



Universität für Bodenkultur Wien
University of Natural Resources
and Life Sciences, Vienna

Master Thesis

The effect of network connectivity and
environmental conditions on the hydro-chemical
characteristics of a Danube floodplain system

submitted by

Sheilla ATUKUNDA

in the framework of the international Joint Degree Master programme

Limnology and Wetland Management

in partial fulfilment of the requirements for the academic degree

Master of Science

Vienna, April 2022

Supervisor:

Univ. Prof. Dr. Thomas Hein
Institute of Hydrobiology and Aquatic Ecosystem Management
Dept. of Water, Atmosphere and Environment
Univ. of Natural Resources and Life Sciences, Vienna

Affidavit

I give my solemn word that I have compiled and submitted this master thesis solely and without external help, have not utilized any assistance/sources outside those permitted, and the sources used have been given verbatim or quoted textually in the places indicated. I hereby declare that I have authored the work and herein is my own except where explicitly stated otherwise. All ideas, concepts, approaches in wording, or basic content from unpublished sources or published studies were duly cited and precise references were written against them.

I further declare that this master thesis report has not been submitted, in whole or in part, in the same or related form, to any other educational institution as a requirement for an academic degree. I am conversant with scientific writing ethical conduct and integrity, and I upheld good scientific practice hence this work complies with scientific standards and guidelines.



Wien, 08.04.2022

Sheilla ATUKUNDA

Preface

This research was conducted with insurmountable and great support from the IPGL- training Programmes in Limnology and the fellowship from the Austrian Development Cooperation (ADC) that made my study conducted at the Institute of Hydrobiology and Aquatic Ecosystem Management (IHG) at the University of Natural Resources and Life Sciences, Vienna throughout August 2021 to April 2022. The research presented in this master thesis was conducted in the framework of two projects.

1. Christian Doppler Laboratory for Meta Ecosystem dynamics in Riverine landscapes - Research for sustainable river management (CDL-MERI) funded by Christian Doppler Forschungsgesellschaft (CDG), Sensengasse 1, 1090 Wien, Austria in cooperation with Österreichische Bundesforste, Austria, Verbund AG, Am Hof 6a, 1010 Wien, Austria and via Donau, Donau-City-Straße 1, 1220 Wien, Austria
2. Functioning of vertebrate metacommunities in dynamic riverine landscapes: an innovative approach using eDNA metabarcoding. Austrian Science Fund (FWF) Project RIMECO (I 5006), funded by Fonds zur Förderung der wissenschaftlichen Forschung (FWF), Sensengasse 1, 1090 Wien, Austria

Acknowledgment

I would like to acknowledge the hand of God from the beginning when I trusted him for this fellowship, and all through leading to my research, the Lord has been faithful. I thank God for helping me through all the trimesters of this course that have tremendously contributed to the general knowledge of all I know now in my field of study. God, I have experienced your guidance, truly your light is a lamp unto my feet which you have led in all these great nations during my study. Steadily you have helped me day by day to finish my degree, I will keep on trusting you for my future endeavors.

Secondly, I would like to acknowledge my Supervisor Univ. Prof Thomas Hein, Head of the Institute of Hydrobiology and Aquatic Ecosystem Management made this work possible as you read and commented on my thesis chapters. Your guidance, immense knowledge, advice, and time have seen me from Topic development and through all the stages of writing this thesis. Your brilliant ideas, comments, and suggestions have been a key input, thank you very much.

I would like to extend my gratitude, especially to the co-supervisors Mag. Dr. Andrea Funk and Mag. Dr. Elisabeth Bondar-Kunze from the Institute of Hydrobiology and Aquatic Ecosystem Management for the thoughtful mentorship they rendered during the development of my master thesis. They provided exceptional scientific input and expertise in the design and implementation of my research and the interpretation of the results, especially through the numerous meeting we held and feedback on the thesis chapters. Thanks for your ever-present guidance and support in all the engagements held with you, this could not have been possible without you. I would like to acknowledge C. Griebler and H. Krail from the University of Vienna who helped with the cation and anion analyses.

My earnest thanks go to the technical assistants Annette Puritscher (laboratory and field equipment), Irina Ludwig (day-to-day guidance in the lab and CFA analyses), and Gertraud Steniczka (DOC and TDN laboratory analyses) at the WasserCluster Lunz Biological Station GmbH who provided technical support.

I would like to express my appreciation to my loving, understanding, and supporting husband Henry Simon Kafumbe (Mr.) for taking care of our family while I have been away most especially our wonderful little man Josiah Harry Kafumbe am so blessed to be his mom. You both have been my biggest motivation, you brought cheer through this academic journey. I thank my mom the pillar of our family, I am extremely grateful for your care, love, support prayers, and sacrifices you make. There would be no me without you. I appreciate the love and support from my siblings Phiona, Sandra, Barnet, extended family, and friends while I have been away for my studies, you have kept in touch, and I appreciate that.

Lastly, I would like to shout out to the amazing lecturers that have taught me throughout the course of my study, class of LWM 2020/2022 and Applied Limnology for being a great team to learn from, we shared ideas and knowledge and had a great time. I learned a lot from the assignment discussions and in a special way Oswald, Eunice and Evagzard have been a close-knit group (LWM), the entire Environmental Science group at IHE Delft were a great team too (such a big group, can't mention all of you but I especially appreciate you) and lastly, the AEEM group that we shared classes, fieldwork, and many great memories at Egerton.

Contents

Affidavit	i
Preface	ii
Acknowledgment	iii
List of Acronyms	viii
Graphical abstract	ix
Abstract	ix
CHAPTER 1. INTRODUCTION	1
1.1 Background	1
1.2 Aim of the study	2
1.3 Research questions	3
1.4 Hypotheses	4
1.5 Justification and rationale	5
Chapter 2. LITERATURE RESEARCH	6
2.1 Riverine floodplain concepts, and typology/environmental conditions	6
2.2 Connectivity and waterbody morphology/typology across a spatial gradient	7
2.2.1 Connectivity metrics	8
2.2.2 Ecological relevance of connectivity metrics	9
2.3 Floodplains as spatial networks of habitat patches for resource flow	10
2.3.1 Riverscape ecology - a spatial network assessment	10
2.3.2 Resource flows - a function meta-ecosystem dynamics of floodplains	11
2.4. Roles of floodplain ecosystems	13
2.5 Threats to floodplain ecosystems	14
2.6 Nutrient dynamics in floodplain water bodies	15
2.7 Primary productivity in floodplain water bodies	17
Chapter 3. METHODOLOGY	18
3.1 The Austrian Danube	18
3.2 Study area	20
3.3 Environmental conditions for the Donau-Aeun Floodplain system	21
3.3.1 Hydrological connectivity development after the flood pulse	21
3.3.2 Quantifying the environmental condition variables	22
3.4 Research method and sampling design	22
3.5 Chemical analyses (water and sediments)	23
3.6 Quantifying photosynthetic rates	25
3.7 Quantifying connectivity	27
3.7.1 Connectivity indices- harmonic centrality	28
3.7.2 Connectivity indices- betweenness centrality	28

3.7.3 Probability of connectivity index.....	29
3.7.4 Description and codes for connectivity metrics calculated.....	29
3.8 Statistical design and calculations	31
Chapter 4. RESULTS	34
4.1 Comparison of floodplain hydrochemistry between the three months (August, September, and October).....	34
4.2 Disentangling the influence of network connectivity and environmental conditions on total phosphorus, POM and PIM, DOM, and phytoplankton biomass at the three different water level stages	42
4.3 Variation in floodplain hydrochemistry for the detailed October analyses	49
CHAPTER 5. DISCUSSION	59
5.1 Comparison of floodplain hydrochemistry between the three months (August, September, and October).....	59
5.2 Disentangling the influence of connectivity and environmental conditions on total phosphorus, POM and PIM, DOM, and phytoplankton biomass at the three different water level stages	64
5.3 Hydro-chemical conditions, organic matter contributions, pelagic and benthic algal biomass production along a spatial gradient of the Danube floodplain during the isolated state (October 2021)	68
5.3.1 Spatial variability of ion concentration during the low flow month.....	68
5.3.2 Spatial variation in the nutrient condition during the low flow month.....	69
5.3.3 Spatial variability of particulate matter and phytobenthos chlorophyll-a concentration in October	71
5.3.4 Phytoplankton chlorophyll-a concentration and photosynthesis rate variation along a spatial gradient during the low flow month.....	73
5.3.5 DOC and DOM quality variation along a spatial gradient during the low flow month	74
CHAPTER 6. CONCLUSIONS AND RECOMMENDATION	77
CHAPTER 7. REFERENCES	79
APPENDIX 1	93
APPENDIX 2	95

List of figures

Figure 1: An example from the Ain River, France: (a) spatial gradient of hydrological connectivity at the floodplain scale with an indication of the main factors involved; (b) hydrological connectivity at the water body scale (adapted from (Amoros and Bornette, 2002)).	8
Figure 2: Location of the study site showing the 23 floodplain water bodies (backwater and side-arm systems) in the Donau-Auen National Park and 1 water body (Eberschuttwasser) from the Lobau floodplain along the Danube River in Austria.	20
Figure 3: The development of temporal hydrological connections in the Donau-Auen National Park floodplain water bodies.	21
Figure 4: Comparing between the months with one-way ANOVA.	38
Figure 5: Emission Excitation matrices (EEMs) showing variation in the three months for the Danube River (Site_0) and at a more connected site Röthelstein upstream (Site_3) which is in the downstream part of the floodplain.	40
Figure 6: Emission Excitation matrices (EEMs) showing variation between the 3 months for isolated water bodies that is Witzelsdorfer Arm (Site_15) and Fadenbach bei Orth (Site_21).	41
Figure 7: Variation partition result for August PCA_1 and PCA_2 showing contribution of environmental conditions and connectivity within the floodplain network.	46
Figure 8: Variation partition result for September PCA_1, PCA_2, and PCA_4 showing contribution of environmental conditions and connectivity.	47
Figure 9: Variation partition result for October PCA_1, PCA_2, and PCA_4 showing contribution of environmental conditions and connectivity.	48
Figure 10: Ion concentration variation along a spatial gradient.	51
Figure 11: Nutrient variation along a spatial gradient of the Danube floodplain water bodies.	52
Figure 12: Spatial variation of particulate inorganic matter, particulate organic matter concentrations, sediment organic matter content, and phyto-benthos chlorophyll-a.	54
Figure 13: The relative photosynthetic Electron Transport Rate (rel.ETR) function of minimum saturation irradiance/ PAR irradiance for the floodplain water bodies and the scatter plot represent mean values.	55
Figure 14: Photosynthesis rate and phytoplankton chlorophyll-a variation along the spatial gradient of floodplain water bodies.	56
Figure 15: Spatial variation in DOM quality of floodplain water bodies from the October sampling date	58
Figure 16: Temporal variation of DOM quality (a) humification index (HIX), (b) biological index (BIX), and (c) fluorescence index (FI) between the three months, bars represent means and standard error.	95
Figure 17: Temporal variation in DOM fluorescence peaks	96
Figure 18: Temporal variation of (a) POM concentration and (b) CDOM concentration between the three months.	96

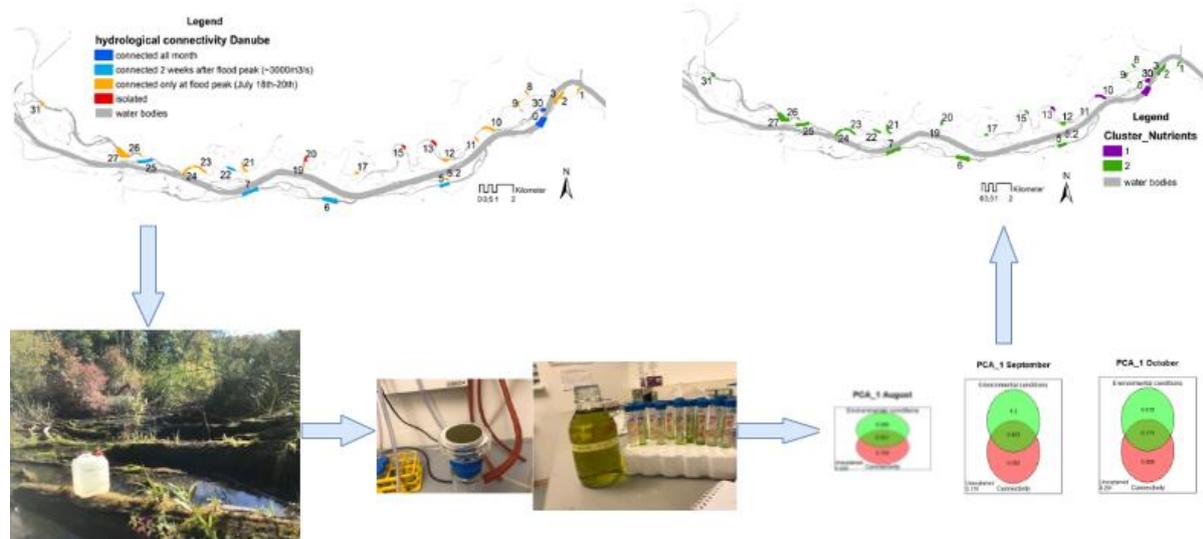
List of tables

Table 1: Description of Dissolved organic matter (DOM) peaks and indices analysed in this study.....	26
Table 2: Factor analysis result showing PCA variable axes of the floodplain hydrochemistry for August 2021.	42
Table 3: Factor analysis result showing PCA variable axes of the floodplain hydrochemistry for September.....	43
Table 4: Factor analysis result showing PCA variable axes of the floodplain hydrochemistry for October 2021.	43
Table 5: Multiple regression results and redundancy analysis for factor analyses in August, September, and October 2021.....	45
Table 6: Variable cluster groups showing how the water bodies clustered which was dependent on similar hydro-chemical conditions.....	49
Table 7: Spatial variation for the ion concentrations in the floodplain water body clusters. ...	50
Table 8: Spatial variation in the nutrient condition during the low flow month.....	51
Table 9: Variation between the 3 clusters for particulate inorganic matter, particulate organic matter concentrations, sediment organic matter content, and phyto-benthos chlorophyll-a along the spatial gradient.	53
Table 10: Variation in photosynthesis rate and phytoplankton chlorophyll-a along the spatial gradient from the 3-cluster solution.....	56
Table 11: Spatial variation for DOM quality in the floodplain water bodies.	57
Table 12: One-way ANOVA result for hydro-chemical differences between the three months as described in results section 4.2.	93
Table 13: Cation and anion correlation with electrical conductivity during the low flow month.	94

List of Acronyms

DANP	Donau-Auen National Park
DOC	Dissolved organic carbon
CDOM	Colored dissolved organic matter
DOM	Dissolved organic matter
POM	Particulate organic matter
PIM	Particulate inorganic matter
P	Phosphorus
N	Nitrogen
TP	Total phosphorus
chl-a	Chlorophyll-a
EEM	Excitation Emission Matrix
UV	Ultraviolet
WCL	WasserCluster Lunz
Phyto-PAM	Phytoplankton-Pulse amplitude modulation
PSII	Photosystem II
Y(II)	Yield estimate of the photochemical use of excitation energy in light
PAR	Photosynthetically active radiation
PCA	Principle Components Analysis
ModEvA	Model Evaluation and Analysis
varPart	Variation Partitioning
PARAFAC	Parallel Factor Analysis
RCL	Rapid Light Curves
$\mu\text{mol photons m}^{-2} \text{ s}^{-1}$	Micro moles of photons per meter squared per second
StaRdom	Spectroscopic analysis of dissolved organic matter in R
RQ1	Research question 1
RQ2	Research question 2
RQ3	Research question 3
H1, H2, H3	Hypotheses 1, 2, and 3
Hazen unit	1 mg/L of Platinum as Chloroplatinate ion 3

Graphical abstract



Abstract

The effect of connectivity and environmental conditions (factors) on the hydro-chemical characteristics of a Danube floodplain system were investigated by comparing hydro-chemical data between three months (August, September, and October 2021) after a flood pulse. The response variables included (total phosphorus), particulate matter, phytoplankton chlorophyll-*a* concentrations, and dissolved organic matter quality. These varied both temporally and spatially as a function of connectivity and environmental factors. August showed the highest TP, PIM, CDOM, and DOM whereas phytoplankton chlorophyll-*a* was highest in October. The directed large distance exchanges in August, undirected river based/whole floodplain network and the Euclidean distance exchanges during mean flow and low flow conditions offered the opportunity to describe the fluxes in the system across the three months. Phosphorus uptake in October by phytoplankton and other autotrophs reduced the nutrient levels in October (total phosphorus). Hence, the sediment aggradation and other inputs like organic matter are a result of a well-connected network mosaic of water bodies. Network connectivity and environmental conditions together significantly explain the functional variability between these heterogeneous aquatic ecosystems.

A detailed analysis of October was carried out, including more variables i.e., ions, nutrients phosphorus and nitrogen forms, sediment organic matter content, DOC, phytobenthos chlorophyll-*a*. Water body clusters represented exchange processes and are indicative of pathways where groundwater enters the floodplain network in this spatially clumped clusters (ions and nutrients) and in contrast, other variable cluster groups represent a laterally large-

scale nutrient gradient. The key attributes of functional variability of lateral floodplain network connectivity differed in both space and time and these help to shape and contribute to a myriad of benefits from floodplains.

Keywords: Floodplain water bodies, network connectivity, environmental conditions, hydrochemistry, temporal and spatial gradients, flood pulse

CHAPTER 1. INTRODUCTION

1.1 Background

Hydrologically, active riverine floodplains are dependent on the pulsing river discharge, timing of the flood (Tockner et al., 2000) characterized by the duration, intensity, and magnitude of its high flows. These are largely driven by rainfall or snowmelt in the upstream watershed area. The pulsing river discharges are the most important aspect that makes floodplain systems the most biologically productive (both autotrophic and heterotrophic) feature with high habitat complexity in riverine systems. Floodplain water bodies and associated alluvial forests provide vital ecosystem services for example nutrient retention, regulate sediment transport (Hopkins et al., 2018), and efficient flood control. The riverine wetlands in the Danube River Basin support very high biodiversity, with thousands of plant and animal species (many endangered) including the recently re-introduced European beaver (Rebelo et al., 2013). They are key regulators of vital ecological processes that are key in the water budget and/or hydrological cycle, including groundwater recharge and retaining flood water (Rebelo et al., 2013), biogeochemical cycling among other ecosystem services. Rivers and their adjacent riparian corridors and floodplains have been known to sustain irrigated agriculture globally (Dryden et al., 2021).

Connectivity greatly influences the exchange of nutrients and organic matter between the river and its floodplain (Tockner et al., 1999) making floodplains vital nutrient sinks (Hopkins et al., 2018) with higher nutrient retention potential than adjacent main channel systems. According to (Thoms et al., 2005), for nutrient dynamics in river-floodplain systems, the most vital factors are the position of the floodplain waterbodies in the network to the river. One other study by (Junk and Wantzen, 2004) reported that both the size and location of floodplain waterbodies, as well as the strong interaction with the parent river, influence physical and chemical conditions in the floodplain. Riedler et al., (2006) reported that during surface water connection with the main river, the water chemistry of the floodplain waterbodies is mainly determined by the quality and the quantity of the imported river water from the main channel. Connection, seepage, and disconnection are distinct hydro-chemical phases, and processes in the post-connection period are the most pronounced and complex (Weigelhofer et al., 2015).

Within a riverscape, fluvial dynamics result in differing mosaics at two spatial scales ie., whole floodplain, and water body scales. At the floodplain scale, water bodies are formed and maintained by fluvial processes through lateral as well as vertical erosion processes, and the

subsequent channel migration and abandonment, including side-arms, backwaters, cut-off braided channels, oxbow lakes, groundwater-fed ponds, and marshes (Amoros and Bornette, 2002). According to (Lamers et al., 2006; Weigelhofer et al., 2015), imported compounds from the main river may alter metabolic processes in the floodplain waterbodies after the surface water connection has ended. For example, suspended matter in the river water may alter light conditions in the backwaters and temporarily limit the activity of primary producers in the post-connection period (Tockner et al., 1999). River inputs like nutrients and dissolved organic carbon (DOC) derived from the adjacent terrestrial system can increase primary and secondary productivity in floodplains (Seekell et al., 2015; Riedler et al., 2006).

Spatial structural heterogeneity, differences in water chemistry, and algal biomass appear to be more pronounced during low river discharge followed by the consequential surface disconnection of water bodies. This key element of the river-floodplain system is the spatial variability/heterogeneity of limnological properties, mostly dictated by water level changes in the network (Tockner et al., 1999; Peršić and Horvatí, 2011). Bishop-Taylor et al., (2015) used graph theory metrics to estimate connectivity over short Euclidean distances in floodplain spatial structure during dynamic flood events on a global scale. They further used in their study visual estimation of spatial connectivity using raster data analyses of betweenness centrality to explain temporal changes at a larger scale. Connectivity of floodplain water bodies is affected by the structure of the water body network and the quality of the mediating landscape mosaic in ways that vary along spatiotemporal scales and because of flood pulses. Bishop Taylor et al., (2018) compared ecosystems prioritizations using graph theoretic centrality metrics like connectivity degree and betweenness centrality to represent 'focal/most central' (main river channel) and 'stepping-stone' (connected side arm systems) water bodies that support large and short-distance connectivity. Urban et al., (2009) point out that using graph theory's effective, spatiotemporally consistent framework (in which ecosystem patches are depicted as network "nodes" connected by various resource flow channels or "edges") is crucial. Graph theoretic metrics have been utilized in a growing number of studies to select particular patches (Estrada and Bodin, 2008) and floodplain water bodies for conservation based on their contribution to landscape- or regional-scale connectivity and importance of floodplain networks in flood retention management (Reckendofer et al., 2013).

1.2 Aim of the study

The study tested information gain due to the integration of connectivity indices that have been developed in landscape ecology which were then incorporated into this study to investigate

floodplain hydrochemistry along a spatial gradient and fluctuating Danube River water levels. There have been numerous studies on the role of riverine floodplains as sinks sources, and transformers of nutrients and organic matter (Natho et al., 2020; Noe and Hupp,2007; Reckendofer et al., 2013; Tockner et al., 1999). The consideration of spatial ecology aspects in floodplain studies to understand resource flows is missing and highlight the general significance of the study. There is an increased realization that systems are not stationary but rather dynamic and spatial flows of resources provide an important part in the dynamic functioning of floodplains.

1.3 Research questions

RQ1. How does the hydrochemistry vary after the flood pulse between high flow in (August), during summer mean flow in September, and relatively low flow conditions in October?

RQ2. What are the unique contributions of network connectivity and local environmental conditions in influencing the water chemistry, particulate matter, phytoplankton chlorophyll-*a* concentrations, and dissolved organic matter quality (within 3 months after a flood pulse)?

Other questions embedded in assessing connectivity,

- a) How do strong directional/large distance transport exchanges during high flow (August) and undirected system distance transport of material during the intermediate connection state (September) and low flow conditions in October impact the floodplain water bodies?
- b) Two network approaches are present in floodplain systems i.e., (a) the permanent pattern (similar across hydrological stages where there is a “classical” lateral floodplain gradient from dynamic network (during connection) to a static network (isolated water bodies), which usually change from autochthonous to allochthonous driven) and (b) Pattern dependent on hydrological conditions where the exchanges under flood conditions or mean water flow are prevalent. Which of the two approaches better represent the Danube floodplain system in this study?

RQ3. How do the nutrient condition (phosphorus and nitrogen forms), sediment organic matter content, phytoplankton, and phytobenthos chlorophyll-*a* concentrations of dissolved organic carbon and dissolved organic matter vary along a spatial gradient of the Danube floodplain waterbodies mean flow conditions in October 2021?

1.4 Hypotheses

The first aim of the study was to disentangle the influence of network connectivity and environmental conditions on water chemistry (inorganic and organic components), phytoplankton biomass, and photosynthesis along a spatial gradient after a flood event at three water level stages i.e., high flow conditions (connected), mean flow (intermediate connected), and the low flow month (disconnected) states. We hypothesized that-

H1- The floodplain hydrochemistry after the flood pulse was expected to shift from mainly autochthonous to allochthonous driven due to high river inputs and pattern dependent on hydrological conditions (exchange under very high flow conditions, mean and low water conditions) a function of fluctuating Danube River discharge. On average, particulate organic and particulate inorganic matter, and nutrients (total phosphorus only) were expected to be highest during high flow conditions, dissolved organic matter (DOM), and phytoplankton chlorophyll-*a* concentrations were expected to be higher in the mean flow and low flow months.

H2- The combined influence of connectivity and local environmental conditions is greater and enhanced during high flow conditions than their independent contributions to the hydrochemistry of the floodplain water bodies. Regarding the different aspects related to connectivity, the following hypotheses were formulated. Strong directional exchange/large distance transport was expected to impact the system during the high flow month and undirected short distance transport/ exchanges of material were expected to be more pronounced during the mean flow (September) and low flow conditions in October.

