows).

patchiness, played a role in the recovery of algae from a drought disturbance. However, this effect was relatively small compared to the main effect of drought, so that algal biomass remained lower in the channels subjected to drought, at the end of the experimental recovery period. Nevertheless, this finding points towards the potential for connectivity with a regional species pool to contribute to a “spatial insurance” for ecosystem functioning against a disturbance (Hagen et al., 2012, Loreau et al., 2003, Matthiessen & Hillebrand, 2006).

Are species traits more responsive to disturbance than species composition?

Traits are typically divided into two categories (**paper I**): (1) **response traits** that reflect the response of species to environmental conditions, such as environmental tolerance or ecological flexibility, and (2) **functional effect traits** that are related to the effects that species have on ecosystem processes, like resource acquisition or biomass production (Hooper et al., 2002, Lavorel & Garnier, 2002, Naeem & Wright, 2003).

First, by extending a trait-based framework for predicting outcomes for functional redundancy and ecosystem functioning (**paper I**), I highlighted the potential for a **greater redundancy of functional traits to allow the maintenance of functioning when an ecosystem is facing a disturbance**. Indeed, an ecosystem process that relies on unique traits acquired by sensitive species is more likely to be the first affected when stressor loads increase. Accordingly, it is possible to explore the mechanisms that link species traits and species interactions to ecosystem processes to further assist in ecosystem assessment and management (Craig et al., 2017).

Departures from trait-based predictions of functioning can be used to indicate where stressors are having a strong influence on ecosystem functioning (**paper I**). Biomass is a key driver of ecosystem processes, in line with basic relationships between body size and individual metabolism and energy requirements, and thus provides a good example of a functional effect trait. However, this was not clearly evident in our data for litter decomposition rates (Figure 6): while some sites with high shredder biomass also had high decomposition (e.g. the most impacted “outlier” site highlighted with an arrow), most of the other sites with high decomposition rates were agricultural sites whit lower total biomass of invertebrate shredders. In this case, it is likely that the high decomposition in more agricultural sites occurring despite the low shredder biomasses in most of these sites reflects the influence of nutrients (Gulis et al., 2006), and possibly high suspended sediments increasing physical abrasion of the litter (Piggott et al., 2012, Sponseller & Benfield, 2001). This example highlights the challenges faced by ecologists in identifying specific traits that can be tightly linked to ecosystem processes and functional diversity (Tilman, 2001).

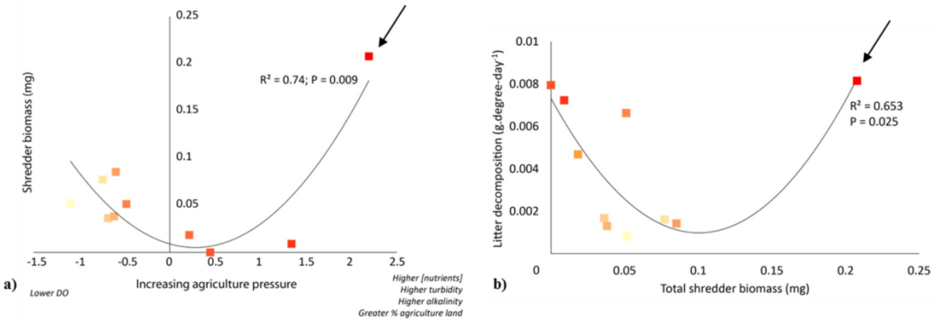


Figure 6. **a)** Impact of agriculture on the total biomass of shredders that can be used as a functional effect trait to explain patterns in litter decomposition along the gradient in **b)**. A colour ramp indicates the strength of impact with the less impacted streams being represented by light-coloured symbols and the most heavily impacted sites being dark coloured. The arrow highlights an outlier discussed in the text.

Finally, using species traits as predictors of ecosystem functioning revealed that **the amount of explained variation in ecosystem functioning was greater when species were characterised by their traits** rather than by their taxonomic identities (**paper III**). In particular, the residual variance dropped from 50% to 44% for the fish community. These results support the general idea that species traits better capture the characteristics of the species regulating ecosystem functioning (Enquist et al., 2015, Lavorel & Garnier, 2002). However, caution should be taken when allocating traits to large-scale datasets as developmental stages of organisms may vary between regions and therefore impact their feeding behaviours (Frainer & McKie, 2015, Layer et al., 2013).

5 Conclusion and future perspectives

In this thesis, I assessed the abiotic, biotic and spatial drivers of ecosystem functioning in streams under anthropogenic pressures using both field and experimental studies (Figure 7). The review paper (**paper I**) synthesised research on ecosystem functioning and highlighted the relevance of human stressors and spatial location when studying ecosystem functioning. This paper also revealed the difficulty of disentangling the effects of various drivers of ecosystem functioning. This challenge was then addressed in **paper II** when studying responses of ecosystem functioning along anthropogenic gradients. This study allowed for pattern identifications but also posed the question of the relevance of space, as the study sites were spread across three geographically-distinct regions. I therefore applied the meta-ecosystem framework on the same data set to take into account the landscape context of the study (**paper III**). With this paper, I was able to partition out the effects of space and revealed the pure effects of environmental variables and community composition on ecosystem functioning. However, a concrete assessment of the mechanisms driving ecosystem functioning in streams under disturbance was still missing. This point was addressed with an experiment in which I studied the stability of ecosystem functioning after a disturbance (**paper IV**). Finally, **papers II-IV** were also designed to address the knowledge gaps identified in **paper I**.

Although agriculture, river regulation and drought impact both community structure and ecosystem functioning, a higher proportion of functional metrics responded to anthropogenic gradients than the community structure metrics I tested. However, ecosystem processes did not respond concordantly to the gradients and this is likely due to the contrasting effects of abiotic variables that are often associated with a pressure gradient. Indeed, abiotic factors can interact with each other and impact ecosystem processes either directly or indirectly through effects on communities, potentially decoupling the responses of community structure and ecosystem functioning. Effects on community structure depended on the pressure gradient of interest, with different organism groups displaying changes in species composition, richness or evenness along different gradients. Furthermore, species traits explained more variation in ecosystem functioning than did community composition. Finally, I showed that both local and regional scales influenced communities and the ecosystem processes they mediate, sometimes even exceeding the amount of variation explained by abiotic factors. In particular, the spatial distribution of habitat patches and the level of regional connectivity moderated the responses and the recovery of communities to disturbance in my experiment, enhancing the maintenance of ecosystem functioning.

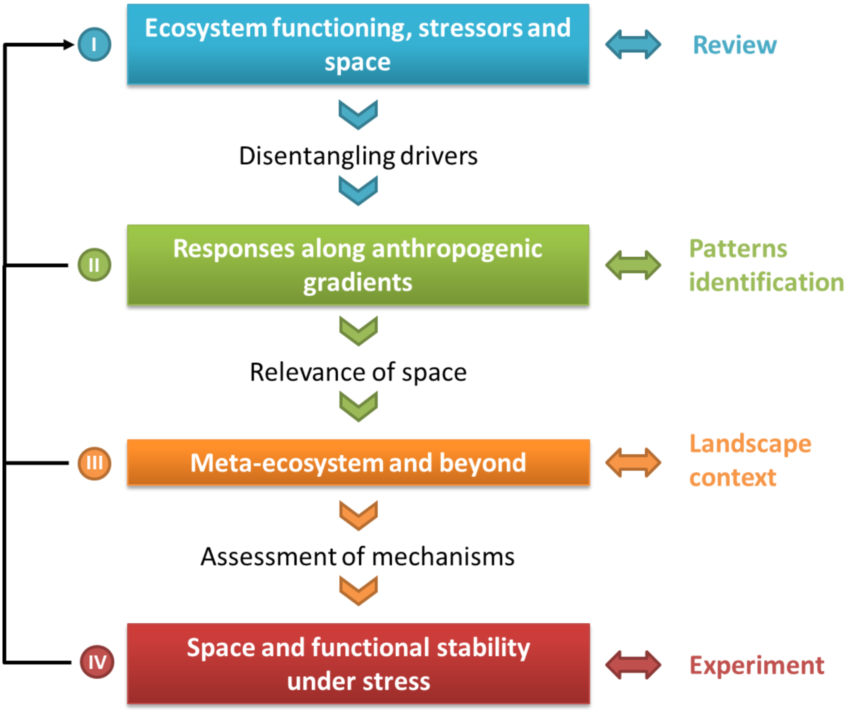


Figure 7. Summary figure of the structure of my thesis.