The second aim was to get deeper insights into the spatial analysis of floodplain hydrochemistry where spatial clusters for local exchanges versus large scale gradients during October sampling became more relevant. Regarding to nutrients (phosphorus and nitrogen forms), sediment organic content, pelagic algal photosynthesis rate, phytoplankton and phytobenthos chlorophyll-*a* concentrations, dissolved organic carbon and dissolved organic matter we hypothesized that-

H3- From the detailed spatial analysis of the October sampling, we expected the backwaters and/or side-arm to be in different spatial clusters due to differing hydrochemistry. We expected local exchanges depicting a more relevant lateral gradient for the hydrochemistry common to fluvial dynamics in floodplains than an inconsistent large-scale gradient in the network.

1.5 Justification and rationale

The degree of connectivity is crucial in influencing the relative importance of autochthonous and allochthonous sources of organic and inorganic nutrient outputs and inputs respectively and their processing in riverine floodplains. There have been numerous studies on the role of riverine floodplains as sinks, sources, and transformers of nutrients and organic matter. This study will add to existing knowledge about how the degree of connectivity along a spatial gradient of floodplain water bodies to the main river channel control floodplain hydrochemistry. In an assessment of the fluvial dynamics regarding lateral exchanges that contribute to the uniqueness of floodplain networks, this study hopes to build on the existing knowledge base for actors who are active in the management of such systems. Also, to inform policy development, society practices for livelihoods, about the continued need for protection of the remaining somewhat intact floodplains, rehabilitation of impacted and modified systems to a degree to ensure that human well-being and a range of ecosystem services from them are sustained over time.

Chapter 2. LITERATURE RESEARCH

2.1 Riverine floodplain concepts, and typology/environmental conditions

Channel avulsion and meander processes can result in the abandonment and cut-off channels, which, when combined with a fluctuating water level associated with river discharge fluctuations, can result in a diverse range of aquatic ecosystems. Ponds, backwaters, stream confluences, sidearm channels, vegetated and gravel islands, riparian forests, and huge wood deposition areas are all examples of floodplain patch typology (Stanford et al., 2005). Dawidek and Ferencz, (2014) argue that, in the case of floodplain lakes/water bodies, "the hydrological (basin filling) and biological status is largely determined by the sort of linkages that the water body/lake has to the parent river". Vannote et al., (1980) study of the River Continuum Concept (RCC), possibly the most prominent concept in stream ecology in the twentieth century, projected patterns and processes along linear channels covering the longitudinal profile of systems from headwaters to mouth and thus did not consider river systems as networks. Junk et al., (1989), explain how the floodplain is the principal source of material and energy that supports food webs in floodplain rivers, according to the classical Flood Pulse Concept (FPC). They detailed how floodplains are inundated by flood pulses, that serve as stimulants for material transport and primary production, as well as the exchange of materials and energy from the floodplain into the main channel, and emphasis was then more on lateral connectivity than on a longitudinal continuum (Junk et al., 1989).

Humphries et al., (2014) proposed to synthesize the prominent classical river ecosystem concepts (Fish Zones Concept, the RCC, FPC, Riverine Productivity Model, and the Riverine Ecosystem Synthesis) into the River Wave Concept (RWC) concept, The RWC was defined by the following premises: The wave is a desirable model for river flow because waves appear everywhere; they are hypothetical and have been used as models for natural phenomena. Consequently, a wave has the potential to be used as a model for river flow, features, and behavior. Humphries et al., (2014) further explain that the location and source of autochthonous production or allochthonous inputs, as well as the transport, transformation, and storage of the material and energy derived from that production and inputs, are largely a function of the temporal or spatial position on the river wave. Dolph et al., (2017) note that the RWC hypothesizes that local autochthonous output and local allochthonous inputs should dominate energy budgets at low/base flow, and they are increasingly requisite as river discharge increases.

2.2 Connectivity and waterbody morphology/typology across a spatial gradient

Riverine floodplains are landscapes with high structural heterogeneity, they support a shifting patchwork of aquatic habitats because of different degrees of hydrological connectivity gradient with the adjacent main river where overbank flows interact with floodplain geomorphology to generate a network of transient water body inter-connections. Less-impacted/near-natural floodplains are composed of different aquatic habitats that vary from lotic to semi-lotic and lentic habitats (Lasne et al., 2007), isolated (no surface connection and further away) to those with temporal and permanent connections, groundwater-fed ponds to surface-water connections. They consist of numerous hydrogeomorphic units characterized by distinct drainage and morphological patterns (typology) which consist of braiding with islands, meandering or anastomosing (Thorp et al., 2006), connected side arm channels, groundwater-fed ponds, and backwaters all with distinct connectivity degrees to the main river (Tockner and Stanford, 2002). In natural rivers (Junk et al., 1989) and anthropogenically altered channels (Thorp et al. 2006), productivity and diversity vary with structural and hydrological connectivity due to fluvial distance between backwaters and the main river channel or flood pulses in sporadically isolated floodplain water bodies during high discharge periods (Junk et al., 1989; Tockner et al., 2000).

As defined by (Amoros and Bornette, 2002) floodplain hydrological connectivity (lateral) is “the permanent and/or temporal connections between the main river channel and the different waterbodies in the alluvial floodplain”. Hydrological connectivity determines numerous water body characteristics that include flow velocity, topography, and slope (Thorp et al., 2006), physical parameters (oxygen, temperature, pH), substrate size/composition, and processes e.g., erosion, transport or deposition, woody debris movement and vegetation cover succession (Tockner et al., 1999). The numerous forms of hydrogeomorphic units vary in chemical conditions, biocomplexity, productivity, community structure, system metabolism, organic matter, and nutrient dynamics (Thorp et al., 2006). This inference is consistent with the extensively acknowledged hydrological characteristics in the ecosystem structure and function of most floodplains around the world.

The ever-evolving mosaic of waterbody typology for example side-arm channels, backwaters, cut-off braided channels, oxbow lakes, floodplain ponds, and marshes through lateral as well as vertical erosion, and the consequent channel movement and abandonment (Amoros and Bornette, 2002). The diversity of biotically significant water body conditions (morphology) at

the floodplain scale (see Figure 1) are pre-determined by (1) the distance between the floodplain water body and the main river channel; (2) the presence of permanent versus temporary river connections; and (3) the size and shape of the water body, which can be described by its length, width, depth, and sinuosity (Amoros and Bornette, 2002). Recolonization may occur more easily in lotic than in lentic water bodies due to higher connectivity. The more lentic systems have more internal processing and settling of sediments while the lotic ones have less interaction due to the washing of the sediments.

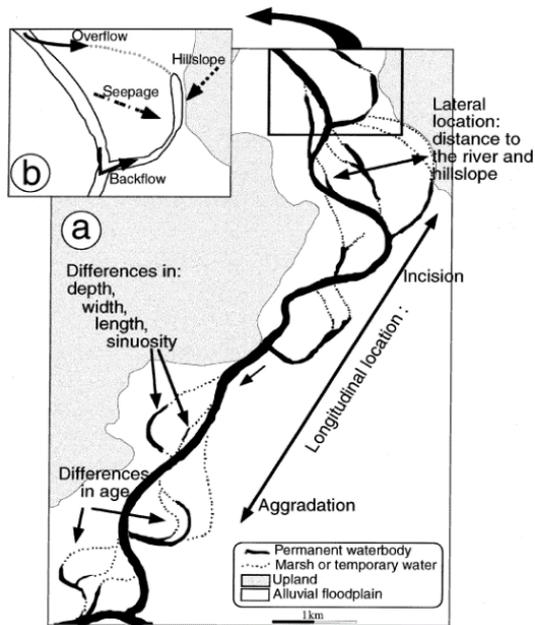


Figure 1: An example from the Ain River, France: (a) spatial gradient of hydrological connectivity at the floodplain scale with an indication of the main factors involved; (b) hydrological connectivity at the water body scale (adapted from (Amoros and Bornette, 2002).

2.2.1 Connectivity metrics

Considering spatial flows as influenced by the degree of connectivity, it becomes imperative to assess the connectivity of the Danube River floodplain water bodies. There have been various connectivity metrics used in landscape ecology but how well these metrics explain ecological processes, especially resource flows are fairly known. Incorporating knowledge from landscape ecology studies such as (Calabrese and Fagan, 2004; Fortin et al., 2012; Gounand et al., 2018), where spatial heterogeneity has been used to explain species distribution, behavior, habitat preference, dispersal ability, and measures for their conservation, etc. based on interactions between the species of interest and landscape components. Based on landscape ecology ideas into the riverine network, we can explain resource flows exchanges between interconnected floodplain aquatic habitats and their adjacent river.

Calabrese and Fagan, (2004) differentiated between three classes of connectivity metrics, and borrowing from their study, the classes are explained here as; (1) Structural connectivity depends mainly on physical attributes of landscape elements such as interconnectivity (shortest inter-patch distance), (2) Potential connectivity which depends on physical attributes but also on the probability of hydrological connectivity to other interconnected water body patches or the main river channel (if the distance between water bodies is greater, then they are likely not to have specific surface connections) and lastly (3) Actual connectivity which is based on existing permanent surface connections between either the water bodies or water body and main river channel. According to (Erős and Lowe, 2019), some geostatistical models have been used to explain stream network characteristics in analyzing data from spatial connectivity such as biogeochemistry, species density, and dispersal. By explaining the spatial dependence of data, therefore, it is possible to separate the effects of in-stream versus landscape-scale processes on hydrochemistry.

Ecological understanding is, however, of crucial importance for any spatial connectivity metrics to make them useful in conservation and management (Estrada and Bodin, 2008). To attain such criteria, landscape ecology studies such as (Calabrese and Fagan, 2004; Saura and Pascal-Hortal, 2007) elaborate that, is an efficient, spatial-temporal consistent structure and an increasing number of studies have used graph theoretic metrics to prioritize individual habitat patches for conservation based on their contribution to landscape- or regional-scale connectivity (Calabrese and Fagan, 2004; Estrada and Bodin, 2008; Saura and Pascal-Hortal, 2007). Other studies have used remote sensing methods since the graph theory assumes a static habitat network that does not properly convey potential temporal variations in availability and degree of connectivity for the habitat patches over time (Bishop-Taylor et al., 2018).

2.2.2 Ecological relevance of connectivity metrics

Landscape connectivity studies in dynamic surface water ecosystems have widely studied connectivity between static networks of habitat patches during pre-defined dry or wet time-intervals, or by using modelled surface water availability or flood events (Bishop-Taylor et al., 2017) and some have assessed connectivity across both time and space (e.g. Erős and Lowe, 2019; Saura and Pascual-Hortal, 2007; Thorp et al., 2006) for the inclusion of dynamic nature of these river network systems. The relative importance of individual ecosystem types depends on the morphology, landscape characteristics of the interfaces (e.g., shape, hyporheic exchanges, leaf litter fall, other vegetation, sediment composition, and terrestrial-aquatic interface foraging organisms) that control cross-ecosystem fluxes (Tockner, 2021).

Spatial-temporal surface-water dynamics are likely to inordinately impact freshwater ecosystems like floodplains, their hydrochemistry, productivity, and biota that inhabit them because they have varied and fragmented network structures (Bishop-Taylor et al., 2017), hence more research should call for direct quantification of the exchange of materials, energy, and organisms along channels and across ecosystem boundaries. This “meta-ecosystem” view integrates the full spectrum of spatial connections among landscape elements, thus combining the fundamental concepts of landscape ecology into a unified framework for spatial ecology research, specifically such study is by (Gounand et al., 2018). The study of connectivity across spatial and temporal scales is a hugely challenging task, but there is no doubt that these approaches will offer an unparalleled understanding of the structure and function of riverine floodplains.

2.3 Floodplains as spatial networks of habitat patches for resource flow

Spatial ecology aims to investigate and simulate the importance of various spatial properties that shape ecological processes and patterns. Fletcher and Fortin, (2018) highlighted why space is crucial for ecology and conservation, as well as how the different aspects/spatial arrangements in landscapes affect ecological dynamics and processes. Floodplains contain a large mosaic of hydrogeomorphic patches with various network characteristics such as hydrological and sediment regimes, nutrient, and organic matter composition all of which are significant factors that influence ecosystem processes and patterns (Tockner et al., 2009).

Floodplains consist of patches of biophysical space occupied by great morphological heterogeneity and biodiversity (Stanford et al., 2005). Fluvial processes such as channel avulsion and cut-and-fill alluvial flooding modify the spatial patchwork of floodplain habitats over time, resulting in variable patterns and rates of surface water, hyporheic, groundwater exchanges, and related biogeochemical phenomena. These fluvial processes in floodplains create surfaces for vegetative recruitment and growth, producing a dynamic mosaic of linked aquatic and terrestrial habitat patches (Tockner et al., 2010). The structural composition and spatial arrangement of these habitat patches regulate the movement of organisms, resource flow exchanges between adjacent patches, and individual habitat ability to process inputs is also determined by the nutrient composition of adjacent patches and exchanges with the main river channel.

2.3.1 Riverscape ecology - a spatial network assessment

For more than two decades, graph theory has become a strong tool for ecologists analyzing connectivity within complex spatial habitat networks (Bishop-Taylor et al., 2018)

who has also used remote sensing tools for both static and dynamic connectivity modeling, and this has been known to overcome the limitations of patch-based and gradient models while enhancing the interpretability and applicability of results (Erős and Lowe, 2019). Briefly, graphs are a set of nodes and links (Fortin et al., 2012; Urban et al., 2009) in landscape ecological application, nodes can represent a particular environmental feature e.g., a habitat patch, a focal species, or an assemblage of species, whereas links represent the functional connections among nodes, such as the flow of energy among patches, paths dispersal of individuals among populations or communities (Erős and Lowe, 2019; Gounand et al., 2018; Urban et al., 2009). Graphs can also be depicted using patch-based, grid, or raster data (Erős and Lowe, 2019), using such modelling templates, researchers have applied graph-based indices to characterize ecological patterns and processes in a spatially explicit manner with simple, uncomplicated extensions that help in ecosystem management.

According to (Erős and Lowe, 2019), both patch-based and spatial statistical network models have been successfully applied to riverine networks. As an alternative to the RCC approach that biotic communities are controlled predominantly by continuous, (upstream-downstream) longitudinal gradients in physical conditions, patch-based models have shown that sporadic hierarchies of hydrogeomorphic units can strongly influence the spatial structure (Thorp et al., 2006). Patch-based models are applicable when both intra-patch environmental homogeneity and inter-patch environmental heterogeneity are high and evident and when these criteria are not met, gradient models are preferred (Erős and Lowe, 2019). More ways to analyze connectivity are presented in a study by (Fortin et al., 2012).

Despite relatively long-standing applications in terrestrial landscape ecology, graph analyses have only been recently applied to riverscape ecology (Erős and Lowe, 2019). Assessments based on timing, magnitude, duration, and frequency are critical because whether spatial flows occur as continuous flows or pulses (for example, floods could be seasonal, annual, fifty or a hundred years may be insignificant) constrained in time can have contrasting effects on the stability of recipient ecosystem across spatial scales (Gounand et al., 2018). These pulses are an important part of the dynamics of many biological systems that rely on resource flows from outside the system due to seasonal, yearly, or irregular changes (Hastings, 2012) e.g., high river discharge boosts allochthonous material exchanges, can influence spawning in fish, etc.

2.3.2 Resource flows - a function meta-ecosystem dynamics of floodplains

Earlier landscape ecology studies have examined meta-ecosystem and metacommunity dynamics, assessing connectivity in terms of dispersal and resource flows along connectivity

gradients in landscapes (Bishop-Taylor et al., 2017; Calabrese and Fagan, 2004; Erős and Lowe, 2019; Gounand et al., 2018; and Wu, 2013). Meta-ecosystems provide perspective into understanding ecological attributes that emerge from spatial couplings for example in riverine ecosystem processes and patterns at landscape and regional scales, where they function either as sources or sinks for energy and material flows, control biotic diversity, and productivity patterns (Loreau et al., 2003).

Floodplain water bodies are closely linked to adjacent terrestrial systems through reciprocal flows of energy, materials, and organisms. At the landscape scale, these flows are controlled by the biotic composition, configuration, boundary conditions, and linkage/connectivity of individual ecosystem types, thereby forming a meta-ecosystem (Gounand et al., 2018). The high ecological variability that defines riverine floodplains is due to the flood pulses as a result of varying river discharge, which provides a dynamic mosaic of aquatic and terrestrial habitats (Junk et al., 1989). The ability of flood pulses to produce spatial heterogeneity is determined by the degree of connectivity throughout the riverine environment (Taylor et al., 1993). Water level variations are reported to influence the number of point inputs of materials and autochthonous processes through regulating material exchanges between floodplain water bodies e.g., nutrient uptake and release by biota (Tockner et al., 2000).

Due to their reliance not only on the hydrological and sediment regimes, but also on climate seasonality, waterbody morphology, and position in the floodplain system (Mayora et al., 2020), floodplains are dynamic in time and space, which increases environmental heterogeneity, particularly during disconnection periods where most of the water bodies are isolated (Tockner et al., 2000). In nature, the exchange of materials and energy across environments of varying ages and productivity is in many cases pulsed in nature (Fletcher and Fortin, 2018) which typically occur simultaneously but are separated in time and space. Small pulses are physical drivers (for example, a seasonal increase in river discharge) and can drain huge amounts of nutrients and sediment load, initially limiting primary production in nearby aquatic patches due to increased turbidity and eventually may be enhanced during post connection phases after water and sediment interaction.

Pulsed connection and disconnection cycles, for example, are widespread in a variety of environments but are most prominent in floodplain ecosystems (Junk et al., 1989; Tockner et al., 2000). Nutrient mineralization, microbial development, greenhouse gas losses, and denitrification are all affected by wet-dry cycles in floodplain biogeochemical cycling.

While the presence of these various flood pulses shaping spatial dynamics within landscapes is widely accepted based on past field study observations, quantitative data on meta-ecosystems resource flows along such gradients is still scarce. Gounand et al., (2018) explained how resource flows in meta-ecosystems exist at a small scale, spanning the boundaries of neighbouring ecosystems (e.g., litterfall, insect exchanges at the river/lake-forest interface during emergence), they also stressed the need to gather such data to advance spatial ecology. Furthermore from the study by (Gounand et al., 2018), the effects of spatial flows at the landscape scale provide tools to investigate spatial dynamics via ecological processes (primary production, nutrient cycling) and biogeochemical fluxes (carbon, water, nitrogen) which are global cycles and in turn induce ecosystem services. Quantifying spatiotemporal connectivity over the different time steps (3 months) into indices accounts not only for the spatial flows of materials and energy but also for the probability of connectivity for these exchanges. This approach provides estimates of the temporal dynamics of connectivity and water body morphology that can explain hydro-chemical changes in the floodplain. After a thorough literature review and borrowing from landscape ecology, there is no existing work yet using this approach, to understand the ecological implications of connectivity on resource flows in floodplains.

2.4. Roles of floodplain ecosystems

Large riverine floodplains are biodiversity hotspots across the world (Tockner and Stanford, 2002) and provide a variety of ecosystem functions. The merits that people obtain from ecosystems are termed ecosystem services (MEA, 2005), including the provisioning of food, timber, and water, regulations such as flood control, climate modification, pollination, and the supporting service of nutrient cycling, primary production, and sediment retention. Floodplains are ecotones rich in biological diversity, especially when they are coupled with spatial-temporal variation (Ward and Tockner, 2001). Many species benefit from intermediate perturbations at the water-terrestrial interface (Crandall et al., 2003) influenced by flood dynamics (Thomaz et al., 2007). Floodplains also play an important regulatory role in ecology e.g., reduction of flood impacts through absorbing water and retaining nutrients (Forshay and Stanley, 2005), preventing damage to human settlements, and safeguarding groundwater quality. Floodplain ecosystems store considerable amounts of carbon in soil and live biomass due to their high productivity, helping to mitigate climate change effects as they are vital carbon sinks for other terrestrial ecosystems (Robertson et al., 1999).

2.5 Threats to floodplain ecosystems

There are many stressors in floodplains, large towns have developed, and agriculturally intensive areas especially around big rivers (Natho et al., 2020). Despite their immense ecological and socio-economic importance, floodplains in temperate regions have been largely separated from rivers by flood protection embankments, levees, dams /dykes, and enormous changes in land use (Opperman et al., 2010). Numerous pressures on riverine systems, such as hydro-morphology, continuity, and water quality deterioration, have effects on the processes and functioning of aquatic ecosystems and the provision of ecosystem services. Due to land use and cover changes such as urbanization, agriculture, hydropower generation, settlement, and the climate change effects at play exacerbating the anthropogenic ones are not foreign to the Danube River Basin (DRB) (Schinegger et al., 2012), floodplains have been decreased by 68 percent in the DRB (Hein et al., 2016). The Danube river, floodplains, and its tributaries have been subjected to massive anthropogenic activities during the last century, resulting in considerable changes in the hydro-morphology of the river-floodplain ecosystem (Hohensinner and Drescher, 2008).

Land reclamation and channel engineering have resulted in substantial losses of floodplain habitat, leading to the reduced functionality of these systems across the world (Tockner et al., 2010). Reduction in river length, siltation, and cut-off of side-arm channels, bank stabilization structures, and the construction of groins and reservoirs have resulted in functional decoupling of river and floodplain, which has been exacerbated by riverbed incision (Natho et al., 2020). Hydrological discontinuity caused by river engineering projects for flood protection dams, navigation, hydropower, settlement, and recreation threatens the ecological integrity of existing floodplains (Funk et al., 2019) by reducing the occurrence of resource flows and lateral exchanges, between the floodplain and adjacent river channel.

The capacity of floodplain systems to regulate flood water has trade-offs as a result of their decline and deterioration (Hein et al., 2016), making areas more flood-prone (Habersack et al., 2015), while vital floodplain functions, such as groundwater recharge, nutrient cycling, and storage (Hein et al., 2004), and water treatment benefits have also declined in value (Hein et al., 2016). Flood protection dams along the Austrian Danube isolate sections of the floodplain ecosystems, reducing the intensity of groundwater oscillation and as a result of altered water balance behind flood protection dams, (Hager and Schume, 2001) hence may have less structural and hydrological connectivity.

2.6 Nutrient dynamics in floodplain water bodies

Water quality has sparked a widespread concern since it is not only necessary for all biological development and reproduction, but it also interacts with other processes that vary in both time and space (Li et al., 2019). The measurement and interpretation of water level and temperatures variations dissolved organic matter quality (Sankar et al., 2019), allochthonous versus autochthonous particulate organic matter (Hein et al., 2003), phytoplankton production (Hein et al., 1999), etc. Many other studies have also examined nutrient dynamics in floodplain systems after flood conditions/water level fluctuation effects on floodplain hydrochemistry (Preiner et al., 2020), dissolved organic, carbon anion, and cation dynamics (Weigelhofer et al., 2015).

The importance of nutrient loading and the dominance of distinct algal communities in predicting future developments and determining the most effective approaches for ecosystem protection is critical in floodplain systems (Bondar-Kunze et al., 2009). Phosphorus (P) and nitrogen (N) are essential nutrient elements in aquatic ecosystems and have been closely linked to carbon cycling influencing primary production and further immobilization and mineralization of organic matter in floodplain water bodies (Gmitrowicz-Iwan et al., 2020). Water chemistry in floodplain lakes varies as a function of river water inputs and local activities during connection phases (Castillo, 2020). During phases of a connection, river water can change the physical and chemical parameters of the surface water, affecting dissolved oxygen, conductivity, turbidity, and nutrient levels (Weigelhofer et al., 2015). According to (Gmitrowicz-Iwan et al., 2020), P and N depend on inherent conditions in the water body as well as the conditions of the water and sediment inputs from the interconnected water bodies and adjacent rivers.

During low flows and high temperatures, anaerobic conditions can prevail and cause denitrification whereas high flow conditions are believed to increase oxygen in the water body, as well as low flows coupled with relatively low temperatures such as in autumn and winter, aerobic conditions favor high nitrification rates. Phosphorus is adsorbed onto sediment surfaces and can be released back into the water column through internal loading/cycling. Weigelhofer et al., (2018) report that under aerobic conditions, dissolved organic and inorganic P forms complexes with metal oxides and hydroxides to form precipitates while in anaerobic conditions P can be precipitated along with calcite when high pH conditions prevail usually as an outcome of photosynthesis by macrophyte vegetation and benthic algae. P release has also been linked to increased temperatures and oxygen depletion at the sediment-water interface when iron-

bound phosphorus is released from the sediment. River engineering, on the other hand, has diminished the importance of hydrological connectivity of floodplain ecosystems across the world (Tockner et al., 2010) and the disconnection of the floodplain from the main river profoundly alters floodplain dynamics, since internal processes became more important (Gmitrowicz-Iwan et al., 2020; Preiner et al., 2020).