My findings have major implications for the development and use of ecosystem functioning in monitoring of aquatic ecosystems. Biomonitoring of aquatic environments is essential in order to detect changes in ecosystem properties that might impact biodiversity and the delivery of ecosystem services, and provide a solid empirical basis for guiding the development of management programs. Ecological assessment programs are usually designed to investigate if ecosystem attributes are adequate to sustain biodiversity, ecological processes and services of interest (Friberg, 2010, Friberg et al., 2011). In recognition of the importance of freshwaters for biodiversity and ecosystem services, the European Union’s Water Framework Directive (WFD) set the goal that all water bodies in Europe should achieve “good” ecological status by 2015 (WFD, 2000). In this context, the selection of the methods to assess human impacts on streams, and to assist in identifying which impacts are having the strongest effects on ecological integrity, is crucial (Feld et al., 2009, Pardo et al., 2012). For instance, if the focus is on biodiversity conservation, community structures would be monitored as a first choice. On the contrary, if priority is set on final ecosystem functioning and service delivery then ecosystem processes should be monitored closely.

Although direct measurements of ecosystem processes are likely to be essential in understanding human impacts on ecosystem dynamics (Gessner & Chauvet, 2002, Young & Collier, 2009, Young et al., 2008), they remain under-used in stream monitoring programs (Bunn, 1995, Chauvet et al., 2016b, Feld et al., 2009), mainly because environmental policies such as the WFD do not give clear guidelines regarding which functional properties to include. Gessner & Chauvet (2002) recommended using litter decomposition as the primary indicator of stream functional integrity, since decomposition rates reflect the effects of disturbance on multiple organism groups across multiple spatiotemporal scales. However, given the contrasting responses of ecosystem processes to anthropogenic gradients, my results rather point towards the need for a multi-functional approach (i.e. quantification of multiple ecosystem processes at the same time). Moreover, species traits could be integrated in monitoring programs and used to detect losses of functional diversity and redundancy, and therefore predict the impacts of anthropogenic stressors on communities, ecosystem functioning and services.

Finally, my results highlighting spatial structuring of ecosystem functioning, reflecting the multiple spatial scales over which species and stressors operate and interact, advocate for the development of spatially explicit monitoring programs. Indeed, integrating functional-based approaches into monitoring programs have great potential to account for ecological connectivity among habitat patches at the regional or national scale and its subsequent consequences on ecosystem functioning at the local scale, using for example nested sampling designs encompassing different spatial scales (Downes et al., 1995, Durance et al., 2016, Göthe et al., 2013).

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Popular science summary

How do streams cope with stress?

Two years ago, I was challenged to take part in a competition that required presentation of my PhD project within two minutes. And guess what? I failed! But this made me think about how to present my research theme using non-scientific words. I am ready now to take up this challenge.

No one can deny that human population is growing at unprecedented rates. For being able to meet the needs of this growing population, we are putting more and more stress on ecosystems. For example, agriculture is becoming more and more intensive to increase productivity per square meter of farmland, ever-larger hydropower dams are being constructed on rivers in order to get electricity, and forests are managed to maximise wood production and efficiency of forest harvesting. What I have tried to understand during the past four years is how streams respond to the stress imposed by these human activities, and to consider not just how the local environment has changed, but also the importance of where a particular stream is positioned within the landscape.

To do so, I went out in the field and collected some data on the organisms living in streams, such as fish, insects, plants and small algae and fungi. These organisms play important roles in rivers: by their activities, they ensure efficient cycling of energy and nutrients, underpinning good functioning of the ecosystem. Healthy ecosystem functioning of freshwaters is essential for provision of key ecosystem services, like delivery of clean water for drinking and agriculture purposes. Organisms also act at different spatial and temporal scales. For instance, fungi and bacteria develop for some time on a pack of leaves trapped among some rocks in a stream but also play important roles for the whole stream ecosystem, such as respiration and nutrient cycling. I therefore decided to quantify some of the organisms' activities by using simple measures: the speed with which algae and fungi grow or leaves degrade.