With hydrology as a primary driver of soluble reactive phosphorus (SRP) availability in the Lower Lobau floodplain (Weigelhofer et al., 2015), phosphorus adsorption/desorption processes have a pivotal function in P retention and primary production in this floodplain. Weigelhofer et al., (2018), showed that phosphorus adsorption occurs at high SRP concentrations in the surface water, while desorption is favoured by low SRP concentrations in the surface water. Nitrate-N can be an indication of hydrological connection in the Danube floodplain, between the nutrient-rich main channel and floodplain water bodies (Tockner et al., 2000). The ability of phytoplankton to take up nutrients is important for assessing floodplain waters, as nutrient influx from rivers was apparent during periods of high connectivity. The temporal dynamics of nitrate and orthophosphate concentrations show outstanding deterioration after high flow connections to major rivers like the Danube (Hein et al., 1999). Most large rivers have been reported to have higher nitrate concentrations than their corresponding side arm systems and backwaters where nitrogen depletion is common this has been reported for the Mississippi-Wisconsin riverine floodplain by (Forshay and Stanelly 2005) and a Danube River floodplain in North-Eastern Croatia by (Peršić and Horvatić, 2011).

Primary production and denitrification are the major processes controlling nitrogen reduction, especially after flood events in side-arm channels. The duration of nitrate reduction can be affected by high concentrations and osmotic supply, which have a significant effect on backwater at average water levels (Hein et al., 1999). (Castillo, 2020). Differences in phosphorus (P) between the river and the floodplain vary based on P inputs from river discharge and sediment flushing (Tockner et al., 1999; Weigelhofer et al., 2015). Both biotic and abiotic processes influence carbon and nutrients (P and N) cycling in river-floodplain meta-ecosystems, and these are dependent on climate, hydrology, primary producers, and decomposers' functional roles (Weigelhofer et al., 2018) and morphological connectivity factors that in turn influence the exchanges between and loading of these systems with organic matter and nutrient flows.

2.7 Primary productivity in floodplain water bodies

Spatial heterogeneity of water chemistry and phytoplankton biomass increase with decreasing water levels in the river's main channel and is accelerated by the subsequent disconnection of water bodies. As a result, one of the key elements of the river-floodplain system is spatial variability of limnological properties, which is predominantly driven by water level changes. Some studies suggest that nutrient inputs during connection are often coincided with phytoplankton, bacterioplankton, and zooplankton successions, resulting in rapid water chemistry recovery during the disconnection phase (Riedler et al., 2006) and changes in pelagic processes happen quickly over short periods (Weigelhofer et al., 2015). Phytoplankton formation in floodplain waterways peaks after floods, according to (Peršić and Horvatić, 2011) and nutrient availability may influence algal biomass and ecosystem production. Backwaters have higher amounts of chlorophyll-a because low water exchange rates and increased transparency support phytoplankton growth and biomass build-up (Castillo, 2020).

At low river discharge, the water level gets back to the pre-connection levels during the disconnection phase, a lot of sediments aggradation on the banks/shores of the water bodies. These variations show that floodplains can act as nitrate and sediment sinks, supplying the river with dissolved organic carbon, coarse particle organic matter, and algal biomass (Tockner et al., 1999). Nutrients bound to humic compounds and terrestrial DOC inputs released by photolysis according to (Seekell et al., 2015) shield phytoplankton from harmful ultraviolet light and increase dissolved carbon dioxide concentrations because of photochemical reactions and bacterial mineralization thus stimulating primary production in floodplain water bodies.

Chapter 3. METHODOLOGY

3.1 The Austrian Danube

The Austrian portion of the basin spans a large region of approximately 80,600 km², (Rebelo et al., 2013) and accounts for 10% of the entire area of the DRB which drains over 96 percent of the country's territory. The Austrian Danube River 350 km long according to (Arnold et al., 2017) enters Austrian territory near Passau from Germany and exits at Bratislava into Slovakia (Hager and Schume, 2001). According to (Hager and Schume, 2001), the Danube river's total length within Austria is approximately 350km with large alluvial plains, among other parts, are also found East of the city of Vienna and are regions with major distributions of floodplain forests. Alluvial forests are relatively rare and confined in their sections of the Danube River, east of Vienna, where the floodplain is less than 15 kilometers wide (Hager and Schume, 2001).

In Vienna (Austria), it's a mean annual discharge of 1,950 m³/s, and an annual flood discharge above 5,800 m³/s (Chaparro et al., 2018). At Vienna, the Danube is a 9th order river (Preiner et al., 2008) and drains an area of 104,000 km², annual flow is characterized by an alpine hydrological regime (Arnold et al., 2017; Preiner et al., 2020), highly variable patterns coupled with summer floods after heavy rains and snow melt from the catchments of its alpine tributaries (Preiner et al., 2020). High and very fluctuating river discharge from the Alps defines the hydrological conditions along the Danube's Austrian length (Schiemer et al., 1999). From the 19th to the mid-20th century, the Danube River had been channelized and protective dikes have been established (Höfle et al., 2014; Staska et al., 2014). Although strongly impacted by regulation measures, the key functional attributes of floodplains include dynamic hydrology with flood and/or flow pulses, and bed load transport are partially operative (Preiner et al., 2008).

Historically braided, the floodplain has been constrained by major regulations that began in 1875. A study by (Schiemer et al., 1999) reported that following side-arm restoration, it now contains sections of differing hydrological connectivity, ranging from predominantly lentic water bodies to areas of intermediate and high connectivity with the river main channel. The floodplain water bodies for the study include connected side arm channels and backwaters, some water bodies are behind the flood-protection dam barrier. The Donau-Auen National Park is a green belt with alluvial forests that connects Vienna and Bratislava (ICPDR website, Danube Basin-Austria, accessed on 02.11.2021). It is the largest natural floodplain landscape of its kind in central Europe, where the Danube River still has the dynamic character of a

mountain river (Natho et al 2020). At coordinates 48° 7' 49" N, 16° 44' 10" E, the National Park extends 9300 ha (Höfle et al., 2014; Staska et al., 2014) was established in 1996 to protect extensive floodplain habitats along a 50 km-long section of the Danube. The size of the National Park area comprises 65% floodplain forest, 20% water area, and 15% meadows and fields Reckendorfer et al., (2006). The area has a mean temperature of 10°C and a mean annual rainfall of 600 mm.

3.2 Study area

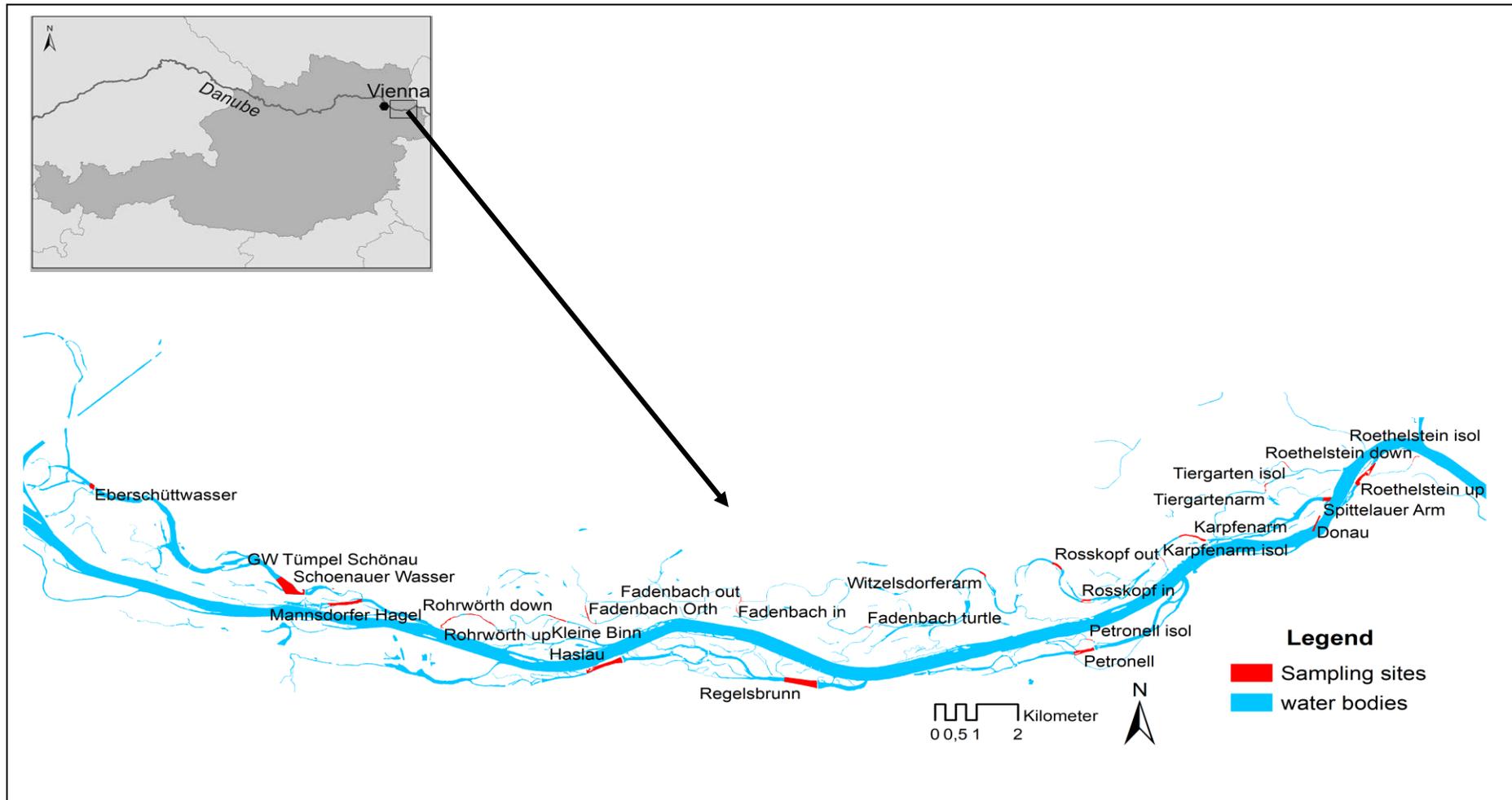


Figure 2: Location of the study site showing the 23 floodplain water bodies (backwater and side-arm systems) in the Donau-Auen National Park and 1 water body (Eberschüttwasser) from the Lobau floodplain along the Danube River in Austria.

3.3 Environmental conditions for the Donau-Aeun Floodplain system

3.3.1 Hydrological connectivity development after the flood pulse

Temporally the flood peak was in July 2021, and below is the development afterward to show which sites were connected and for how long? and sites that were not connected at all during the study. A group of environmental condition variables were investigated to broadly represent the local environmental conditions at water body scale.

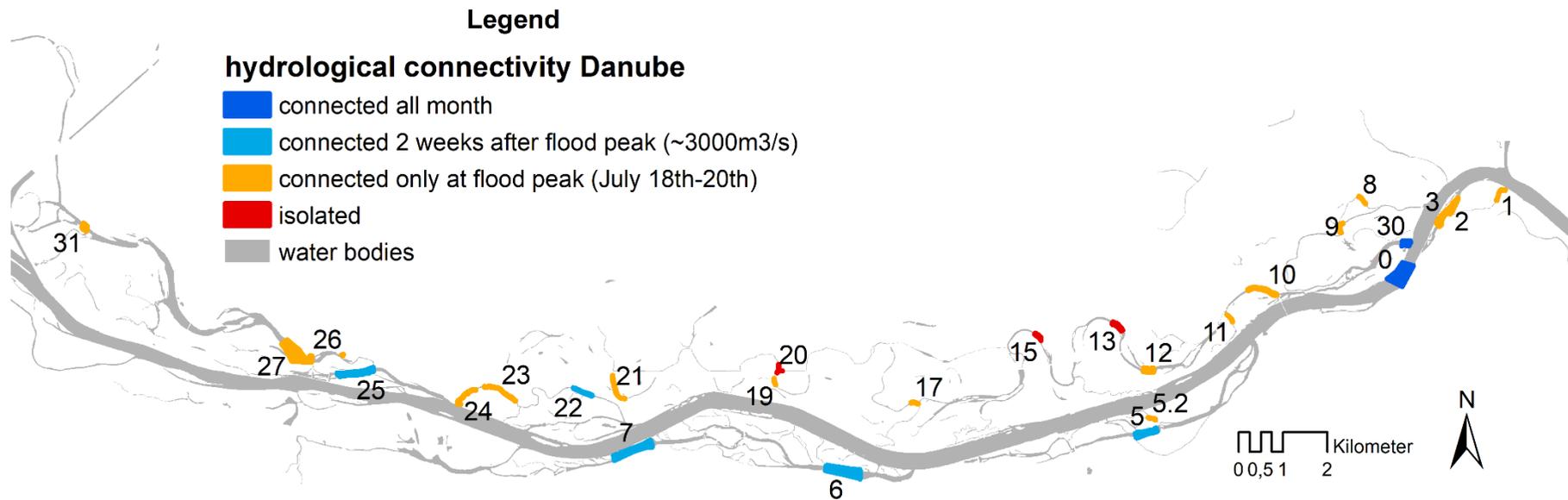


Figure 3: The development of temporal hydrological connections in the Donau-Aeun National Park floodplain water bodies.

The most dynamic sites (dark blue) were connected at all sampling occasions, less dynamic (light blue) were still connected 2 weeks after the flood (at the August sampling) and in the September disconnected for 2 weeks and for the October sampling 2 weeks plus 1 month. More isolated sites (orange) were connected only at the flood peak which was 2 weeks before the August sampling isolated (red) sites are outside of the dam and where *never connected*.

3.3.2 Quantifying the environmental condition variables

Environmental conditions assessed in this study include (1) instream condition (emergent, submerged, macrophyte, floating, surface algae, open water, woody debris percentage), (2) shoreline condition (percentage cover of fringing vegetation up to about 1m from the shoreline, woody ie trees, herbaceous,, artificial with concrete or riprap and percentage of canopy cover), (3) modelled flow velocity at high flow $\sim 5000\text{m}^3/\text{s}$ of the Danube (Gabriel et al., 2014), (4) water depth (at low, $980\text{ m}^3/\text{s}$ mean, $1900\text{ m}^3/\text{s}$ and high flow, $5000\text{m}^3/\text{s}$ of the Danube, Gabriel et al., 2014), (5) substrate cover determined in the field (gravel substrate (2-20 cm), Sand/Psammal (0.063-2 mm) and Psammo-pelal ($< 0.063\text{ mm}$)), (6) land use and/or cover within a 500m buffer zone around the water body in percentage (agricultural, urban, forestry, aquatic and pasture land based on CORINE landcover data from (EEA, 2018), (7) water body size (area and perimeter), hydrological connectivity (total and upstream connections expressed in days/year calculated as a mean value over a period of 20 years, (Reckendorfer et al., 2006) and lastly was sun exposure of the side arms was calculated using the “Area Solar Radiation” extension for ArcGIS (ESRI) expressed in watt hours per square meter (WH/m^2). From the environmental conditions factor, the total and upstream hydrological connectivity were used to observe if the site was connected at especially mean water and hence this is the pattern that is shown with the connectivity parameters (Donau River information Services (DoRIS) website accessed on 26.03.2022 <https://www.doris.bmk.gv.at/fahrwasserinformation/pegelstaende-und-prognosen/jahresverlauf>).

3.4 Research method and sampling design

Temporal variation in floodplain hydrochemistry between three months in the year 2021 was investigated; August following high river discharge ($6500\text{ m}^3/\text{s}$ \sim HQ5-flood event with a mean recurrence time of approx. 5 years), September during a summer mean flow ($3000\text{ m}^3/\text{s}$), and October low flow month ($1500\text{ m}^3/\text{s}$) in the Danube and floodplain water bodies (side-arms and backwaters). Samples were taken following a multi-scale sampling design (Thoms et al., 2007) to examine innate spatial and temporal floodplain complexity. In the Donau-Auen National Park (DANP) and Lobau floodplain, 24 individual water bodies (Figure 2) were

sampled within multiple side-arm systems, and the sampling design for the water bodies was stratified along the connectivity gradient, limited by the accessibility of the water bodies via the road network and due to nature protection law.

Sampling was done for two weeks each month, and 2-4 sites were sampled per day. Per site, one representative water sample was taken 20-40 cm below the water surface depending on the water level of sites and stored in pre-washed 10-liter polyethylene jerrycan. Total phosphorus, total suspended solids, particulate inorganic matter, particulate organic matter, chlorophyll-*a* concentrations and dissolved organic matter (DOM) via excitation emission matrix (EEM) were determined during this sampling campaign. In October additionally, dissolved nutrients (nitrate, nitrite, ammonium, soluble reactive phosphorus) were analysed and pulse-amplitude modulated (PAM) fluorometry was conducted to measure the relative electron transport rate (rETR). In-situ parameters i.e., water body temperature, pH, electrical conductivity (EC), and dissolved oxygen (DO) concentrations were measured at all dates with portable meters at each site using WTW 330, Hach Lange HQ40d probes.

Sediment sampling (3-10 sub-samples) followed a degree of morphological heterogeneity of the substrate to have a good representation of the site and dependent on the accessibility of the water body shoreline/bank, sediment samples were collected during the October sampling only were placed in resealable plastic bags.

3.5 Chemical analyses (water and sediments)

To determine TSS, 200-1000 ml of water sample (depending on turbidity) were filtered using muffled (490°C for 2.5 hours) Whatman Schleicher & Schuell 47 mm GF/F filter papers immediately after sampling and dried at 80°C for 24 hours and muffled again at 490°C for 2.5 hours to quantify organic (POM) and inorganic (PIM) contributions to particulate matter. Chlorophyll-*a* concentration, a pigment present in all green algae was extracted using organic solvent (Acetone) and ultrasonic cell disruption (Steinman et al., 2017). About 200-1000ml water samples (dependent on the suspended sediment load) were filtered through Whatman glass microfiber GF/C filter papers (diameter 47 mm) and approximately 5g of sediment sample was kept at -20°C until extraction with 90% Acetone under dark conditions for 24 hours (Steinman et al., 2017). All samples were centrifuged at 2500 rounds per minute for 10min and a supernatant decanted for spectrophotometric analysis on Hach Lange DR 3900 Photometer at multi-wavelength (664, 665, and 750). The ion concentrations, samples were filtered through pre-muffled (at 450°C) Whatman GF/F filters (0.7 µm mesh size) for analyses of potassium,

sodium, magnesium, calcium chloride, and sulfate ions according to standard methods (APHA, 1998).

Water samples (300-500 ml) were filtered with Whatman GF/F filter papers, pore size 0.75 μ m immediately after sampling, and a filtrate (stored in one 50 ml plastic vial), at 4°C until laboratory analysis. The Hazen color test uses a Pt/Co solution to determine the yellowness of the water sample, standard row was prepared according to (ISO EN 7887, 2011) on a progressive scale from (0, 5, 15, 25, 50, and 75 mg Pt L⁻¹), using the Platinum Cobalt color comparison solution (Hazen), up to 75 Hz because Austrian natural waters are not so humic rich. Water samples and standard row solution (10 ml) were placed in a 3 cm cuvette for comparative reading at both 440 and 750 nm using DR 3900V Hach GmbH photometer. DOM composition was determined via optical characteristics using DOM absorbance spectra measurements (Baker, 2002; Hudson et al., 2007; Weigelhofer et al., 2020) performed between 200 and 700 nm in 0.5 nm intervals with a UV-VIS spectrophotometer (UV 1700 Pharma Spec, Shimadzu Corporation, Kyoto, Japan; 5 cm quartz cuvette). The absorbance analyses were done using a UV-Probe program and data was exported from the program as Excel and text delimited files. Fluorescence data were obtained using a fluorescence spectrophotometer with a xenon lamp (Hitachi F-7000, Hitachi High Technology Corporation, Tokyo, Japan).

DOM excitation emission matrices (EEM) from fluorescence spectroscopy were measured over a range of wavelengths to produce 3D scan fluorescence graphics (Murphy et al., 2013). The excitation (Ex) wavelengths ranged from 200 to 450 nm and emission (Em) 5 nm wavelengths from 200 to 600 intervals in a 1 cm quartz cuvette. Measurements were blank-corrected against milli-Q, corrected against inner-filter effects, and normalized to water Raman units as in (Lawaetz and Stedmon, 2009). DOM quality was analyzed using the peak picking method with the R package staRdom (Pucher et al., 2020) and the peaks A, B and T along with indices HIX, BIX and FI were used for further statistical analyses (see their description in Table 1). For dissolved organic carbon (DOC) and total dissolved nitrogen (TDN), water samples were filtered using Whatmann membrane filters (0.45 μ m pore size and 47 mm diameter), and filtrate was stored in 50ml pre-muffled (4 hours at 450°C) glass vials. The DOC concentrations were determined using the TOC-L analyser which adopts the 680°C combustions catalytic method developed by Shimadzu. For total nitrogen, the TOC analyser has a TNM-L Total Nitrogen Unit which performs simultaneous TOC and TN measurements. TDN concentration was then determined by 720°C catalytic thermal decomposition/chemiluminescence measurement method. Dissolved nutrients concentrations (N-NH₄, N-NO₃, N-NO₂, and P-PO₄)

were measured spectrophotometrically using a continuous flow analyzer (Flowsys, Systea Analytical Technology, Italy) according to standard methods (APHA, 2005).

3.6 Quantifying photosynthetic rates

Water samples were transported in a cooling box to the lab and measured the same day. A Phyto-PAM (pulse-amplitude modulation) coupled with a Phyto-WinControl Software V 1.45 (Heinz Walz GmbH, Effeltrich, Germany) was used to produce rapid light curves (RLCs) (Kühl et al., 2001). The instrument measures the effective quantum yield of PSII ($Y(II) = F/F_m$) at a series of nine light steps of increasing irradiance without prior dark acclimation (16, 32, 164, 364, 564, 964, 1364, 1664 and 2064 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). According to Heinz (Walz GmbH, 2003), measurements with the Phyto-PAM require the application of a saturation pulse and that is the measurement that involved the assessment of the fluorescence yield before the saturation pulse (F) and the maximum fluorescence yield (F_m).

The duration of the irradiance steps was 15 seconds (Serôdio et al., 2008) and the relative Electron Transport Rate (*rel.ETR*) was calculated at each level of irradiance, as the product of the effective quantum. Relative ETR ($rel.ETR = (YII \times PAR \times ETR - factor)$) whereas for the ETR-factor the default setting of 0.42 was used (Genty et al., 1989). Alpha electrons/photons (α) are the initial slope of rapid light curves (RCL) which is related to the quantum efficiency of photosynthesis. The minimum saturating irradiance (I_K) was calculated as, $I_K = \frac{ETR_{max}}{\alpha}$. The $Y(II)$ value estimates the photochemical use of excitation energy in the light and PAR is the photosynthetically active radiation. While formal units of $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$ apply for relative ETR, in practice normally “rel. units” are used (Schreiber et al., 2011). The light response of rETR (rETR/ I) curves was constructed with the WinControl software using the model (Eilers and Peeters, 1988). This model allowed estimating the maximum rel.ETR (rel.ETR_{max}) as a measure for photosynthetic activity.

Table 1: Description of Dissolved organic matter (DOM) peaks and indices analysed in this study.

DOM Peaks and Indices	Description	References
T	Peaks indicative of biological activity or protein-like material include tryptophan-like peaks	
B	Peaks indicative of biological activity or protein-like material include tyrosine-like peaks	
C	Terrestrial humic-like peak C is considered an indicator of allochthonous carbon in aquatic systems	(Cobble, 1996; Stedmon and Markager, 2005)
HIX	Humification Index - degree of DOM humification, highly humified organic substances are generally resistant to degradation and are expected to persist in the environment longer than substances with a low degree of humification. HIX is low (<5) for fresh DOM derived from plant biomass and animal manure and generally increases with the degree of decomposition	(Ohno, 2002; Stedmon and Markager, 2005)
BIX	Biological Index - relative contribution of autochthonous DOM. Values of BIX between 0.8 and 1.0 correspond to freshly produced DOM of biological or microbial origin, whereas values below ca. 0.6 are considered to contain little autochthonous OM	(Fellman et al., 2006; Huguet et al. 2009; Stedmon and Markager, 2005)
FI	Fluorescence Index - a metric for distinguishing CDOM derived from terrestrial and microbial sources. FI values of 1.4 or less indicate DOM of terrestrial origin and values of 1.9 or higher correspond to microbially-derived material. May represent fluorescent, water-soluble, extracellular substances excreted by microorganisms, detritus resulting from apoptosis	(McKnight et al., 2001; Stedmon and Markager, 2005)

3.7 Quantifying connectivity

By combining remotely sensed surface-water time series and landscape connectivity metrics based on the graph theory network analysis (Erős et al., 2012), indices, and models, researchers have been able to analyze connectivity across large spatial extents. Different from landscape ecology studies such as (Erős et al., 2012; Gounand et al., 2018; and Uroy et al., 2021) where the approaches emphasize the importance of connectivity in understanding biodiversity patterns, this study provides quantitative and spatial frameworks to understand how the hydrochemistry, productivity, distribution/spatial arrangement, and availability dynamics are influenced by the degree of connectivity in the system and to the adjacent Danube River and their influence on resource flows. We used connectivity indices for the network of water bodies important for resource flows and expressed the water bodies as nodes and their connectivity linkages within the system and to the Danube are the basis of the calculation where the peripheral water bodies are less connected hypothetically.

The floodplain water bodies in this study were considered both dynamic fluvial aspects (during the high flow month) and static networks because assessments were done for changes along a spatial gradient of connectivity and temporal variations between 3 months. Additional to the centrality metrics, an important predictor variable was "hydrological connectivity"/inundation frequency, quantified as the average days per year a waterbody has a surface water connection to the Danube main River which ultimately depends on the river discharge and water body position in the network (Reckendorfer et al., 2006). Calculations were based on a network (network edges) representing the side-arm and backwater systems in the Donau-Auen National Park, polygons of water bodies (nodes) and temporal change quantified based on "hydrological connectivity", for a detailed description see (Reckendorfer et al., 2006).

Network analysis was done using ArcGIS 10.6 software (ESRI, Redlands, CA) with an ArcGIS Network Analyst Extension. Harmonic centrality and betweenness centrality were calculated using the igraph package (<https://igraph.org/>) for R and the igraph software package for complex network research by (Csardi and Nepusz, 2006). The probability of connectivity was calculated using the software package Conefor Sensinode 2.2 to quantify the importance of individual water body patches (Saura and Torné, 2009). The network-related indices were calculated for connectivity in a static approach (for the whole river-floodplain network), as well as dynamic, for all levels of hydrological connectivity ranging from 0 (completely isolated backwaters of the network are included) to 365 days (only permanent connected side-arm systems are included) and their parent River the Danube (Uroy et al., 2021). Connectivity

indices are further calculated for both directed and undirected networks where the directed network accounts for directional transport in the system whereas the undirected network accounts for the total connectivity in the network e.g., where water is flowing bidirectional dependent on the water level of the Danube, an inflow during a flood and outflow after the flood.

3.7.1 Connectivity indices- harmonic centrality

The harmonic centrality (hc) is a distance-based index, hence summarizes the distance to all other water bodies which were the most central and hence have the highest value and are the most influential nodes in the network (Andrade and Rêgo, 2019). RoCHAT et al., (2009), explain that hc seeks to include the unreachable nodes (water bodies) by calculating the sum of all the inverse of the shortest path distances from a specific node to all the other nodes. Harmonic centrality for the node x is calculated as:

$$hc(x) = \sum_{y \neq x} \frac{n-1}{d(y,x)} \dots\dots\dots \text{Equation (1)}$$

Where a node “x” is defined as the sum of the reciprocal of the distances between that node x and every other node in its graph not including itself. For example, to calculate the (hc) for node x, the distance between x and y nodes is calculated, and then take the reciprocal of the value got (distance reciprocal). Then calculate the distance reciprocal for all the nodes in the network a, b, c, d... keeping node x constant and the sum of all the distance reciprocal values of all these nodes from node x is the harmonic centrality of x (hc(x)). Nodes closer to most other nodes in the graph have higher harmonic centrality.

3.7.2 Connectivity indices- betweenness centrality

The importance of a node is characterized by its centrality in the network, the shortest paths between each pair of nodes are determined as the Betweenness centrality (Barrat et al., 2005). Many paths pass through one or more other nodes so that nodes may be part of more than one shortest path and the nodes that are part of many paths are more central in the network because any change at this particular node will affect large parts of the system (Marra et al., 2014). Betweenness centrality (bc) gives higher importance to nodes that act as connectors for different parts of the network, i.e., the water body with the highest ‘bc’ value connects most of the other nodes in the system especially the Danube River is a more central and relevant node compared to all the floodplain water bodies. The water bodies that follow with higher ‘bc’ values will follow in importance for the resource flow/exchanges in the system after the Danube. The side-arm channels and backwaters with high ‘bc’ values may have a central

position or if they have the biggest water body area (size) usually included in calculating some connectivity indices. In the equation below, as defined by (Barthélemy, 2011).

$$g(i) = \sum_{s \neq t} \frac{\sigma_{st}(i)}{\sigma_{st}} \dots\dots\dots \text{Equation (2)}$$

Where, σ_{st} is the number of shortest paths going from s to t and $\sigma_{st}(i)$ is the number of shortest paths going from ‘s’ to ‘t’ through the node ‘i’. This quantity ‘g(i)’ thus characterizes the importance of node “i” in the organization of flows in the network.

3.7.3 Probability of connectivity index

Another metric based on a static network; the probability of connectivity (PC) is a graph-based habitat availability metric that quantifies functional connectivity. It is defined as the probability that two points randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) given a set of n habitat patches and the links (direct connections) among them as elaborated by (Saura and Pascual-Hortal, 2007) is denoted by:

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{i,j}}{A_L^2} \dots\dots\dots \text{Equation (3)}$$

Where a_i and a_j are the attributes of patches ‘i’ and ‘j’ (Saura and Rubio, 2010), ‘ A_L ’ corresponds to the total landscape area (in the case of the floodplain water bodies ‘ A_L ’ is the Area of water bodies and ‘p’ is a distance decay function between ‘i’ and ‘j’).

3.7.4 Description and codes for connectivity metrics calculated

Description and codes for connectivity indices were calculated and the nodes/water body patches were weighed by size and distance between the patches to better represent their contribution to connectivity. For this study, they include, (a) the Euclidean distance (eu) which assumes resource flows along a straight line between two nodes, (b) the river-based model (rb) which assumes resource flow exchanges through the entire water body network (after establishing pairwise connections, graph-theoretic applications like igraph can be used to calculate the connectivity of the whole floodplain network), and lastly (a) the directed flow (dir) which are the resource exchanges along with the longitudinal flow of the river. The nodes/water body patches were weighed by size and distance between the patches to better represent their contribution to connectivity as below.

(1) Harmonic centrality (hc) by (Rochat, 2009) captures the notion that the “closer” the node is, on average, to the other nodes in the network, the more central it is.

(2) Betweenness centrality (bc) is explained by (Barrat et al., 2005) as the shortest path between each pair of nodes.

(3) Probability of connectivity (PC) which helps to analyze individual water body importance (Saura and Pascual-Hortal, 2007) thereby allowing one to know and rank the water bodies that contribute most to general connectivity.

(4) Connector - the role of the water body as a connecting element in the floodplain system which depends solely on its position in the network (Saura and Rubio, 2010) and

(5) Flux - Area-weighted flux through the connections of a water body from all the other relevant water bodies in the system (Saura and Rubio, 2010)

The distinct types of floodplain water body networks were also categorized as below

$o_y \Rightarrow$ represents the floodplain water body network during flood conditions (bank-full flow) calculated over a standard year when the side-arm channels are connected or disconnected

$o_c \Rightarrow$ represents the floodplain water body network during flood conditions (bank-full flow) calculated for the connected state.

$mean_y \Rightarrow$ mean connectivity estimated over an average year (calculated dependent on hydrological connectivity)

$mean_c \Rightarrow$ mean connectivity estimated for all connected stages for the specific water body

$eu \Rightarrow$ Euclidean distance calculated between two water bodies.

$dir \Rightarrow$ calculated for directed connectivity that follows the longitudinal connectivity and flow of the Danube River.

$rb \Rightarrow$ calculated for the undirected transport, whole river-based network connections (lateral, vertical, and longitudinal connections for all the floodplain water bodies).

The threshold distance here has only been used for the probability of connectivity index (PC) where-

- (a) 100 \Rightarrow represents the mean transport distance of 100 meters - short distance (Saura and Pascual-Hortal, 2007)

- (b) 1000 => mean transport distance of 1000 meters - medium distance (Saura and Pascual-Hortal, 2007)
- (c) 10000 => mean transport distance of 10000 meters - large distance exchanges

3.8 Statistical design and calculations

The study had a multivariate-ordination statistical design specifically a regression design due to distributions along an environmental (spatial) gradient. Statistical hypotheses where the; Null hypothesis (H_0) the variables are independent to the degree of connectivity and water body environmental conditions whereas, the alternative hypothesis (H_A) the variables are dependent on influence from local environmental conditions and degree of hydrological connectivity. Pearson's correlation tests to determine the relationship among the response variables (nutrient (total phosphorus), particulate matter, DOM quality parameters (biological index (BIX), DOM-peaks B, T, and C, fluorescence index (FI), and humification index (HIX), and phytoplankton Chlorophyll-a).

Principal Components Analysis (PCA) reduced the number of the response variables (Rotation method: Varimax with Kaiser Normalization. ^a) measured in all three months i.e. (nutrient (total phosphorus), particulate matter, DOM quality parameters, and phytoplankton Chlorophyll-a) using IBM SPSS Statistics for Windows Version 26 (also used to graphically illustrate between month comparisons). A linear model for the relationship was assumed for the independent variables/environmental gradients (connectivity and environmental conditions) estimated for the entire variation (sum of all eigenvalues) in the dependent (response) variables. Data were checked for normality using histograms, Quantile-Quantile plots (QQ-plots), and homogeneity of variance using the Shapiro-Wilks test and log transformed if necessary. Differences in nutrient condition, particulate matter, and dissolved organic matter quality between and within the three months were done by one-way ANOVA (all analyses done using R Software Version 4.1.2).

According to (Borcard et al., 1992) in their study on "Partialling out the spatial component of ecological variation", variation partition aims at quantifying the various unique and combined fractions of variation explained by (1) connectivity and (2) environmental conditions in this study. A linear regression trend was considered to show the source of variation in the response variables explained by the two factors above. Linear regression analyses were used to test for a linear trend (Borcard et al., 2018), which was incorporated distinctly in the variation partitioning process only if it was a statistically significant model without forward

selecting the explanatory predictor variables from two factors connectivity and the environmental conditions. This guaranteed that any linear trend, big or small was incorporated in the variation partition analysis (Borcard et al., 2018). Before variation partition, linear regression models incorporated a forward selection which was singly used to regress the response with each set of explanatory variables in the multiple regression analyses.

Multiple linear regression summarized the variation where consequently the response variables were explained by explanatory variables from the two factor groups with variation partitioning in R Software 4.1.2 using the ModEvA package and varPart function. The overall variation was partitioned as follows in terms of the amount of variation explained by either of the two factors. Variation partitioning comprised of (a) the non-spatial variation in the response variables as a function of only local environmental conditions, (b) the variation in the response variables that is explained by both local environmental conditions and connectivity, a common variation that is partially a consequence of the interaction of these explanatory predictors, (c) variation in the response variables which was explained solely by the spatial connectivity metrics and (d) is the fraction of variation in the response variables (nutrients (only total phosphorus), DOM, PIM, POM, and phytoplankton Chlorophyll-a) that is neither explained by connectivity no local environmental conditions.

Hierarchical cluster analysis (Ward's method, squared Euclidean distance) was used to divide the detailed variable dataset from the October sampling into five cluster groups-

1. Nutrients group - (Orthophosphate (P-PO₄), total phosphorus (TP), Ammonium (N-NH₄), Nitrate (N-NO₃), Nitrite (N-NO₂), and total dissolved nitrogen (TDN)),
2. DOM water quality - (DOM indices (HIX, BIX, and FI) and peaks (B, T, and C), and DOC).
3. Ion concentrations group - Sodium, Potassium, Magnesium, Chloride, Sulfate, and Calcium.
4. Phyto-PAM Photosynthesis rate analyses group - (relative electron transport rate (relativeETR₄), minimum saturation irradiance (I_k), Alpha (α) the slope of the initial linear, light-limited part of the rapid light curve in the phytoplankton analyses) and pelagic/phytoplankton chlorophyll-a concentration.
5. PM and Chl-a group - Particulate matter (PIM and POM), CDOM, sediment organic matter content, and phytobenthos chlorophyll-a.

The 3-cluster solution mainly provided a good representation of heterogeneous gradient analyses in the floodplain network, and as for the ions and nutrients cluster groups, 2-cluster solutions were used as there was not much variation in the floodplain network. The results were analyzed graphically using IBM SPSS version 26 and variation across a spatial gradient for each cluster group was illustrated using maps developed in ArcGIS version 10.6. Spectroscopic analysis of dissolved organic matter in R (StaRdom package) by (Pucher et al., 2019) was used to separate components of the excitation-emission matrices using R version 4.1.2 provided a quick understanding and quantification of DOM composition for the samples. StaRdom was used to analyze spectroscopic data (both fluorescence and absorbance) to examine the DOM composition (Pucher et al., 2019) from the floodplain water body samples. Pre-processing of the fluorescence data included spectral correction, blank correction, inner-filter effect correction, Raman normalization, scatter removal, interpolation, and noise correction was possible by the template in (https://cran.r-project.org/web/packages/staRdom/vignettes/Basic_analysis_of_DOM_samples.html; accessed on 20 January 2022). The R software was used to perform parallel factors analyses (PARAFAC) by (Murphy et al., 2013) of the excitation-emission matrices (EEMs) which included DOM peak picking of EEMs, and as well calculated the DOM indices (HIX, BIX, and FI) Blank correction was done according to (Murphy et al. 2013; Massicotte 2019), calculating fluorescence peaks and indices (Massicotte 2019), autochthonous productivity index/freshness index (BIX) according to (Huguet et al. 2009; Fellman et al., 2006). Classical peaks (Coble, 1996), based on the manual peak picking (B, T, M, A, and C) were analysed for DOM quality, peaks (M and A) were excluded in further analyses, fluorescence index (FI) was calculated according to (McKnight et al., 2001) and lastly the humification index (HIX) according to (Ohno, 2002).

Chapter 4. RESULTS

4.1 Comparison of floodplain hydrochemistry between the three months (August, September, and October).

Differences between the months were determined using Analysis of Variance (one-way ANOVA) for all variables measured for statistically significant between means of the different variables in the three sampling dates see ANOVA results in (result in Appendix 1). During all the months, the Danube River and floodplain water bodies differed significantly in water body temperature $F(2, 66) = 129.9, P < 0$. DOM quality also differed significantly in the floodplain as shown by the biological index (BIX) with $F(2, 66) = P < 0.001$, humification index (HIX) with $F(3, 66) = 3.344, P < 0.01$ and marginal significant differences in the Florescence index (FI) $F(3, 66) = 2.957$ and $P < 0.05$ ($P = 0.0517$.) in the three months.

In August, the following sites had the highest PIM concentrations Donau (Danube main channel), Mannsdorfer Hagel, Rohrwörth downstream, Kleine Binn, Karpfen Arm, Regelsbrunn, Petronell-Carnuntum, Röthelstein upstream and Tiergarten Arm isoliert. Noticeably, Tiergarten Arm isoliert was the only isolated water body with high PIM concentrations during the high flow month, the rest are all connected side-arm systems with central positions in the network. Backwater systems had lesser PIM as expected during August. Higher concentrations in the connected side-arm channels were due to the increased river discharge and lateral exchanges. In September, Donau, Röthelstein upstream, Regelsbrunn, Petronell-Carnuntum, Rosskopf Arm innen, Fadenbach bei Orth and Tiergarten Arm isoliert had the highest PIM concentrations. The last two sites do not have surface connections to the Danube. For October, Donau, Röthelstein upstream, Regelsbrunn, Petronell-Carnuntum, Karpfen Arm, Fadenbach turtles, Fadenbach bei Orth and Tiergarten Arm isoliert, here the pattern starts to get more heterogeneous in terms of spatial variation (Figure 4).

The water bodies also had statistically significant differences in total phosphorus $F(2, 66) = 11.84, P < 0$, particulate inorganic matter $F(2, 66) = 5.793, P < 0.001$ and phytoplankton Chlorophyll-a concentrations $F(2, 66) = 5.59, P < 0.001$ graphical results shown in Figure 5. The remaining variables CDOM/ Color, particulate organic matter, conductivity, DOM water quality peaks (B, T, and C) showed no statistically significant differences in their means $P < 0.05$. To examine between which months are there significant differences for the above variables, Post hoc returned pairwise comparisons using the Tukey HSD (Tukey multiple comparisons of means at 95% family-wise confidence interval) in R indicated which months

differed significantly from each other ($P < 0.05$). Total phosphorus and Particulate inorganic matter differed significantly between the months October and September, and September and August $P < 0.05$. Phytoplankton Chlorophyll-a concentrations differed significantly between October and August, and September and October $P < 0.05$ (Figure 4 (c)) whereas water temperature differed significantly between all the three months (pairwise) $P < 0.05$. DOM quality indices BIX, HIX, and FI also differed significantly between September and August, $P < 0.05$.

The yellowness color of water is what was referred to as Colored dissolved organic matter (CDOM) in a bid to clarify what “CDOM” mean in this study. CDOM was highest in August during the high flow condition and lowest in October, most of the sites with high CDOM are isolated sites. CDOM ranged between from 10.06 at Haslau to 78.09 Hazen units at Grundwasser Tümpel Lobau, other sites with values higher than 25 Hazen were Tiergarten Arm isoliert with 76.58 Hazen, Fadenbach aussen had 47 Hazen, Fadenbach Turtle had 33.5 Hazen and Witzendorfer Arm with 29.7 Hazen units. In September, CDOM ranged from 4 Hazen units at Mannsdorfer Hagen to 58.9 Hazen units at Grundwasser Tümpel Lobau. Sites with values higher than 25 were Tiergarten Arm isoliert and Fadenbach Turtle with 54.1 and 34.2 Hazen units respectively. Whereas in October CDOM ranged between 2.81 Hazen units at Röthelstein isoliert and 84.18 Hazen units at Grundwasser Tümpel Lobau. One water body with a value above 25 Hazen units was Faden bei Orth with 52.76 Hazen units. Between the months CDOM varied greatly, especially for the high flow month, and mean values were 26.19, 19.16, and 18.45 Hazen units for August, September, and October respectively. The Danube River values also decreased temporally i.e., 16, 11.2, and 5.23 Hazen units in August, September, and October respectively.

Total phosphorus (TP) varied greatly both spatially and temporally where August had the highest mean concentration of 137.77 $\mu\text{g/L}$, then 80.8 $\mu\text{g/L}$ in September, and 58.4 $\mu\text{g/L}$ in October. The Schönauer Wasser had the least TP concentration 58.3 $\mu\text{g/L}$ and Haslau had the highest 239.4 $\mu\text{g/L}$ of TP in August. In September Fadenbach aussen had the least TP concentration while Fadenbach bei Orth had the highest TP 262 $\mu\text{g/L}$. In October, Regelsbrunn had the least TP concentration of 9.6 $\mu\text{g/L}$ and Fadenbach bei Orth had the highest TP i.e., 221 $\mu\text{g/L}$. The Danube River had a consistent decreasing trend in TP concentration between the 3 months i.e., 108.2 $\mu\text{g/L}$, 29.2 $\mu\text{g/L}$, and 22.4 $\mu\text{g/L}$ in August, September, and October respectively (Figure 4 (b)).

The Danube River had the lowest values for DOM fluorescence peaks B and T. DOM fluorescence peak B concentration for example was highest Roskopf Arm innen (a more connected site downstream), and least in Kleine Binn (connected arm) for August, Fadenbach Turtles (isolated water body) had the highest DOM fluorescence peak B concentration least in Kleine Binn (connected arm) whereas for October it was the Tiergarten Arm isoliert (isolated) that had DOM fluorescence peak B concentration and the Spittelauer Arm (permanent connection to the Danube) had the least concentration. This result corresponded to “Hypothesis 2 (H2)- Particulate matter, dissolved organic carbon (and DOM), nutrient and pelagic algal biomass (Chlorophyll-*a*) are expected to be higher in floodplain water bodies than in the Danube River, with greater values in the more isolated waterbodies and generally during the disconnected period”. The only deviation to the H2 was that DOM was highest in August (connected floodplain state) rather than the set expected to be higher in October (during the isolated state of the floodplain).

Mean phytoplankton Chlorophyll-*a* concentrations were highest in October during the isolated state of the floodplain water bodies at 26.58 µg/L and least in September at the intermediate connection state to the Danube River at 10.6 µg/L. In August, phytoplankton Chlorophyll-*a* concentrations ranged from 0.64 µg/L (at Spittelauer Arm) to 58.74 µg/L (at Röthelstein isoliert), while in September ranged from 2.32 µg/L (at Rohrwörth upstream) to 29.9 (at Spittelauer Arm) and for October ranged from 5.02 µg/L (at Rohrwörth upstream) to 91.21 µg/L (at Regelsbrunn) result in Figure 4 (c) below. Particulate inorganic matter also yielded significant differences between the mean for the temporal variation.

Particulate inorganic matter concentration varied greatly both spatially and temporally where August had the highest mean concentration of 0.022 g/L, then 0.0055 g/L in September and 0.0086 g/L in October. Fadenbach bei Orth had the least PIM concentration 0.001 g/L and Kleine Binn had the highest 0.088 g/L of PIM in August. In September, Rohrwörth downstream had the least PIM concentration of 0.0003 g/L while Petronell-Carnuntum had the highest PIM of 0.0162 g/L. In October, the Schönauer Wasser had the least PIM concentration of 0.002 g/L and the Tiergarten Arm isoliert had the highest PIM i.e., 0.0481 g/L. The Danube River had a steady decrease in PIM concentration between the 3 months i.e., 0.086 g/L, 0.011g/L, and 0.0056 g/L in August, September, and October respectively (Figure 4 (a)).

Values of BIX for the floodplain water bodies were generally > 0.7 in all months and ranged between 0.72 and 0.95 Raman units at Grundwasser Tümpel Lobau and the Tiergarten Arm respectively in August. BIX values ranged between 0.72-0.98 Raman units at the Grundwasser

Tümpel Lobau and Karpfen Arm respectively in September and 0.74-1.3 Raman units at the same sites in October. Values of HIX for the floodplain water bodies were generally > 0.6 for all months and ranged between 0.69 and 0.92 Raman units at Rosskopf Arm aussen and the Grundwasser Tümpel Lobau respectively in August. BIX values ranged between 0.76 to 0.92 Raman units at Haslau and Grundwasser Tümpel Lobau respectively in September and 0.62 to 0.88 Raman units at Mannsdorfer Hagel and Fadenbach turtles in October. For all months, the FI values for all water bodies were >1.5 Raman units, highest FI values of 1.7 Raman units were observed at Karpfen Arm in September and at Mannsdorfer Hagel, Rosskopf Arm aussen, and Karpfen Arm in October.

Generally, peak A (terrestrial humic derived from both terrestrial and autochthonous sources common to a wide range of freshwater systems) was the highest observed fluorescence peak from the DOM quality analysis noticeably at excitation (ex) < 250 nm and emission 500 nm. DOM peak B, excitation (ex) 280 nm and emission (em) 344 nm the Tryptophan-like fluorescence peak derived from autochthonous sources and corrected to fluorescence material in a forested watershed. DOM peak B values ranged between 0.09 and 0.59 Raman units at Kleine Binn and Rosskopf Arm innen respectively in August, 0.07 to 0.46 Raman units at Kleine Binn and Fadenbach Turtles respectively in September. October peak B values ranged between 0.01 and 0.76 Raman units at the Spittelauer Arm and Tiergarten Arm isoliert respectively.

The Tyrosine-like fluorescence peak T (excitation (ex) 270 nm and emission (em) 344 nm) values range between 0.11 and 0.47 Raman units in August, between 0.06 and 0.46 Raman units in September, and between 0.06 to 1.1 in October. Peak C values ranged between 0.14 and 1.2 Raman units in August, between 0.77 and 0.98 Raman units in September, and lastly from 0.06 to 1 Raman unit in October. Fluorescence spectroscopy was used to characterize dissolved organic matter (DOM) in the Danube floodplain water bodies and several fluorescence signals such as humic-like, tyrosine-like (peak B) and tryptophan-like (peak T) was observed. Humic-like fluorescence stimulated by the visible excitation peak C (Ex = 350 and Em varied between 450 and 480) and one by the UV excitation peak A (not included in the results data) were most pronounced.