I was able to rank the stressors I studied: stress imposed by agriculture and dams were the worst for the organisms living in rivers. But that said, organism groups responded differently to a given stress, with small organisms being more affected than expected. Also, I could demonstrate that it was not all about what the species groups are made of, but what they actually do. Finally, I was able to prove that spatial scales indeed regulate organisms' interactions and their activities – where a stream is in a landscape is important for understanding the way it functions and the biodiversity it supports.

I know what you are thinking… What for? This kind of research is actually of everyone's concern. We take advantage of rivers in our everyday life without even noticing. Have you ever thought about a life without drinking water? What if we cannot grow crops anymore because we are lacking water and the streams are not able to absorb the excess nutrients and pollutants we subjected them to? To really understand these impacts, we need to integrate more information in monitoring programs not only on what organisms are present, but also on how the streams purify water or absorbs nutrients. It is going to take some time until policies really take into account the importance of using measures of organisms' activities. Fortunately, the methods for quantifying how ecosystem functions already exist, as demonstrated by their use in my research!

Populärvetenskaplig sammanfattning

Hur orkar vattendragen med stress?

För två år sedan blev jag utmanad att delta i en tävling som gick ut på att presentera mitt doktorandprojekt på mindre än två minuter. Vad hände? Jag misslyckades! Men det fick mig att tänka på hur jag kan beskriva mitt forskningsområde i enklare ordalag. Jag är nu redo att återuppta utmaningen!

Ingen kan förneka att världens befolkning växer snabbare än någonsin förr. Vi utsätter våra ekosystem för mer och mer stress och påfrestningar för att kunna möta behoven för den växande befolkningen. Till exempel blir jordbruket mer och mer intensivt för att öka produktiviteten per kvadratmeter jordbruksmark, större och större dammar byggs längs våra vattendrag för att producera elektricitet och skogsbruket bedrivs för att maximera virkesproduktionen och effektiviteten vid skörd av skogen. Det jag har försökt förstå mig på under de senaste fyra åren är hur bäckar och mindre åar (vattendrag) påverkas av de störningar och påfrestningar som mänskliga aktiviteter har på vår miljö, och att ta hänsyn till inte bara hur den lokala miljön har förändrats, utan också betydelsen av ett vattendrags position i landskapet.

För att åstadkomma detta så åkte jag ut i naturen och samlade data om organismerna som lever i bäckar. Organismerna kunde vara fisk, insekter, växter och små alger samt mikroskopiska svampar. Dessa organismer spelar en viktig roll i vattendragen. Genom sina aktiviteter försäkrar de att energi och material rör sig och omvandlas i miljön, och på så sätt bidrar till ett välfungerande ekosystem. Välmående ekosystemfunktioner i sötvatten är avgörande för att tillhandahålla grundläggande ekosystemtjänster, som rent vatten att dricka och jordbruksprocesser.

Organismer verkar också på olika skalor, både i tid och rum. Som exempel, på den lilla skalan kan mögelsvampar och bakterier växa en tid på en grupp med löv, fångad bland några stenar i vattendraget, men också spela en viktig roll i hela ekosystemet i vattendraget, så som respiration och näringscirkulering. Därför bestämde jag mig för att uppskatta aktiviteterna för några av organismerna i vattendragen, genom att bruka enkla tillvägagångssätt: hur snabbt alger och mikroskopiska svampar växer till eller hur löv bryts ned.

Jag lyckades med att rangordna de olika påfrestningarna som jag hade studerat. Resultaten visade att påverkan från jordbruk och vattendammar hade värst effekt för de vattenlevande organismerna. Men med det sagt, även inom en viss grupp av organismer så reagerade organismerna olika på samma typ av påfrestning, där de små organismerna blev mer påverkade än väntat. Jag kunde också visa att det inte bara handlar om vilka arter som organismgrupperna bestod av, utan också vilken aktivitet de faktiskt utförde. Slutligen kunde jag bevisa att den rumsliga utbredningen verkligen påverkade organismernas interaktioner och aktiviteter. Var ett vattendrag ligger i landskapet är viktigt för att förstå hur det fungerar och den biodiversitet det stöttar.