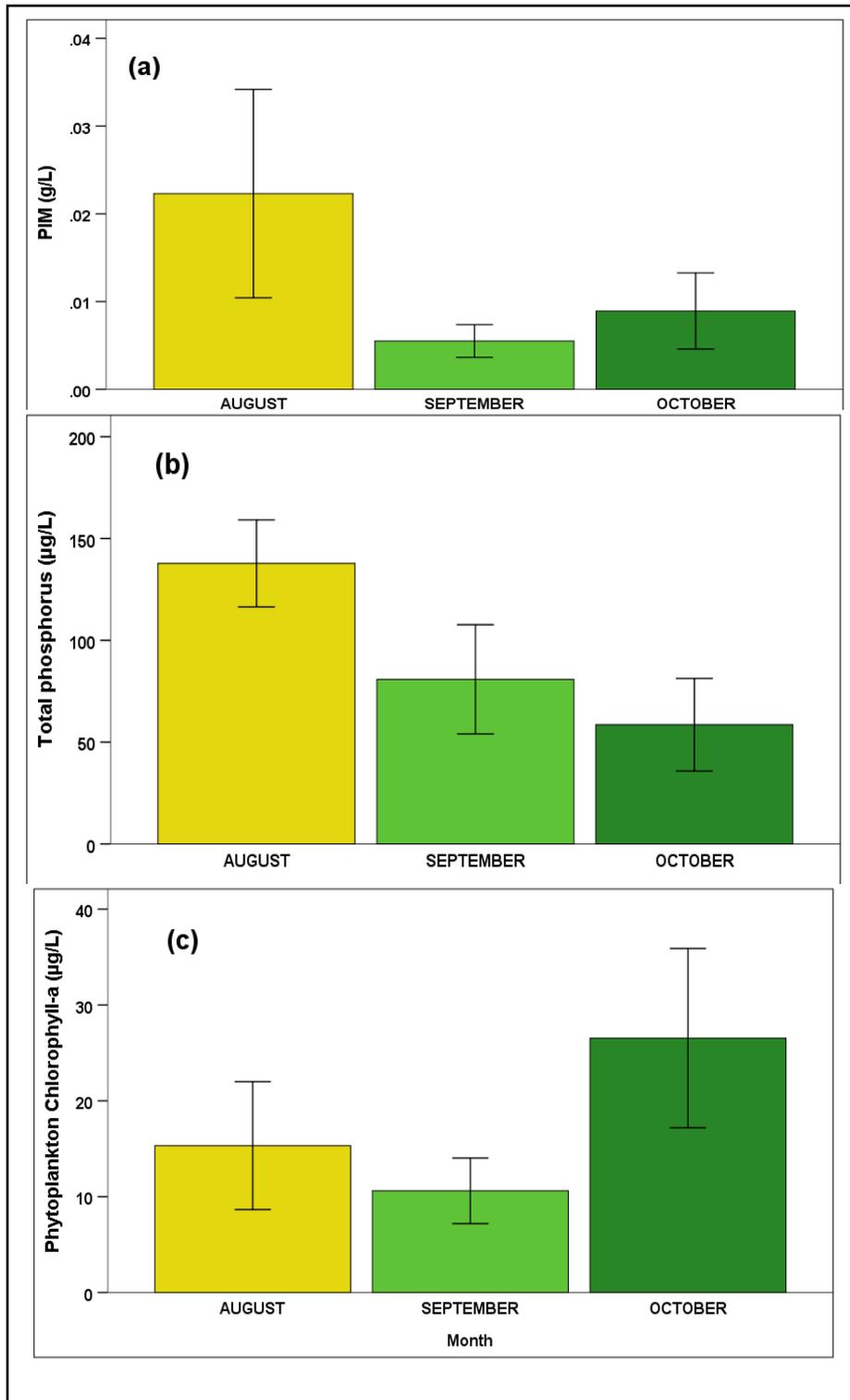


Figure 4: Comparing between the months with one-way ANOVA.

(a) Particulate inorganic matter $F(2, 66) = 5.793$, $P < 0.001$, (b) total phosphorus $F(2, 66) = 11.84$, $P < 0$, and (c) phytoplankton chlorophyll-a concentration $F(2, 66) = 5.591$, $P < 0.001$, bars represent mean \pm standard error.

For all EEMs, three fluorescence peaks were identified that were always detectable. These were (1) fluorescence excited between 300 and 340 nm excitation and emitted between 400 and 460 nm (peak C), (2) fluorescence excited between 220 and 250 nm excitation and emitted between 400 and 460 nm (peak A), and (3) fluorescence excited between 220 and 235 nm and emitted between 330 and 370 nm (peak T). Both peak C and peak A fluorescence are attributed to terrestrial fulvic-like and humic-like aquatic substances, and peak T to microbially and algal derived tryptophan-like substances. Lastly, a vital and most occurring ultraviolet excited peak A values ranged between 0.3 and 2.7 Raman units in August, between 0.18 and 2.2 Raman units in September, and lastly 0.19 to 2.2 Raman units in October.

Overall mean values for the floodplain water bodies analyzed in this study were $Ex_{max}/Em_{max} = 350/480$ nm but the peaks differed between the months August, September, and October (Figure 5 and Figure 6) below. Generally, for all water bodies to fluorescence because the fluorescence peaks/signals were less intense and overall, October fluorescence peaks had the most intense peaks measured in the study. Excitation emission matrices for the Danube River (Site_0) and Röthelstein upstream (Site_3) highly connected water body (Figure 5) and for isolated water bodies that is Witzelsdorfer Arm (Site_15) and Fadenbach bei Orth (Site _21) in (Figure 6).

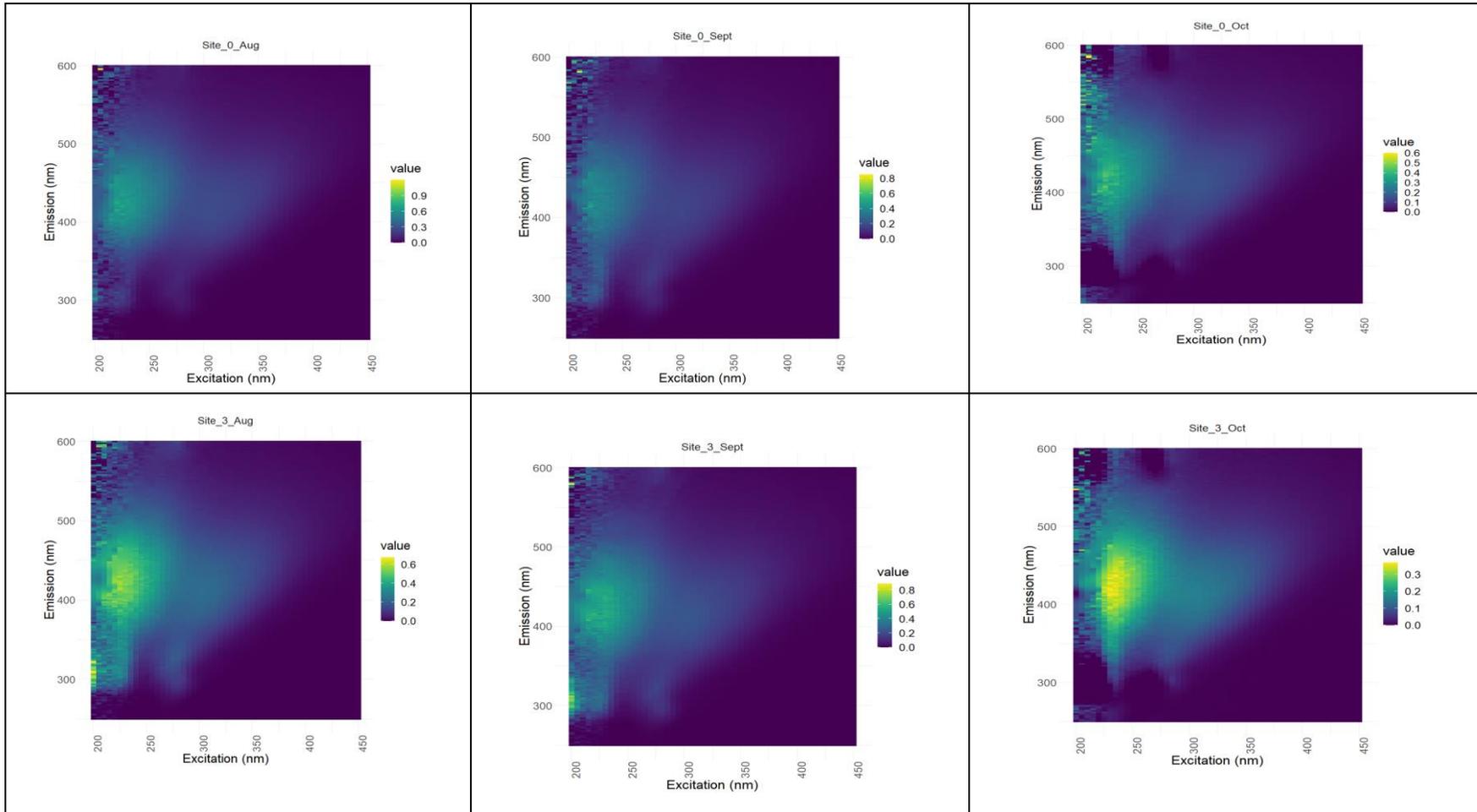


Figure 5: Emission Excitation matrices (EEMs) showing variation in the three months for the Danube River (Site_0) and at a more connected site Röthelstein upstream (Site_3) which is in the downstream part of the floodplain.

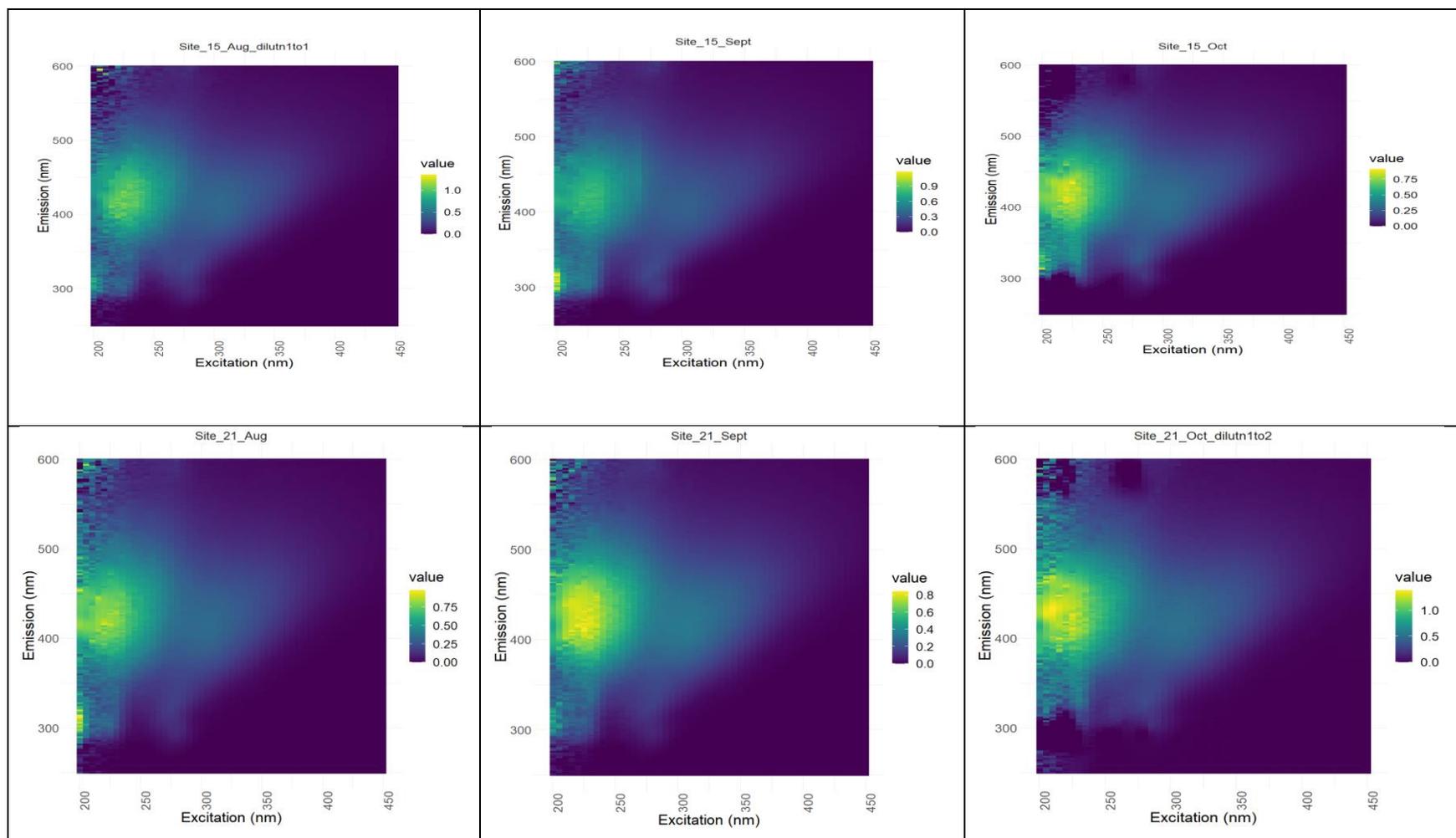


Figure 6: Emission Excitation matrices (EEMs) showing variation between the 3 months for isolated water bodies that is Witzelsdorfer Arm (Site_15) and Fadenbach bei Orth (Site_21).

4.2 Disentangling the influence of network connectivity and environmental conditions on total phosphorus, POM and PIM, DOM, and phytoplankton biomass at the three different water level stages

For the explanation of these variables, it was necessary to examine how the connectivity gradient or environmental conditions influence variation of these variables between the high flow month (August), mean flow (September) and low flow condition in October. This was done looking how much they independently contribute to the floodplain hydrochemistry. The PCA axes represent the main variable gradients in the floodplain network, PCA results for August, September, and October are in Tables 2, 3, and 4 respectively. In the PCA results, the dominant variable(s) appearing in each component axis (with the highest correlation) was determined as the main variable gradient in the floodplain network for the months.

The August and September PCA_1 represented a DOM gradient with fluorescence protein/tryptophan-like peak T, (peak T and protein/tyrosine-like peak B for September) which was indicative of microbial activity, ultraviolet excited terrestrial humic peak C, an indicator of allochthonous organic matter inputs into the water bodies, BIX index for the relative contribution of DOM. Also, in PCA_1 was the CDOM/yellowness color due to chromophoric organic contents that were brought in with other river inputs.

Table 2: Factor analysis result showing PCA variable axes of the floodplain hydrochemistry for August 2021.

Response variables	Component	
	PCA_1	PCA_2
DOM peak C	0.957	
CDOM	0.951	
DOM peak T	0.862	0.408
BIX	-0.687	0.443
PIM (g/L)		-0.864
HIX	0.413	-0.733
DOM peak B	0.483	0.590

a. Rotation converged in 11 iterations

In the August PCA_2, the particulate matter became more relevant whereas in September PCA_2 was dominated by total phosphorus, and DOM index HIX which was related to humification of freshly deposited DOM. For October, the floodplain had largely heterogeneous gradients for DOM, nutrient-total phosphorus, and phytoplankton gradients as internal processing of these becomes more relevant during the low flows. PCA_2 was a CDOM and

humification gradient due to relatively elevated primary production, less humified surface water, but from processing of terrestrial inputs.

Table 3: Factor analysis result showing PCA variable axes of the floodplain hydrochemistry for September.

Response variables	Components	
	PCA_1	PCA_2
DOM peak T	0.962	
DOM peak B	0.937	
CDOM	0.751	0.571
DOM peak C	0.663	0.658
HIX		0.914
TP ($\mu\text{g/L}$)		0.802
BIX		-0.659
FI		-0.453

a. Rotation converged in 8 iterations

Table 4: Factor analysis result showing PCA variable axes of the floodplain hydrochemistry for October 2021.

Response variables	Component	
	PCA_1	PCA_2
DOM peak B	0.944	
DOM peak T	0.918	
POM (g/L)	0.839	
DOM peak C	0.824	0.433
PIM (g/L)	0.721	
Phytoplankton Chlorophyll-a ($\mu\text{g/L}$)	0.614	-0.322
TP ($\mu\text{g/L}$)	0.590	0.531
CDOM		0.823
HIX		0.577

a. Rotation converged in 10 iterations

PCA_1 and PCA_2 axes were considered for all months to show the main gradients, the most relevant explanatory variables and how these differed across the three months. Linear regression analyses revealed the explanatory variables explaining spatial variations in the floodplain hydrochemistry based on both environmental conditions and the connectivity factor groups (Table 5). Connectivity produced significant models from the regression analyses, and the following network connectivity variables were found to be the most relevant in explaining the variation in hydrochemistry between the three months. Firstly, was the directed connectivity, which represented directed transport/exchanges during the high flow month (August). Secondly, the river-based undirected connectivity represented the total floodplain network connectivity which is characteristic to lateral gradients from isolated water bodies to

those having central positions in the network, was found to be relevant for all the three months. Thirdly, the Euclidean distance connectivity, that represented connectivity independent from the river network (usually exchanges between two water bodies or could indicate exchange interaction via the groundwater was most relevant for both September and October.

From the environmental conditions factor group, the explanatory variables that were most relevant in influencing temporal variation in floodplain hydrochemistry included- In August, the upstream hydrological connection to the Danube River was relevant for river inputs into the system, total hydrological connectivity was also relevant for exchanges during this highly interconnected floodplain state. Hydrological connectivity was especially for the directed flow exchanges and undirected, and overland undirected transport of materials in the network at bank-full conditions. Percentage aquatic land cover maintain a connected state, emergent vegetation contributed to trapping of sediment and POM contribution. Local land use and land cover along the shoreline, and buffer zone were important in all the three months.

September mean flow month, the environmental condition variables that explained floodplain hydrochemistry variation include, percentage of shoreline occupied by woody (ie trees) also contributed to POM and DOM concentration. The water body perimeter which is a closed path of the sum of lengths and widths for water body edges that contributes to a more heterogeneous morphology. Depth at high water which explains the mixing effects and light penetration for effect to phytoplankton production. Size (depth and area) and sun exposure were mainly relevant for September, indicating a relevance of the water body size and depth gradient in the floodplain network. Sun exposure contributes to photo-degradation of the organic inputs in the water bodies,

In October they included percentage of land use by agriculture and urban -influenced hydrochemistry at these sites Donau, Röthelstein isoliert, Petronell-Carnuntum, Regelsbrunn, and Haslau, these sites are closest to urban areas and agricultural fields than the rest in the network. Percentage of shoreline occupied by woody (ie trees), canopy cover is a major contributor of terrestrial POM and DOM sources, and was also related to shading effects. Percentage of the herbaceous and emergent vegetation are vital sources of DOM inputs and lastly the total hydrological connectivity in the network which might contribute to seepage flows, important during the low flows. The findings suggest that although environmental conditions were the most influencing factor for temporal variation in floodplain chemistry and network connectivity had lesser but substantial effects depending on the floodplain state (during high, mean, and low flow conditions).

Table 5: Multiple regression results and redundancy analysis for factor analyses in August, September, and October 2021.

AUGUST, 2021					
PCA Components	R	R Square	Adjusted R Square	Std. Error of the Estimate	Explanatory variables
PCA_1_environmental conditions	.798 ^a	0.636	0.619	0.61747014	Percentage of emergent vegetation
PCA_1_connectivity	.678 ^a	0.460	0.434	0.75207410	Rb_o_hc
	.963 ^f	0.928	0.901	0.31397258	Upstream hydrological connectivity, percentage aquatic land cover, total hydrological connectivity, sun exposure, surface algae, emergent vegetation
PCA_2_envirinmental conditions					
PCA_2_connectivity	.828 ^b	0.685	0.654	0.58837824	10000dir_mean_y_dPCflux, dir_mean_c_hc
SEPTEMBER, 2021					
PCA_1_environmental conditions	.789 ^b	0.623	0.585	0.64398251	High water depth, percentage of woody shoreline (ie trees)
PCA_1_connectivity	.652 ^a	0.425	0.398	0.77599507	10000rb_mean_y_dPCflux
PCA_2_environmental conditions	.735 ^b	0.540	0.494	0.71116225	sun exposure, perimeter
PCA_2_connectivity	.694 ^b	0.481	0.429	0.75536470	10000rb_mean_c_dPCflux, 10000eu_mean_y_dPCconnector
OCTOBER, 2021					
PCA_1_envirinmental conditions	.889 ^c	0.790	0.758	0.49163589	Percentage emergent vegetation, canopy cover, total hydrological connectivity
PCA_1_connectivity	.424 ^a	0.180	0.143	0.92593049	10000eu_o_dPCflux
	.645 ^b	0.416	0.360	0.79969872	Total hydrological connectivity, percentage herbaceous land cover
PCA_2_envirinmental conditions					
PCA_2_connectivity	.695 ^a	0.483	0.459	0.73545625	Rb_o_hc

From the variation partitioning analyses, the fraction of explained variation by connectivity metrics was smaller than that of the environmental conditions generally in all the months and their total contribution (within the Venn diagrams) was always greater than the unexplained fraction in August, September, and October (Figures 7, 8 and 9) respectively. The jointly explained variation was higher in all months and always the vital fraction except for October PCA_1 which indicated an independent and stronger influence from local environmental conditions in the disconnected low flow month of October.

In August, variation partitioning using multiple linear regression models, for PCA_1 indicated most of the variation 28.5% was explained by the percentage of emergent vegetation from the environmental condition variables, and 10.9% was explained by connectivity rb_o_hc variable => harmonic centrality calculated for all the water bodies in the network and all undirected exchanges with the Danube River, calculated for the static approach. These two main parameters had a significant partial regression coefficient of for the model $F(2, 20) = 29.169, P < 0.05$ and $R^2 = 0.745$. A significant interaction between the connectivity and environmental condition variables explained 31.5% and 25.5% remained unexplained.

For PCA_2, 25.3% of the variation was explained by the upstream and total hydrological connectivity to the Danube and in the network respectively, percentage of sun exposure, surface algae, and emergent vegetation environmental conditions. connectivity explained only 1% of the variation in PCA_2, the variables and their description were (1) 10000dir_mean_y_dPCflux => directed large distance transport of material exchanges along with the flow of the Danube, calculated for the dynamic approach over a standard year when all side-arms are connected or disconnected. (2) dir_mean_c_hc => harmonic centrality for the water bodies during the directed transport calculated for the dynamic approach during the connected state. These main predictor parameters had a significant partial regression coefficient model $F(8, 14) = 26.385, P < 0.05$ and $R^2 = 0.938$. A significant interaction between the connectivity and environmental condition variables, explained 53.1% and 67.5% while 25.5% and 6.2% for PCA_1 and PCA_2 respectively remained unexplained see Figure 7 below.

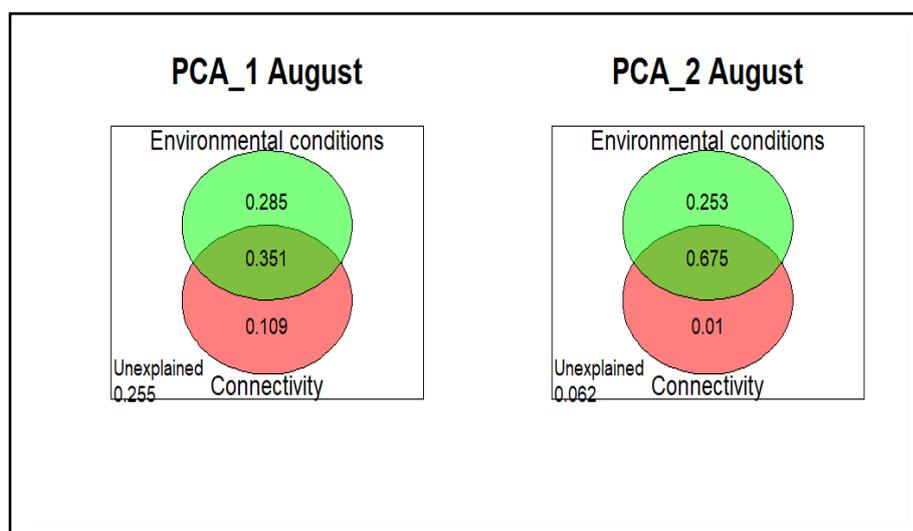


Figure 7: Variation partition result for August PCA_1 and PCA_2 showing contribution of environmental conditions and connectivity within the floodplain network.

In September during mean flow conditions, variation partitioning result in R (Figure 8) for PCA_1 showed that 20% variation in floodplain hydrochemistry was explained by the local environmental conditions. The explanatory variables were depth at high water and percentage of woody shoreline/bank conditions. Connectivity explained 0.2% of the variation and the explanatory variable was 10000rb_mean_y_dPCflux => undirected large distance transport/exchanges within the whole river network calculated over a standard year when all side-arm systems are either connected or disconnected. These PCA_1 explanatory variables had a significant partial regression coefficient model $F(3, 19) = 10.556, P < 0.05$ and $R^2 = 0.625$. For September PCA_2, 17.5% of the variation in floodplain hydrochemistry was explained by environmental conditions. The explanatory variables were amount of sun exposure and water body perimeter. Connectivity explained 11.6% of the variation in PCA_2, the explanatory variables were 10000rb_mean_c_dPCflux => undirected large distance transport of exchanges within the whole river network, calculated for the dynamic approach for the connected state and 10000eu_mean_y_dPCconnector => Euclidean distance calculated for large distance transport overland dynamic approach over a standard year when all side-arms are connected or disconnected. These explanatory variables had a significant partial regression coefficient model $F(4, 18) = 8.57, P < 0.05$ and $R^2 = 0.656$.