Jag vet vad du tänker… Varför behöver vi veta det här? Svaret är att den här typen av forskning är en angelägenhet för alla. Vi utnyttjar våra vattenresurser dagligen i vardagslivet, utan att ens reflektera över det. Har du någonsin funderat över hur vårt moderna liv skulle se ut utan rent dricksvatten? Tänk om vi inte skulle kunna odla mat på grund av vattenbrist och att vattendragen inte klarar av att absorbera all näring och förorening som vi utsätter dem för. För att verkligen förstå denna påverkan måste vi integrera mer information i miljöövervakningsprogrammen, inte bara om vilka organismer som finns, utan också om hur vattendraget renar vatten eller absorberar näring. Det kommer att dröja länge innan policys och styrdokument ser nyttan av att använda organismers aktiviteter som måttstock för ekosystemens välbefinnande. Som tur är så finns det redan metoder for att mäta ekosystemfunktioner, som jag har visat genom deras användning i min forskning!

Résumé en Français

Comment les rivières font-elles face au stress ?

Il y a deux ans, j'ai été mise au défi d'expliquer mon projet de thèse en deux minutes. Et devinez quoi ? Je n'ai pas réussi ! Mais cela m'a permis de réfléchir à comment présenter mon projet de recherche en utilisant des mots simples. Je suis maintenant prête à relever ce défi.

Personne ne peut nier le fait que la population humaine ne fait que de croître. Afin de répondre à tous nos besoins, nous dégradons de plus en plus les écosystèmes. Par exemple, notre agriculture devient de plus en plus intensive de manière à augmenter le rendement des terres agricoles, des barrages de plus en plus gros sont édifiés pour produire de l'électricité et les forêts sont gérées afin de maximiser la production de bois. Pendant ces quatre années, j'ai essayé de comprendre comment les rivières font face aux stress que nous leur imposons en ne considérant pas seulement les changements à l'échelle locale, mais aussi la position de la rivière dans le paysage.

Pour ce faire, je suis allée sur le terrain et j'ai collecté des données sur les organismes vivants des rivières, tels que les poissons, les plantes et les algues et champignons microscopiques. Ces êtres vivants jouent un rôle important dans les rivières: leurs activités permettent le maintien des cycles d'énergie et des nutriments, et de ce fait le bon fonctionnement de l'écosystème. Avoir des écosystèmes aquatiques qui sont en bonne santé est essentiel pour l'approvisionnement en eau potable et l'irrigation des cultures, des fonctions qui sont des services rendus par les écosystèmes aux hommes. Les organismes vivants agissent aussi à différentes échelles spatio-temporelles. Par exemple, des champignons et bactéries peuvent se développer un temps sur un petit agglomérat de feuilles coincé entre deux cailloux, mais ces organismes vivants jouent également un rôle pour l'ensemble de la rivière, tels que la respiration ou le cycle des nutriments. J'ai donc décidé de mesurer certaines des activités de ces êtres vivants en utilisant des mesures simples : la vitesse avec laquelle les algues et les champignons poussent ou encore les feuilles se dégradent.

J'ai pu classer les différents stress étudiés : les niveaux de stress imposés par l'agriculture et les barrages sont les pires pour les êtres vivants des rivières. Ceci dit, les organismes vivants répondent de manière différente au stress, et les microbes ont été plus affectés que ce que je pensais. J'ai également pu montrer que tout ne se ramène pas aux organismes vivants appartenant au même groupe: il faut aussi prendre en compte le rôle qu'ils jouent – la position géographique de la rivière ayant son importance pour comprendre son fonctionnement et la biodiversité qu'elle soutient.

Je sais ce que vous pensez… A quoi bon ? Mon thème de recherche concerne en réalité tout le monde. Nous tirons profit des rivières dans la vie de tous les jours sans même nous en rendre compte. Avez-vous imaginé une vie sans eau potable ? Et si nous ne pouvions plus irriguer nos cultures par manque d'eau ou parce que les rivières ne sont plus capables de supporter tous les nutriments et polluants que nous avons déjà rejetés ? Pour vraiment comprendre l'importance de ces effets indésirables, nous devons intégrer plus d'informations concernant les organismes vivants présents et la façon dont la rivière purifie l'eau et absorbe les nutriments dans nos programmes environnementaux. Cela va prendre du temps pour que les directives changent et prennent en considération l'importance de mesurer les activités des êtres vivants. Heureusement, des méthodes existent déjà, comme je l'ai montré dans mon sujet de thèse !

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