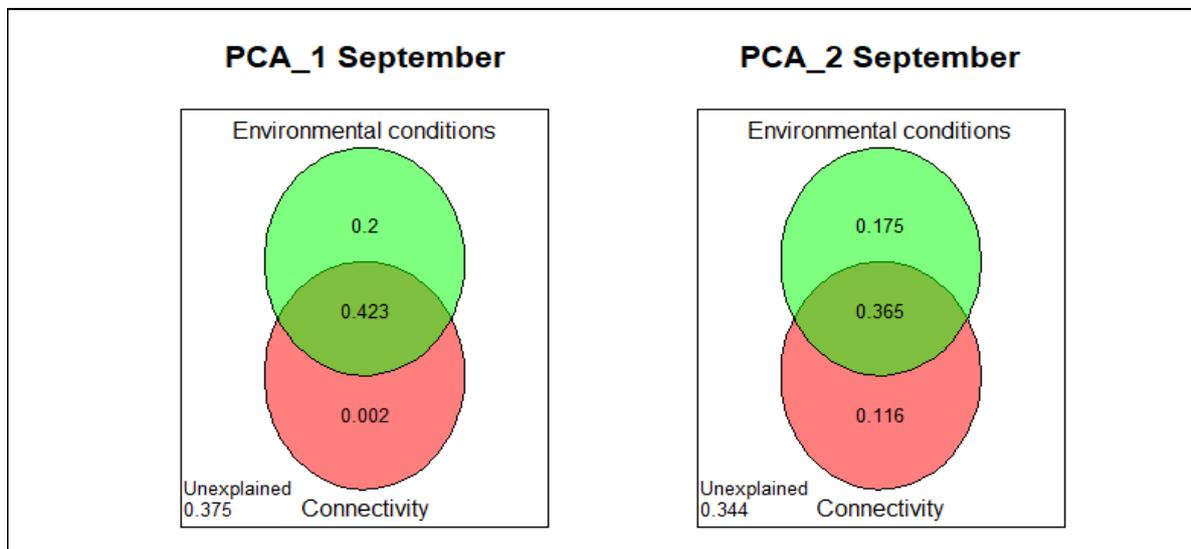


Figure 8: Variation partitioning result for September PCA_1, PCA_2, and PCA_4 showing contribution of environmental conditions and connectivity.

In October during low flow conditions, variation partitioning in R, for PCA_1 most of the variation 61.9% of the variation in floodplain hydrochemistry was explained by local environmental conditions in the network. The explanatory variables/predictors were

percentage of emergent vegetation, canopy cover, and total hydrological connectivity in the network variables. 0.9% was explained by connectivity variable 10000eu_o_dPCflux => large Euclidean distance transport calculated. The PCA_1 explanatory variables had a significant partial regression coefficient model $F(4, 19) = 18.936, P < 0.001$ and $R^2 = 0.799$. For October PCA_2, 11.3% of the variation was explained by the environmental conditions in the network percentage of herbaceous vegetation and total hydrological connectivity. Connectivity explained 18% of the variation in the floodplain hydrochemistry and the explanatory variable was rb_o_hc => harmonic centrality calculated for undirected exchanges in the network, explained 18% of the variation in PCA_2. These explanatory variables had a significant partial regression coefficient model $F(3, 20) = 9.827, P < 0.001$ and $R^2 = 0.596$ (see Figure 9).

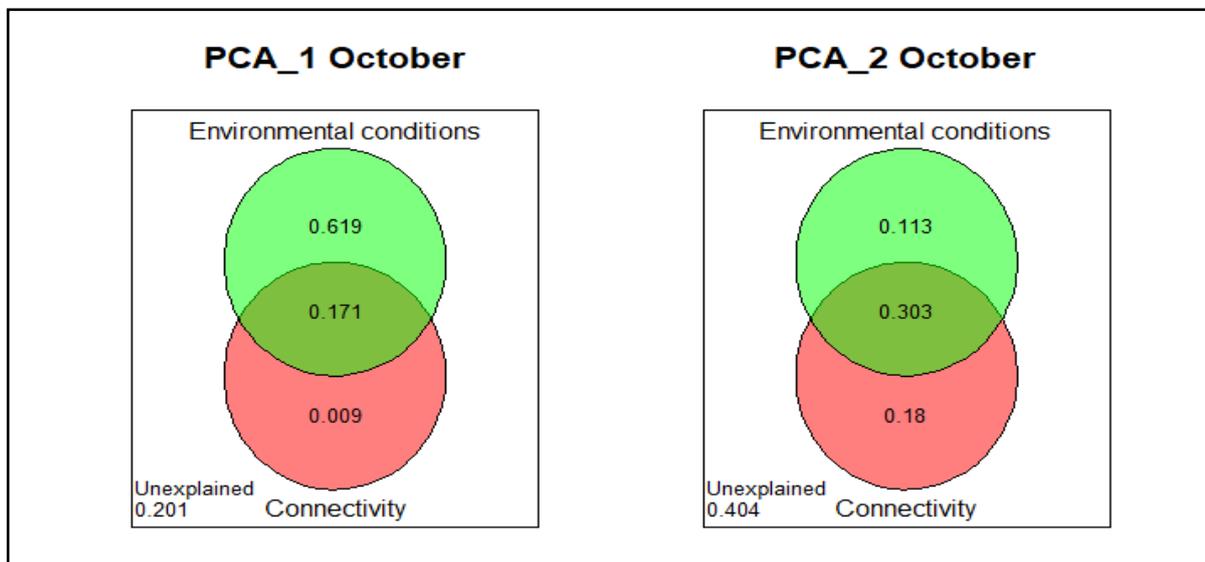


Figure 9: Variation partitioning result for October PCA_1, PCA_2, and PCA_4 showing contribution of environmental conditions and connectivity.

4.3 Variation in floodplain hydrochemistry for the detailed October analyses

The detailed dataset of October followed either a 2 or 3-cluster solution for spatial gradient analyses as shown in Table 6 below.

Table 6: Variable cluster groups showing how the water bodies clustered which was dependent on similar hydro-chemical conditions.

Site code	Site names	Variable Cluster groups				
		Ions	Nutrients	Phytobenthos Chl-a, PIM, and POM	DOC, DOM peaks and indices, CDOM	Phytoplankton Chl-a, rel.ETR, Irradiance, and alpha
0	Donau	1	1	1	1	1
1	Röthelstein isoliert	1	2	2	1	1
2	Röthelstein down	1	2	1	1	2
3	Röthelstein upstream	1	2	1	2	2
5.1	Petronell-Carnuntum	1	2	1	2	2
6	Regelsbrunn	1	2	2	1	1
7	Haslau	1	2	1	1	1
8	Tiergarten Arm isoliert	1	2	2	2	1
9	Tiergarten Arm	1	2	3	1	1
10	Karpfen Arm	2	1	1	1	3
12	Rosskopf Arm innen	2	2	3	1	2
13	Rosskopf Arm aussen	2	1	1	2	2
15	Witzelsdorfer Arm	1	2	3	2	1
17	Fadenbach turtles	1	2	1	2	1
20	Fadenbach aussen	1	2	1	2	1
21	Fadenbach bei Orth	1	2	1	3	1
22	Kleine Binn	1	2	1	1	2
23	Rohrwörth down	1	2	1	2	1
24	Rohrwörth up	1	2	3	2	1
25	Mannsdorfer Hagel	1	2	3	2	3
26	Grundwasser Tümpel Lobau	1	2	3	3	1
27	Schönauer Wasser	1	2	3	1	2
30	Spittelauer Arm	2	1	1	2	1
31	Eberschüttwasser Lobau	1	2	3	2	2

Generally, mean ion concentrations for the floodplain waterbodies were highest in cluster 2 than in cluster 1 for the variation along a spatial gradient, the values below represent the mean \pm standard deviation of the variables below. Cluster 2 water bodies (Karpfen Arm, Rosskopf Arm innen, Rosskopf Arm aussen, and the Spittelauer Arm) had generally the highest ion concentration (except for potassium) and corresponding highest conductivity. These sites are very close to each other according to their spatial location in the floodplain network which is downstream but is very connected to the Danube River. Mean conductivity for cluster 1 water bodies was 476.8 ($\mu\text{S}/\text{cm}$) and 1059.5 ($\mu\text{S}/\text{cm}$) for cluster 2 water bodies, see the spatial variation in (Figure 10).

Table 7: Spatial variation for the ion concentrations in the floodplain water body clusters.

Clusters	N	Ions cluster group					
		Sodium (mg/L)	Potassium (mg/L)	Magnesium (mg/L)	Chloride (mg/L)	Sulfate (mg/L)	Calcium (mg/L)
Cluster 1	20	13.97 \pm 2.8	5.07 \pm 3.38	15.9 \pm 5.7	14.5 \pm 5.34	23.68 \pm 12.41	59.43 \pm 15.41
Cluster 2	4	22.55 \pm 2.32	5.27 \pm 1.6	53 \pm 10.05	65.7 \pm 15.77	162.9 \pm 32.62	117.92 \pm 10.13

Sites belonging to the same cluster (denoted by the color of clusters 1 and 2) had relatively the same ion concentration. Cluster 1 had the highest mean Sodium (Na^+), Potassium (K^+), and Calcium (Ca^{2+}) whereas cluster 2 had the highest mean Magnesium (Mg^{2+}), Chloride (Cl^-), and Sulfate (SO_4^{2-}) concentrations (values represent mean \pm standard deviation for the above-mentioned ion concentrations). For this ion cluster group, there is a clear spatial clustering showing high ion concentration in the network which can be indicative of exchange processes between ground water and the water bodies.

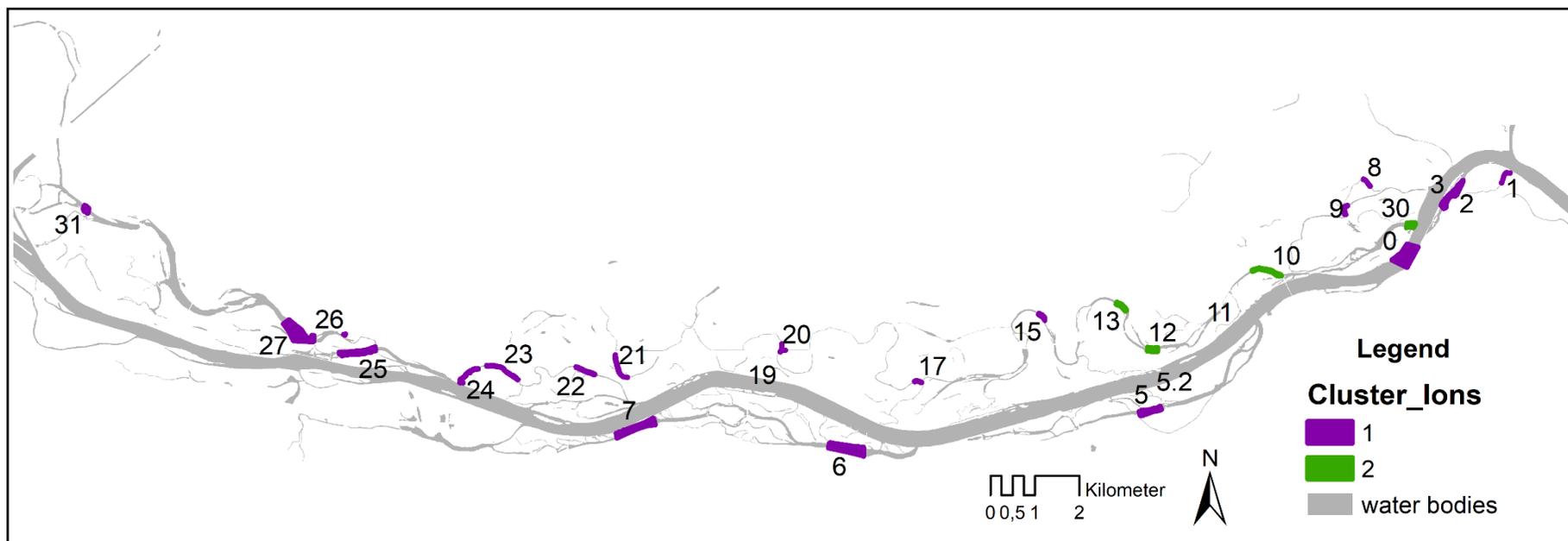


Figure 10: Ion concentration variation along a spatial gradient.

For nutrients cluster group, there is a clear spatial clustering showing high nitrite (N-NO₂) concentration in the network which can be indicative of exchange processes between ground water and the water bodies, see the spatial clusters in (Figure 11).

Table 8: Spatial variation in the nutrient condition during the low flow month

Nutrients cluster group							
Clusters	N	TP (µg/L)	P-PO ₄ (mg/L)	TDN (mg/L)	N-NH ₄ (µg/L)	N-NO ₂ (µg/L)	N-NO ₃ (µg/L)
Cluster 1	4	24.2 ± 4.9	0.93 ± 1.1	1.9 ± 0.6	12.5 ± 13.9	24.5 ± 23.6	1420.8 ± 551.36
Cluster 2	20	22.13 ± 3.31	1.03 ± 1.28	1.61 ± 0.08	12.23 ± 17.03	13.133 ± 7.82	1145.93 ± 51.09

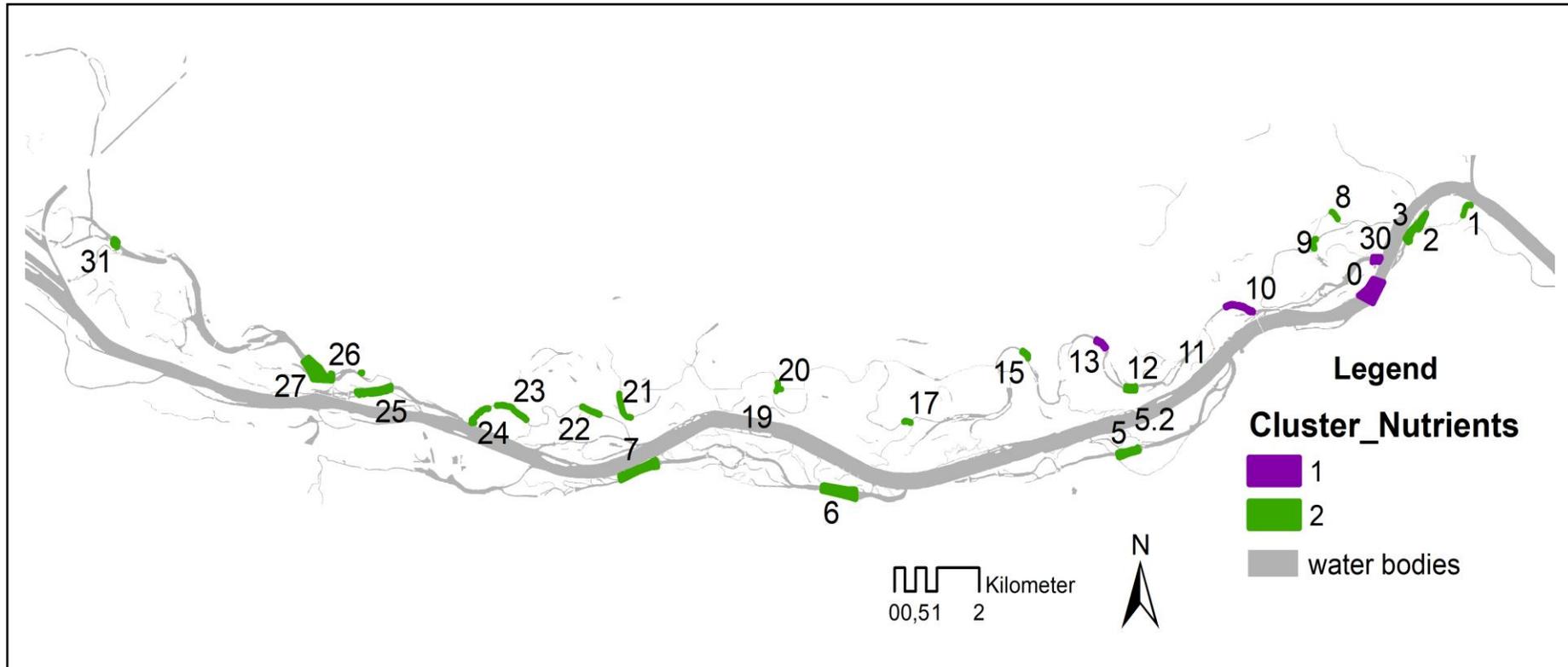


Figure 11: Nutrient variation along a spatial gradient of the Danube floodplain water bodies.

The nutrient conditions in the floodplain water bodies during the October sampling date were highly variable, sites belonging to the same cluster had relatively similar nutrient water quality. Cluster 1 had the highest mean of all variables except for orthophosphate, cluster 2 had the highest mean value for orthophosphate.

Sediment type influences the ratio of biological uptake, adsorption processes are suited to fine sediment. The sediment type/composition in these floodplain water bodies was mostly psammal-pelal (mud) at 12 water body sites, 4 water bodies with equal sand and mud composition and the rest

had higher gravel sediment type especially at Donau, Regelsbrunn, the Spitellauer Arm, and Tiergarten Arm. From the study, the highest phytobenthos chlorophyll-a biomass was observed at Regelsbrunn with $630 \mu\text{g}/\text{cm}^2$, relatively such substrate sizes (gravel >2-20cm) support more filamentous phytobenthos growth. Smaller/fine grain sizes especially mud and sand were more prevalent (< 2 mm) have a large surface area to volume ratio to adsorb phosphorus but these offer a less stable substratum for phytobenthos growth. Some other studies have linked this to the low flow conditions during the isolated floodplain state especially Fadenbach Turtle (isolated water body) and other water bodies that belong to cluster 1 (in the particulates matter and phytobenthos chl-a cluster group) had the least phytobenthos chlorophyll-a measured. Cluster 1 water bodies with more PIM and POM but support the least phytobenthos that was measured. Values for concentrations shown below represent mean \pm standard deviation, see the spatial variation in (Figure 12).

Table 9: Variation between the 3 clusters for particulate inorganic matter, particulate organic matter concentrations, sediment organic matter content, and phytobenthos chlorophyll-a along the spatial gradient.

Particulate matter, phytobenthos chlorophyll-a and sediment organic content cluster group					
Clusters	N	POM (g/L)	PIM (g/L)	Phytobenthos chlorophyll-a ($\mu\text{g}/\text{cm}^2$)	Sediment organic content (%)
Cluster 1	13	0.01 ± 0.001	0.01 ± 0.07	86.17 ± 53.33	6.18 ± 2.42
Cluster 2	3	0.02 ± 0.02	0.02 ± 0.02	255.35 ± 326.32	6.72 ± 4.04
Cluster 3	8	0.01 ± 0.002	0.003 ± 0.002	110.14 ± 93.86	5.19 ± 1.36

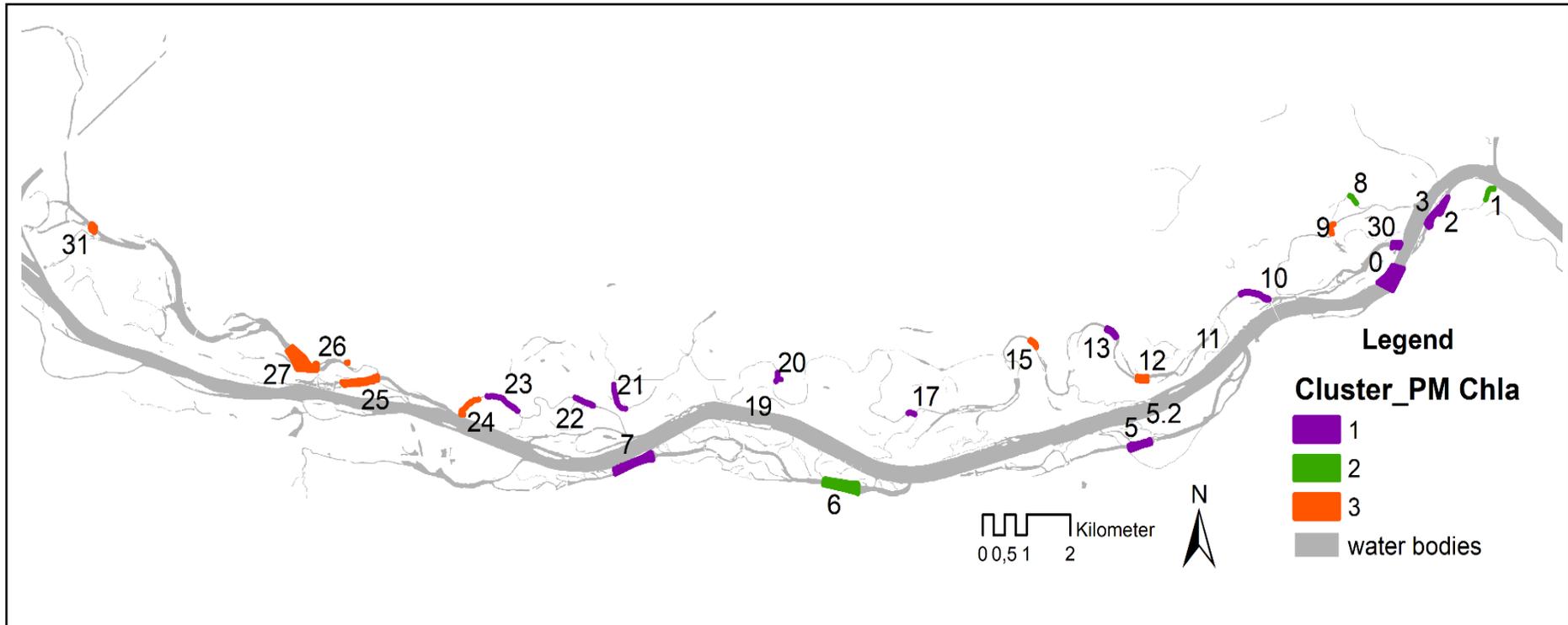


Figure 12: Spatial variation of particulate inorganic matter, particulate organic matter concentrations, sediment organic matter content, and phytobenthos chlorophyll-a.

Floodplain water bodies belonging to the same cluster had relatively similar phytobenthos Chlorophyll-a, percentage sediment organic content particulate organic and inorganic matter concentrations in this cluster group shown in the spatial gradient map above. For this cluster group (PM Chla), there is a clear spatial clustering showing high phytobenthos chlorophyll-a concentration with corresponding highest organic matter in the network.

Variation in photosynthesis rate and pelagic chlorophyll-a among the floodplain water bodies from the October sampling date were denoted as – Cluster_Phyto-PAM cluster membership in the map. sites belonging to the same cluster (denoted by the color of clusters 1, 2, and 3) had relatively similar variables listed below that were used to compute the photosynthesis rate in the floodplain water bodies. Cluster 1 had the highest mean relative photosynthetic Electron Transport Rate (rel.ETR), pelagic/ phytoplankton chlorophyll-a concentration, and alpha value are the initial slope of rapid light curves (RCL) which is related to the quantum efficiency of photosynthesis while Cluster 3 had the highest minimum saturation irradiance/light saturation coefficient (I_k).

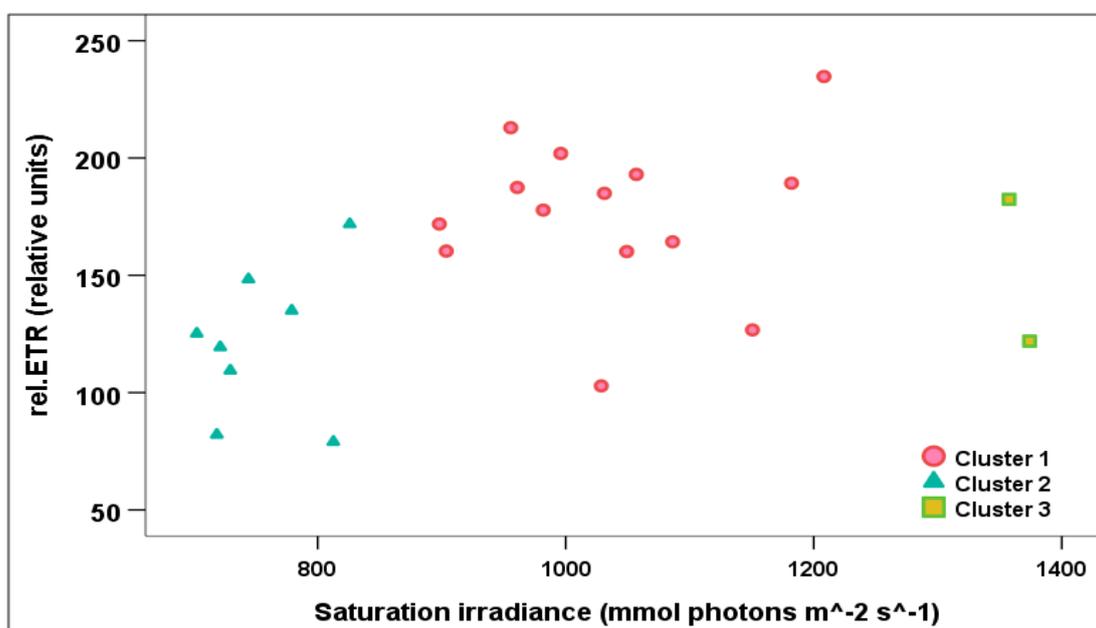


Figure 13: The relative photosynthetic Electron Transport Rate (rel.ETR) function of minimum saturation irradiance/ PAR irradiance for the floodplain water bodies and the scatter plot represent mean values.

The photosynthetic rate and phytoplankton cluster (Cluster_Phyto-PAM) as indicated in the spatial variation map in (Figure 14), for this group, the patterns related to photosynthesis rate and phytoplankton are more complex and might bear a resemblance to different patterns of large gradients, local environmental exchanges, and abiotic conditions.

Table 10: Variation in photosynthesis rate and phytoplankton chlorophyll-a along the spatial gradient from the 3-cluster solution.

Clusters	N	Relative ETR	Irradiance ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)	Alpha	Phytoplankton chlorophyll-a ($\mu\text{g/L}$)
Clusters 1	14	176.3 ± 33.51	1035 ± 96.28	0.17 ± 0.03	30.7 ± 27.04
Clusters 2	8	121.3 ± 31.52	754.2 ± 46.1	0.2 ± 0.03	18.9 ± 8.4
Clusters 3	2	152.2 ± 42.73	1365.8 ± 11.7	0.12 ± 0.03	28.5 ± 18.8

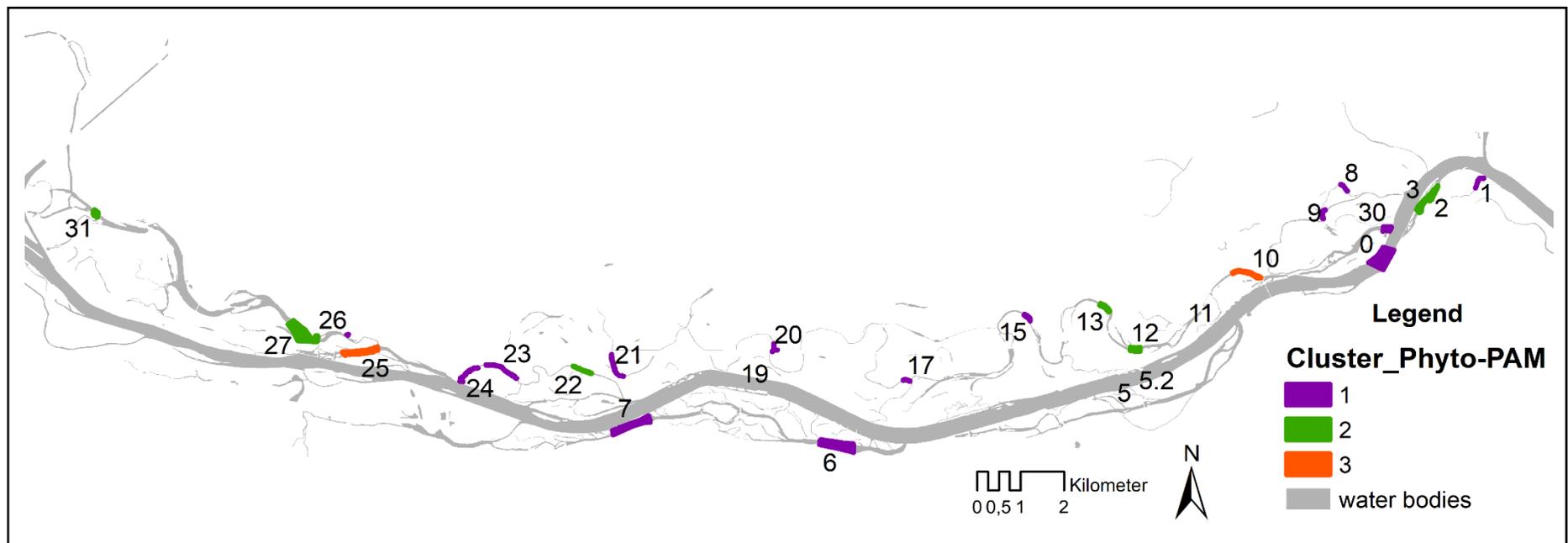


Figure 14: Photosynthesis rate and phytoplankton chlorophyll-a variation along the spatial gradient of floodplain water bodies.

For DOM, the lateral gradient was more visible transcending from the Danube River to the small, isolated water bodies. This is also in concordance with the temporal study (in section 4.2 above) where DOM parameters are widely explained by the river-based whole network undirected connectivity, from the most highly connected site (parent river, the Danube) to the most isolated water bodies with a more peripheral position in the network.

Table 11: Spatial variation for DOM quality in the floodplain water bodies.

Dissolved organic matter, dissolved organic carbon and color/CDOM cluster group								
Clusters	Peak C	Peak T	Peak B	BIX	FI	HIX	CDOM (Hazen units)	DOC (mg/L)
Cluster 1	0.13 ± 0.07	0.15 ± 0.1	0.1 ± 0.07	0.9 ± 0.14	1.54 ± 0.07	0.74 ± 0.07	11.9 ± 5.4	2.8 ± 1.3
Cluster 2	0.23 ± 0.25	0.24 ± 0.3	0.15 ± 0.2	0.9 ± 0.08	1.6 ± 0.07	0.78 ± 0.07	23.6 ± 22.8	4.6 ± 4.2
Cluster 3	0.64 ± 0.38	0.48 ± 0.3	0.26 ± 0.1	0.8 ± 0.04	1.55 ± 0.07	0.82 ± 0.02	20.5 ± 3.4	8.4 ± 4.3

For DOM water quality, cluster 3 water bodies had the least biological index (BIX) but the highest HIX (highest humified organic substances that are usually resistant to degradation (values presented are mean ± standard deviation). Variation between the different clusters along a spatial gradient in the Danube floodplain is shown in (Figure 15).

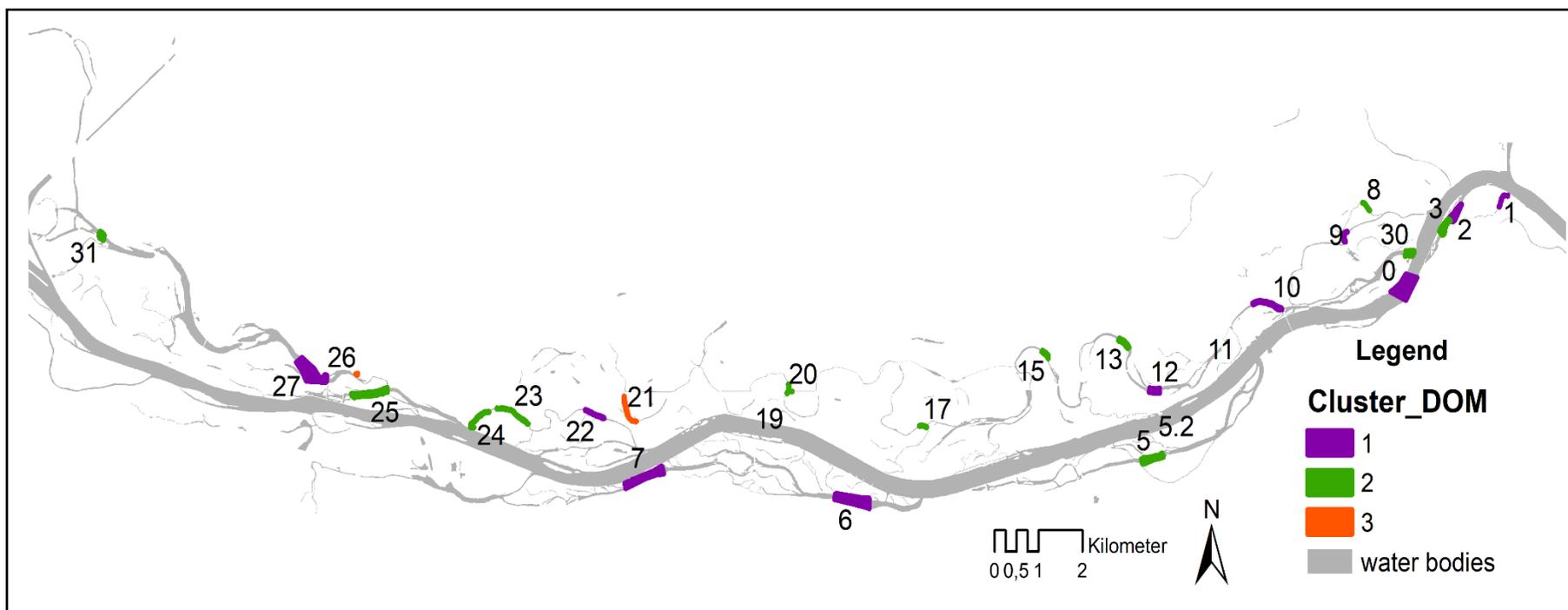


Figure 15: Spatial variation in DOM quality of floodplain water bodies from the October sampling date

The different clusters had relatively similar DOM water quality where cluster 1 had the highest BIX concentration and least mean for all the other variables, cluster 2 had the highest Color/CDOM in Hazen units and FI mean values, and cluster 3 had the highest mean dissolved organic carbon (DOC) concentration.

CHAPTER 5. DISCUSSION

5.1 Comparison of floodplain hydrochemistry between the three months (August, September, and October)

Variation in floodplain hydrochemistry revealed several vital findings. First, the One-way ANOVA determined the differences between the means of nutrient and organic matter conditions between the three months. Specifically, the total phosphorus, particulate inorganic matter, and phytoplankton concentrations showed the most significant differences between the high, mean, and low flow months. Secondly, the processes that influence relatively higher PIM and TP concentrations in the high flow months could easily be linked to the intense transport and exchanges during this connected state.

Temporally, PIM and total phosphorus were highest in August in comparison to the other months, this variation was greatly explained by the hydrological connectivity upstream (transporting the flux inputs), the directed transport of material calculated for the dynamic conditions over a standard year, and the harmonic centrality for the directed transport calculated for the connected state of the floodplain over a standard year. Floodplain water bodies (backwaters, meander-bends, groundwater ponds, and side are channels) differed significantly from the Danube River and in part prior studies such as (Tockner et al., 1999) have expressed that floodplain water bodies differ from other aquatic ecosystems because of their dynamic nature precisely related to water level fluctuations and hydrological connectivity to their parent river.

Increased discharge influences the interconnectedness in the floodplain network, water level and the exchanges increase the particulate inorganic matter concentrations. Longitudinally, PIM was highest in the Danube main channel, water bodies with an upstream connection to the Danube (Rohrwörth upstream), downstream position (Spittelauer Arm had a permanent surface connection throughout the study) and shorter distances from the river that were easily inundated (Kleine Binn, Regelsbrunn and Mannsdorfer Hagel) at high flow in August and this result coincided with findings by (Heiler et al., 1995). They report that PIM is highest in water bodies that are highly connected or had a downstream position because such sites received higher river inputs, sediment resuspension. Generally, PIM concentration decreased from August (highest) to October (lowest concentration) whereas POM had the opposite trend.

On the other hand, reduction of PIM and TP during the mean and low flow months can be attributed to settling processes of the particulates, breakdown of the organic matter, and

adsorption onto sediment particles (for phosphorus). As expected, TP was highest during the high flow month and yielded significant differences temporarily, lowest concentrations were observed during low flow conditions. Low TP concentrations might be attributed to P retention in the floodplain water bodies with the increasing water residence time and sedimentation during low flows consistent with finding by (Castillo, 2020; Mayora et al., 2018). TP concentration was highest during the high flow conditions, likely due to higher particulates exchange within the network considering phosphorus is transported mainly adsorbed onto sediments/particulate form (Castillo, 2020; Reddy et al., 1999). Weigelhofer et al., (2018) also express that floodplain networks have shown to be effective in storing nutrients that can attach to particles.

TP concentration correlates greatly with PIM which was also highest in August as well as POM contribute to TP concentrations in water. Mayora et al., (2018) explains how the hydrological and sediment regimes regulate TP and other water chemistry between contrasting but adjacent ecosystems. Total phosphorus was higher in the Danube River than in half of the floodplain water bodies investigated this could be attributed to higher transport of suspended particulates to which phosphorus adsorbs on (Mayora, 2020). Aggradation processes were evident for most floodplain water bodies and, in such sedimentation, processes following high flows, sediment-bound phosphorus comprises vital phosphorus sinks in floodplain water bodies. Such adsorbed phosphorus might be released back into the water as this has been reported to be dependent on their adsorption capacity highest in clay and sand at the sediment-water interface (Reddy et al., 1999). Sand/psammal (0.063-2 mm) and mud/Psammo-pelal (< 0.063 mm) combined are the largest substrate type of the water bodies in this study and this phenomenon was more likely in this case.

High phytoplankton chlorophyll-a during the low flow conditions could be explained by the internal (biotic and abiotic) processing of the river inputs which enhanced pelagic primary production (Weigelhofer et al., 2015). Increased phytoplankton chlorophyll-a biomass has been linked to reduced connectivity for backwaters, improved transparency and low water turnover/increased residence time that enhance pelagic primary production during low flows (Castillo, 2020). High phytoplankton production during low flows was also reported by (Rechendorfer et al., 2013). Lowest phytoplankton biomass for August might have been influenced by poor underwater light climate, high turbidity from the suspended particulates and higher flow velocity scouring effect.

Color/ CDOM as used in this study, might have been a result of leaching processes of soil from adjacent forests, riparian leaves as these Danube floodplain water bodies are surrounded by an alluvial forest expanse and dense herbaceous vegetation, woody debris that was transported along with other inputs during high water connections and lastly decaying detritus were all contributing factors to the overall color measured (Coble, 2007). Water containing high CDOM appears brown (encountered during high river discharge exchanges with the floodplain) usually as sediment and organic matter runoff from terrestrial humic-rich systems. Other sources as identified by (Coble, 2007) include river inputs from soil/sediment humus carried with flow, phytoplankton and phytobenthos pigments and their protein amino acids, and microbial organic pools. The highest yellowness color was observed for Grundwasser Tümpel Lobau (and other sites that had values above 25 Hazen units see section 4.1 for CDOM results) for all months and during the high flow month in August when material inputs and resuspension of sediment and as allochthonous materials were being transported and/or deposited into the water bodies. CDOM was least in October because of less interconnectedness in the water body network (low connection and increase in internal processes such as settling increased transparency of the water bodies) and as well as mineralization of photochemically and microbially degraded CDOM.

The findings reveal that temporal variation in the DOM gradient are vegetation driven DOM. This finding was not consistent with study hypothesis 1 because we had anticipated higher DOM in October related to high autochthonous sources. This is because the water-mediated exchanges were significantly sufficient for allochthonous sources from river inputs and overland transport from adjacent terrestrial systems to dominate and outweigh autochthonous derived DOM. The sources of the DOM in the network were vital to what DOM quality is present and its rebounding effects in the water bodies with time. Physical and chemical characteristics of the recipient floodplain water bodies for example their underwater light climate, temperature, pH, and nutrient condition affect the degradation of DOM (Weigelhofer et al., 2020) but more importantly is the source of the DOM (Birdwell and Engel, 2010; Ohno, 2002). Highly humified DOM are said to be recalcitrant in the system (Birdwell and Engel, 2010) and a sign of the DOM age and can last longer in these ecosystems up to multiple years (Kirschner et al., 2001). Sankar et al., (2019) reported that these mainly are sourced from catchment-scale mainly the humic-like, aromatic terrestrial DOM such as from forests, woody shoreline conditions, herbaceous vegetation. Kirschner et al., (2001) in their study examined how production and degradation of emergent and submerged macrophyte biomass in a

backwater system can also be hindered by flood pulses increasing DOM immobilization and territorialization of isolated water bodies.

Generally, the side arm channels, and the Danube River didn't show high DOM fluorescence and the isolated floodplain water bodies had the highest DOM composition, this finding was consistent with hypothesis 1. DOM has been known to affect light penetration in aquatic systems (Sankar et al., 2019) through its degradation, this influenced the availability of inorganic nutrients (bioavailable) that phytoplankton utilize to fix biomass. They explain how photochemical mineralization of DOM and microbial degradation avail the DOM-bound nutrients in floodplain water bodies especially with less canopy cover and high percentage sun exposure. In this study sun exposure was among the predictor variables from the environmental conditions factor explaining the variation in September hydrochemistry (section 4.2). The water bodies displayed the low temporal variation but high spatial variability in the DOM quality across the 3 months (see Figure 17 in Appendix 2) The findings for peak B and T indicated a multitude of transformational processes acting on these DOM components especially in October where in-situ processing could explain microbial activity to produce these protein-like DOM.

The fluorescence index (FI) ratios have been applied to explain changes in DOM compounds. The FI values from the floodplain show substantial changes in DOM fluorescence acquired from allochthonous sources in August and autochthonous sources in October (McKnight et al., 2001). The FI ratio is calculated for fulvic acids in aquatic systems which may be from either allochthonous or autochthonous sources (McKnight et al., 2001) and FI has been linked to ultraviolet excited humic-like peak C where values of ≤ 1.4 indicate terrestrially sourced DOM while values of ≥ 1.9 correspond to microbially derived DOM according to (Birdwell and Engel, 2010). The values from this study were in the range typical for algae and aquatic plants 1.5-1.7 which are above the lower limit for terrestrial derived DOM but also lower than the lower limit of microbial DOM. High values for FI for some water bodies relatively in all the three months suggested that there was an increase in humic-like DOM from microbial activity whereas relatively low BIX coincides with a reduction of humified substances (Sankar et al., 2019).

Hence, the FI, which is a ratio of microbially derived DOM had higher fluorescence than the terrestrially derived and this makes the relative proportion of PCA_2 for all months depend on both microbially and terrestrially derived DOM. There was a strong absorption in the ultraviolet band in the fluorescence peak A region for almost all the water bodies in the dataset which indicates the presence of terrestrially derived fulvic acids present in these floodplain

water bodies (Stedmon and Markager, 2005). In October (isolated floodplain state), the allochthonous organic matter could be principally from riparian leaf litter. The increases in BIX values during September and October showed fresh autochthonous derived DOM in the water bodies. In-situ processing of DOM through photodegradation or microbial degradation or other interacting effects can influence the quality and quantity of DOM (Stedmon and Markager, 2005) and this meant that terrestrial DOM was being photochemically/biodegraded to simpler forms (Sankar et al., 2019).

The inconsistent trend in October cannot be explained by network connectivity but rather the local environmental conditions that became pronounced during the low flow conditions. These findings were consistent with study hypothesis 2, where PIM was expected to be higher during the high flow month and lowest during the low flow condition in October. This is very analogous to any prior studies of this kind where TP is transported as particulate P with the highest concentrations during high flows (August) after hydrological connections (Natho et al., 2020). During the high flows in August (connected state of the floodplain), imported river water improved water body aeration and other input materials that are exchange, resuspension, and aeration of sediments in turn elevating mineralization of organic matter and subsequent release of phosphorus into the water column (Weigelhofer et al., 2015).

Phytoplankton chlorophyll-a concentration was highest in October exactly as expected, these floodplain dynamics are more probable and were expected because they emerge from the internal processing/biogeochemical processing of materials and energy imported into the floodplain water bodies by the exchanges with the river water and inherent connections in the floodplain network (Lamers et al., 2006; Weigelhofer et al., 2015). Settling processes of the particulates to the benthic zone improved light penetration for light-limited algal communities to photosynthesize. Some studies have explained the light limitation factor where the continued supply of nutrients, while the phytoplankton is lightly limited, would not yield substantial primary production (not investigated in this study). In this study, both betweenness and harmonic centrality were considered and as well the probability of connectivity index.

The directed (along with the longitudinal flow of the Danube River), river-based/whole floodplain network, and the Euclidean distance exchanges offer insurmountable connectivity for the fluxes between the three months. Therefore, a conclusion about the sediment aggradation and other inputs like organic matter is a result of a well-connected network mosaic of water bodies. We did not measure phytobenthos chlorophyll-a largely because of high water levels in both August and September. However, we cannot discredit/discount that there was

probably some phytobenthic assimilation of the nutrient enhancement from the river inputs in these months as an additional variable in our investigation. Nonetheless, we predict a combination of this summer flood pulse (maximum peak in July 2021) with effects seen through the following two months (3 peaks in August and 1 at the beginning of September before leveling down to mean flow). The flood pulse effects intertwined with the connectivity and interaction with environmental conditions influenced the temporal variation in floodplain hydrochemistry. The high flow conditions in August contributed to reduced autotrophic uptake, increased total phosphorus and PIM concentrations attributed to inputs from the river, and large distance transport overland of terrestrial material as water moved laterally in this Danube floodplain system.

5.2 Disentangling the influence of connectivity and environmental conditions on total phosphorus, POM and PIM, DOM, and phytoplankton biomass at the three different water level stages

Environmental conditions and network connectivity were investigated to quantify their influence on floodplain hydrochemistry following a flood pulse in a Danube floodplain water body network. The flood pulse peaked in July 2021, and the variation in hydrological connectivity between August, September, and October 2021 was the focus of the study see section 3.3 (Figure 3). In riverine floodplains systems, network connectivity and local environmental conditions (the two factors) are for the most part intrinsically linked (Amoros and Bornette, 2002). According to hypothesis 1, variation in floodplain hydrochemistry variables between the three months was explained to a greater extent by both network connectivity and the local environmental conditions and as well there were some unexplained variations in the dataset shown in the result section 4.2 (Figures 7, 8 and 9). The unexplained variation could be a result of other factors not covered by this study.

Variation partitioning showed that the PCA factor 1 was mainly composed by dissolved matter components (Table 2-4) was explained during the connected phase (August) by environmental conditions but also by a combination of connectivity and environmental conditions (Figure 7). This pattern shifted then in the disconnected phase (October) to a clear explanation by environmental conditions, The main explanatory variables were shoreline vegetation and emergent vegetation (Table 5). This means that emergent vegetation and other littoral macrophytes at the terrestrial-aquatic interface contribute greatly to the composition and amount of DOM a water body receives (Wetzel, 1992). Mayora et al., (2018) further reports

that in transiently connected floodplain water bodies, dominated by emergent vegetation cover exudate high DOM. Between aquatic macrophytes, emergent and free-floating species produce striking biomass and usually produce high DOM and aromaticity compared to other macrophyte vegetation. A study in the Danube Lobau floodplain revealed how emergent macrophytes contribute to the detritus pool (Kirschner et al., 2001). In their study on degradation of emergent and submerged macrophyte biomass production in a backwater system found out that emergent macrophyte have relatively longer degradation time especially the stems and leaves of some of the species they investigated. It was found that the decay time was 3-4 years for leaves of some of the species in their study.

Kirschner et al., (2001) also reports that fluctuating water levels in backwaters have a remarkable impact on the degradation rates and characteristic drying and rewetting during flood pulses might in due course slow degradation rates further. They explain that detrital material continuously is buried and with such processes coupled with longer residence times (months to years can lead to anaerobic conditions further slowing down the decay and increasing intractable DOM in the system. Sankar et al., (2019) express how a combination of photo biodegradation can reduce the intractable DOM to simpler forms, hence amount of sun exposure reaching the littoral benthic zones and in shallow backwaters is crucial in these systems.

For both August and September, the environmental conditions independently explained higher variation in the response variables and only for PCA_1 in October (which is majorly a DOM gradient coupled with PIM, TP, and phytoplankton) than independent contribution from network connectivity. In October DOM fluorescence peaks, phytoplankton Chlorophyll-a and total phosphorus concentrations all correlated to PCA_1 and the local environmental conditions solely explained the most variation. This is because internal processes are more prominent and evident during the low flow month when most of the water bodies were disconnected than during the high flow month in August. At high water levels river inputs and undirected exchanges between the interconnected water bodies homogenize the hydrochemistry as also reported by (Mayora et al., 2013; Mayora et al., 2020, Thomaz et al., 2007), especially the DOM gradient in floodplain network as allochthonous materials are flushed laterally into the water bodies.

This result is in line with some deductions by (Weigelhofer et al., 2015) who noted that during “the connection state hydro-chemical differences between sites are not so evident due to mixing effects”. This clearly explains the impact of the surface hydrological connection to the Danube

River in August, while the great influence of network connectivity in the system (mainly short distance transport) increased during the low flow month. Directed transport from the Danube River was also vital for connected sidearm channels with permanent connections in the low flow month such as the Spittelauer Arm. Internal processes after the flood pulse was shifted from mainly autochthonous to allochthonous material carried with high river inputs and pattern dependent on hydrological conditions (exchange under very high flow conditions, mean and low water conditions) a function of fluctuating Danube River discharge (Preiner et al., 2008).

Overall, the local environmental conditions influenced most of the temporal variation in floodplain hydrochemistry, though some significant variation was due to network connectivity. Large distance directed transport influenced the temporal variation in floodplain hydrochemistry in August while the river-based undirected transport and Euclidean distance exchanges were more crucial in September and October sampling which were undoubtedly as expected. The interconnections in the floodplain water body network evident from short distance transport exchanges were more pronounced in September and October and generally, October had the highest explanatory values from connectivity. The group of the predictor variables that explained variation in floodplain hydrochemistry in these two mean flow months (intermediate connection state) and low flow month (isolated floodplain states) further stresses the importance of interconnected water bodies in large floodplains like the Donau-Auen. Furthermore, riverine floodplain networks often consist of numerous continuous geomorphologic units with varying hydrological connectivity patterns (Thorp et al., 2006). Even though the phenomena involved in the complexity of these systems are scale-dependent (Thorp et al., 2006), their ecological heterogeneity becomes inadequately assessed when spatiotemporal scale variations are not considered.

In accordance with the second hypothesis of this study, the combined influence of network connectivity and local environmental conditions was expected to be greater and enhanced during high flow conditions than their independent contributions to the hydrochemistry of the floodplain water bodies as compared to the joint explained variance during the mean and low flow conditions. In general, variation was explained purely/ entirely by network connectivity and environmental conditions (Table 5), from the variation partitioning result, there was always a higher interaction/overlap that explained jointly much of the temporal variance in floodplain hydrochemistry (Figures 7, 8 and 9). This huge overlap meant that not all variables embedded in these two factors were significant to influence the water chemistry but rather there were

some redundant variables in the factor datasets hence only the predictor variables in (Table 5) were significant.

There was an inconsistent pattern between what factor explained the most variance and thus the study could not ascertain which of the two factors explains the most temporal variation in floodplain hydrochemistry singly as they both fluctuated highly between the three months (Figures 7, 8, and 9). This was due to the single month analyses, and the most variation that was consistent in the 3 months was the DOM gradient in the floodplain water bodies, and was well October was still significantly different with TP and phytoplankton chlorophyll-a variation becoming more pronounced in the network. The composition and concentration of DOM (main variable gradient) can be controlled by the productivity in the aquatic ecosystem as well as exchanges from adjacent terrestrial ecosystem. Many studies have highlighted the role of whole catchment contribution of DOM inputs (Sankar et al., 2019; Stedmon and Markager, 2005; Wetzel, 1992). The area of the catchment that is inundated during high river discharge and flood pulses for example forested, agricultural and or pastureland can influence DOM inputs that recipient ecosystems like floodplain water bodies will characterize. Junk et al., (1989) explained how the flood pulse the amount and composition of allochthonous and autochthonous sources of DOM in floodplains. They further expressed that seasonal and multi-year recurrence floods that influence variation in depth, extent of flooded area, emergent, floating, and herbaceous vegetation cover expansion, or contraction hence the influence of flood pulses and inherent network connectivity in mobilizing DOM in floodplain water bodies. The influence of fluctuation flows because of increased Danube River discharge becomes more pivotal for the intrinsic temporal and spatial complexity affecting ecosystem processes and patterns, fauna and flora diversity, and nutrient conditions therein. Phosphorus uptake in October by the phytoplankton and other autotrophs reduced the nutrient levels in October (total phosphorus). Phytoplankton chlorophyll-a was highest in the isolated state of the floodplain (October) and this result was found to be consistent with findings of (Weigelhoefer et al., 2015). The emergent and macrophyte vegetation also contribute immensely to the assimilation of the particulate matter-bound phosphorus in the water bodies.

Most importantly the study reveals how directed exchange and large distance transport influence the floodplain hydrochemistry during the high flow month, undirected river-based and Euclidean distance transport were found to be more important during the summer mean flow and low flow conditions. Jointly network connectivity and environmental conditions

explain large variance in temporal hydrochemistry of floodplain water bodies than independently.

5.3 Hydro-chemical conditions, organic matter contributions, pelagic and benthic algal biomass production along a spatial gradient of the Danube floodplain during the isolated state (October 2021)

The position of the water bodies in the floodplain network dictates to what degree they are influenced by the local environmental conditions and network connectivity hence the resulting fluvial dynamics across spatial scales (Amoros and Bornette, 2002). Low flow conditions disconnect the backwaters in the Danube floodplain network and water supply is guaranteed by groundwater seepage according to (Heiler et al., 1995). During October, internal processes such as uptake of bioavailable nutrients by phytoplankton, phytobenthos and macrophytes, sedimentation and resuspension of particulates and mineralization of organic matter, influence hydro-chemical characteristic of Danube floodplain network. The Danube River was the most central water body responsible for hydro-chemical dynamics that were investigated in October.

The cluster groups were distributed at the different sites that were also accorded the various variables. The aim of the cluster algorithm was to reduce variability within each cluster while maximizing the between cluster variation hence the floodplain water bodies from the October sampling date had that belonged to the same variable/ parameter cluster group had a high degree of association regarding the similar hydrochemistry. Overall, the cluster groups could help in identifying the hidden exchange patterns and explore more lateral exchange gradients.

5.3.1 Spatial variability of ion concentration during the low flow month

Ion concentrations differed greatly between the two clusters where cluster 2 water bodies that are Spittelauer Arm, Karpfen Arm, Rosskopf Arm innen, and Rosskopf Arm aussen had the highest concentrations of all the ions that were investigated in the study, and cluster 1 had the least ion concentrations. From the ion concentration correlation with the conductivity values from this low flow month, all the ions had high and significant correlations $P > 0.01$ with the electrical conductivity from the water bodies which were found to be related to lateral connectivity gradients (see Table 13 in Appendix 1). Electrical conductivity of water is frequently linked to water flow because of water level fluctuations. Variations in conductivity caused by variations in water level are particularly obvious in floodplains. Weigelhofer et al., (2015) described ions as “conservative” since changes owing to biological or chemical processes are small in comparison to mixing effects with Danube River during high flows. The

ions showed a clumped spatial clustering especially for the cluster 2 water bodies which could also be indicative of pathways where groundwater enters the system and exchange processes between the water bodies. Along the floodplain, the areas with increasingly higher ion concentration than others as for cluster 2 water bodies, the findings show a corresponding increase of ion concentration.

Katutis and Rudzianskaitė, (2015) report that in floodplain soils containing high amounts of organic matter, especially like this low flow conditions that prevailed in October sampling, sulfate is known to increase the mobilization of phosphate. The high cation concentration especially calcium could be due to the residual effect of the flood. It is reported that long after floods, ion concentrations do not reflect river inputs deposited from the catchment, but these depend on the flow velocity and soil properties of the adjacent terrestrial systems through cation and anion exchange processes (Katutis and Rudzianskaitė, 2015).

5.3.2 Spatial variation in the nutrient condition during the low flow month

Overall, floodplains have been known globally as nutrient sinks (Tockner et al., 1999). For the nutrients, there is a clear spatial cluster showing high nitrite (N-NO₂) concentration indicating a pathway where groundwater enters the floodplain system. Cluster 2 water bodies had the highest nitrite concentration which was almost twice as high as that of cluster 1 water bodies which have a temporary surface connection, and most are isolated water bodies. Generally, N-NO₃ was the dominant N-compound (Gordon et al., 2020), a more soluble and mobile nutrient, and due to the porous nature of the groundwater aquifer, inputs through seepage inflow become more relevant, (Heiler et al., 1995). The same cluster 2 water bodies had the highest ammonium (N-NH₄) concentration, indicating some ammonification processes in these water bodies. (Forshay and Stanely, 2005; Wohl, 2021) have explained how nitrogen-rich organic matter inputs in the floodplains water bodies promote transformation of nitrogen compounds.

The Danube main channel, Roskopf Arm aussen, Karpfen Arm and the Spittelauer Arm belonged to cluster 2 (nutrients). Natho et al., (2020) reports how the Spittelauer Arm is groundwater-fed and with findings from (Heiler et al., 1995) that the Danube is characterized by high amounts of nitrate, then river inputs into this permanently connected water body can explain the high nitrate concentration in this spatial cluster. On one hand, cluster 2 water bodies represent nutrient exchange processes in this spatially clumped cluster and on the other hand, cluster 1 waterbodies represent a laterally large-scale nutrient gradient.

The findings were not consistent with hypothesis 3 because from the detailed spatial analysis of the October sampling, we expected the backwaters and side-arm to be in different spatial clusters due to differing hydrochemistry. Dissolved N concentrations and chemical form change as the water reacts with the surrounding matrix, especially in slower, subsurface flow, or as biotic communities such as microbes or algae take up some of the N compounds and biochemically transform them (Wohl, 2021). We expected local exchanges depicting a more distinct lateral gradient for the hydrochemistry common to fluvial dynamics in floodplains than an inconsistent large-scale gradient in the network. Such contrastingly higher nitrate compared to other nitrogen-compounds in the floodplain water bodies and suggest how floodplains are vital sinks for nitrate (Natho et al., 2020). Lower nitrate concentrations observed for most backwaters can be related to greater nitrogen assimilation by phytoplankton, phytobenthos and other primary producers in these systems (Natho et al., 2020).

Other factors, such as inputs from local environmental conditions like land use and cover affect differences among floodplain lakes, particularly during low water levels. Nitrate can be leached from agricultural fields into the porous aquifer hence through subsurface/ seepage flow transport large amounts of nitrate into this floodplain. Land use type such as agriculture covering 23.61% of this floodplain landscape may have an influence. Fluctuating water levels on floodplains create aerobic and anaerobic conditions that enhance nitrification and denitrification in sediments respectively (Wohl, 2021).

Cluster 1 water bodies had the highest TP concentration while cluster 2 water bodies had the highest P-PO₄. Orthophosphate (P-PO₄) concentrations were higher in cluster 2 water bodies than in cluster 1 water bodies which include the main Danube channel during this low flow month. This would potentially allow for a high level of P-PO₄ adsorption (Preiner et al., 2020), long water residence time (predominant lentic conditions), sediment sorption and desorption, phytobenthos uptake and their mineralization during low flows, less sediment-water interaction, could be why there was less orthophosphate (House, 2003). We postulate that other P-PO₄ release mechanisms, such as reductive P-PO₄ release, overlaid the adsorption and/or desorption processes since P-PO₄ concentrations were higher in cluster 2 water bodies during disconnected floodplain state. Possible restriction of P-PO₄, indicated by the low P-PO₄ concentration for the cluster 1 water bodies findings during the October analysis could be due to phytoplankton uptake of this bioavailable phosphorus (Hein et al., 2004). High-water residence time, decreased depth, and resuspension could be related to greater TP concentrations in cluster 1 (Reckendorfer et al., 2013). Phosphorus release from sediments could also have

contributed to increased phosphorus concentrations particularly considering the high productivity of the water bodies (Castillo, 2020). TP and P-PO₄ concentrations are controlled by both biotic and abiotic processes in the water and sediments but mainly biotic processes predominantly (Preiner et al., 2008) influence phosphorus during the floodplain disconnected state.

Overall, orthophosphate was relatively low compared to other nutrients during this isolated state, this can be attributed to the internal processes eg assimilation by phytobenthos, and the precipitation with the Ca ions (Co-precipitation of P with calcite) at the sediment-water interface according to (Withers and Javie, 2008). Findings from this study indicated a clear low concentration of orthophosphate for both clusters that according to (Wohl, 2021) coincides with retention by these floodplain water bodies i.e., they removed phosphorus from the water column through physical, chemical, and biological processes. Though one water body the Grundwasser Tümpel Lobau stands out with a striking 65 µg/L of P-PO₄ which might be attributed to high inorganic matter mineralization. The main input of phosphorus to the water body benthic zone in side-arm channels and backwaters was via the settling of particulates during this low flow month (Reddy et al., 1999). Phosphorus sedimentation includes the settling of inorganic suspended particles and the accretion of organic matter. Phosphorus can also be taken up and released by vegetation and microbial activity (Reddy et al., 1999; Withers and Javie, 2008). Floating aquatic, emergent, and submerged macrophytes, fringing vegetation present at most of the sites could account for a high P-PO₄ uptake hence a reduction in water column phosphorus. On the other hand, (Wohl, 2021) reports that this makes up for limited storage because much of the phosphorus is released back into the water as these plants die and are degraded.

5.3.3 Spatial variability of particulate matter and phytobenthos chlorophyll-a concentration in October

Increased discharge influences the interconnectedness in the floodplain network, water level and the exchanges increase the particulate inorganic matter concentrations. Longitudinally, PIM was highest in the Danube main channel, water bodies with an upstream connection to the Danube (Rohrwörth upstream), downstream position (Spittelauer Arm had a permanent surface connection throughout the study) and shorter distances from the river that were easily inundated (Kleine Binn, Regelsbrunn and Mannsdorfer Hagel) at high flow in August and this result coincided with findings by (Heiler et al., 1995). They report that PIM is highest in water bodies that are highly connected or had a downstream position because such sites received higher river

inputs, sediment resuspension. Phytobenthos chlorophyll-a, PIM and POM, were in the same cluster group because PIM and mineralization of POM are the biggest contributors to sediment nutrients which are then utilized by phytobenthos growing on the sediment surface.

The cluster 2 water bodies ie Röthelstein isoliert, Regelsbrunn, and Tiergarten Arm isoliert had the highest phytobenthos chlorophyll-a concentration and the same trend sediment organic content. Noticeably in all the 3 clusters, there was an inconsistent pattern between side-arm channels and backwater concentrations. Cluster 3 water bodies had the least phytobenthos chlorophyll-a, and the Danube River falls under this cluster which was expected but rather the cluster is a mixture of both isolated water bodies and connected sidearm systems. On one hand, the Donau had the least phytobenthos chlorophyll-a measured during October, one would expect that the large gravel at this site would correspond to higher phytobenthos growth, this was not the case. The high flow conditions in the Donau 9th order stream with a nival flow regime (Natho et al., 2020) and it being a major transport route in Europe (highly navigated on a daily) do not provide a good physical habitat because the shear stress threshold may have played a big role in influencing low phytobenthos production. Higher nutrient loading could be a reason for the observed high phytobenthos growth for cluster 2 water bodies.

POM and PIM concentration were significantly different between the 3 clusters, but a clear distinction can be made for cluster 2 water bodies (Röthelstein isoliert, Regelsbrunn, and Tiergarten Arm isoliert) which had twice higher POM cluster 1 and 3. Cluster 1 water bodies had 6 times higher PIM than cluster 3 and twice higher than cluster 1 water bodies. Significant differences between the clusters can be attributed to low flow velocities especially in the backwaters and disconnected side-arm system head to sedimentation processes (Natho et al., 2020) that reduce POM and PIM form from the pelagic zone. Cluster 1 PIM and POM concentration was more less the same (0.01 g/L) but variation within the cluster was ± 0.001 and ± 0.07 g/L respectively. This big variation could have been due to significant upstream and downstream position. This is a clumped spatial cluster which indicates exchange processes in the upstream section of the floodplain.

Heiler et al., (1995) report that PIM is highest in sites that are highly interconnected or are located downstream along the river's longitudinal connectivity. This is usually where deposition of river inputs during high flow conditions is highest. Along the lateral gradient, PIM decreases with increasing distance from the Danube main channel (Heiler et al., 1995), Overall POM compounds entering the aquatic POM pool can be from terrestrial leaf litter mainly in autumn (October) and primary production by phytoplankton and the macrophytes.

In summary, hydrological connection is critical for the ecology and evolution of particulate matter in backwaters as in such water bodies, autochthonous processes contribute to deposition and locally driven algal blooms after mineralization of high POM (Reckendorfer et al., 2013). Primary production in the floodplain, from algae in floodplain water bodies to larger organic detritus from floodplain forests, can introduce POM to the floodplain and, through breakdown, infiltration, and burial, move POM into the subsurface zones (Wohl, 2021).

For the Röthelstein isoliert water body, the site had no surface connection, a very dense canopy cover hence tremendous leaf litter in the water could have contributed to high POM. The Tiergarten arm insolirt had large woody debris deposits in the water body and is the site that at the time of sampling had high beaver activity in the water hence this could have also influenced the results from resuspension as they moved through their dams. Based on these sediment trapping mechanisms, the submerged vegetation could increase water clarity and could complement further macrophyte growth (Bondar-Kunze et al., 2009). Regarding the PIM, most connected side arm systems acted as sources for the backwaters which had relatively lesser PIM. Decreasing water levels expose and alienate the shoreline zone of the water bodies coupled with low flow can lead to immobilization of accumulated fine sediment. Reddy et al., (1999) and Weigelhofer et al., (2018) noted how floodplain networks are effective in accumulating/storing nutrients that are transported in these systems in particulate form and that especially in isolated water bodies nutrient mobilization is relatively low as aggradation of fresh sediment on top of existing old sediment during periods of high flows is more prevalent.

5.3.4 Phytoplankton chlorophyll-a concentration and photosynthesis rate variation along a spatial gradient during the low flow month

Relative ETR_{max} and α are highly variable with environmental conditions and phytoplankton community structures. They change with water temperature (Côté and Platt, 1983), light intensity (Van Oijen et al., 2005), macronutrient level (Platt et al., 1992), and taxonomic composition of phytoplankton assemblage (Allali et al., 1997). The relative electron transport rate was highest for cluster 1 water bodies and corresponding with the highest phytoplankton chlorophyll-a values. This can be due to good underwater light availability (Castillo, 2020), seen in lower PIM/POM values. For the most part in this study, the interaction between how much percentage of sun exposure a water body had, how open the water bodies were determined how much incident solar radiation the water bodies received. The Donau, Röthelstein upstream, Eberschüttwasser Lobau, Petronell-Carnuntum Arm, Rosskopf Arm innen, Rosskopf Arm aussen, Witzelsdorfer Arm, Fadenbach Turtles, Mannsdorfer Hagel,

Spittelauer Arm, Schönauer Wasser all had high sun exposure amounts above 2000-watt hours/square meter (WH/m²) except for the Grundwasser Tümpel Lobau which had 0 (WH/m²). Additionally, lower phytoplankton chlorophyll a was found in these water bodies, so less possibility for nutrient competition may occur (Table 9). Shading effects due to dense canopy cover, turbidity, color, humic DOM, and highwater depth might explain relatively lower phytoplankton chlorophyll-a and relative ETR (photosynthesis rates) in cluster 2 water bodies. This can be underlined with the very low saturation irradiance, found in this cluster (Table 10). In general, this photosynthesis rate and phytoplankton biomass cluster group represents a laterally large spatial gradient of contrasting but adjacent water bodies with evidently different pelagic primary production. We hypothesized that stable patterns similar across the “classical” lateral floodplain gradient from dynamic (most connected water bodies -the side-arm systems) were expected to differ from completely isolated water bodies (backwaters) this was not consistent with the findings from this study. However, in conclusion, rapid light curves, (although data are not shown separately at each irradiance for all sites) can give a great understanding of photosynthesis rates of pelagic algal communities.

5.3.5 DOC and DOM quality variation along a spatial gradient during the low flow month

Concentrations of dissolved organic carbon are important because this material provides the energy source for the bacteria that facilitate transformations of material and nutrient inputs in the floodplain and do not correlate well with high river discharge (Preiner et al., 2008). There was no clear consistent trend for DOC as it was high in both side-arm systems and isolated backwaters having high DOC values and clustered differently. Grundwasser Tümpel Lobau and Fadenbach bei Orth which belongs to cluster 3 had the highest mean DOC, and cluster 1 water bodies had the least DOC concentration. This finding was contrary to studies that reported side-arm systems as functional DOC sinks (Preiner et al., 2018) because the highest DOC values were observed in cluster 3 backwaters. Schiemer et al., (2006) correlated microbial activity “fluorescence index” from (McKnight et al., 2001) that helps to differentiate DOM sources. Low FI values represent DOC derived from terrestrial plant material, whereas high FI values as for the case of all the clusters (mean values were > 1.5) represent DOC derived from aquatic primary production such as from phytoplankton.

The high DOC variation along the spatial gradient can be explained by inputs like dissolved oxygen, DOM, and nutrients into the floodplain, thereby accelerating primary production in the water column and the sediments of the backwaters (Hein et al., 1999; Lamers et al., 2006; Preiner et al., 2008). Increased dissolved organic matter in the floodplain water bodies might

explain the considerably high DOC concentrations in cluster 2 and cluster 3 (Tockner et al., 1999) had similar findings. In addition, the DOC quality may play a role in phosphorus production. The enhanced nutrient concentrations in the Donau-Auen floodplain waterbodies after the connection with the Danube stimulated an increase in algal biomass (Schiemer et al., 2006). Preiner et al., (2008) reports that autochthonous production in the Regelsbrunn Arm, make it a vital source of high DOC amounts and phytoplankton chlorophyll-a that are laterally exchanged with the Danube main channel. This may have increased the proportion of autochthonous DOC in the water column, thereby accelerating benthic microbial mineralization rates further (Preiner et al., 2008) in most of the side-arm (in cluster 1 and 2) which were mostly disconnected in October.

The allochthonous humic material were indicated by fluorescence peak C indicator of allochthonous carbon in the water bodies. The cluster 3 water bodies show higher relevance of allochthonous inputs than autochthonous production than the rest of the clusters the mean values of terrestrial humic-like fluorescence peak C in (section 4.3, Table 11). There were negligible differences for FI between the clusters as the observed explaining presence of fluorescent, dissolved extracellular material from microbial activity, fresh detritus from cell death and/or lysis, and other humic substances. Terrestrially and microbially derived humic material in the ultraviolet excitation band peak A (McKnight et al., 2001) had the highest concentration in all water bodies. This may be due to recalcitrant terrestrial soil humic-like DOM that was transported into the water bodies during the high flow month (connected state) and processing of leaf litter as these water bodies are surrounded by large alluvial forest cover. More intractable DOM can be from autochthonous protein-like DOM. The dominant protein-like fluorescence tyrosine-like peak B and tryptophan-like T were a result of microbial autochthonous internal processes like the high phytoplankton biomass production that was measured during this month. Generally, the degradation and cycling of aquatic-derived DOM is very fast compared to the catchment-derived (terrestrial) OM (Junk and Watzen, 2004).

We expected DOM gradient in the floodplain water bodies during these low flow conditions to reflect mainly primary productivity of the floodplain (autochthonous derived DOM). This was not the case as intractable organic matter from allochthonous sources was still prevalent in the network. DOM inputs have also been reported to reflect dissolution rates of organic matter and transport duration (Tockner et al., 1999). Characteristics like the composition of leaf litter and residence time of the leaf litter in a water body influence the rate of DOM leaching from the leaves and the ability of microbes to utilize the leached DOM (Wohl, 2021). Findings reveal

that such floodplain water bodies like the Grundwasser Tümpel Lobau, Fadenbach bei Orth, Fadenbach turtles, Röthelstein isoliert, Witzelsdorfer Arm, Rohrwörth downstream had the highest humic terrestrial peak C (irrespective of their clustering and would drain from them (leaf leachate) and hence had especially high DOM concentrations (Sankar et al., 2019).

Therefore, the humic-like DOM and high degree of humification could not only be resistant to microbial degradation but also are an indicator of the material's age according to (Ohno, 2002). The intractable nature towards degradation of most humic material could render them to stay longer in these ecosystems that are faced with continuous river inputs, aggradation and burial due to changes in hydrological connectivity (Birdwell and Engel, 2010). There was no clear pattern for the DOM cluster group because it was a laterally large spatial gradient with inconsistent trend between the clusters except for cluster 3 that stands out with just two water bodies ie Grundwasser Tümpel Lobau and Fadenbach bei Orth. They had the highest mean values for fluorescence peaks C, B, T, highest DOC and humification index. Grundwasser Tümpel Lobau has a dense canopy cover could be contributing to high humic-like terrestrial DOM and other intractable protein-like DOM. Cluster 2 water bodies had the highest CDOM values, BIX and FI correlating to biological processing of autochthonously sourced DOM which coincides with findings in section 4.3 and discussions in 5.3.4 above (had the highest phytoplankton biomass). Values of BIX were between 0.8 and 1 for the 3 clusters (cluster 1 with the highest BIX mean value = 0.9) which correspond to freshly produced DOM from microbial activity. There was less variation for humification indices of the clusters and values were less than the same as for BIX.

To summarize, the study did not investigate the real processes fundamental to the temporal floodplain dynamics (hydrochemistry) that were pivotal to this study. However, the connectivity degree and environmental conditions were assessed to explain their influence on hydrochemistry. The study, therefore, concludes that both network connectivity and environmental conditions together significantly explain the functional variability between these heterogeneous aquatic ecosystems. The key attributes of functional variability of lateral floodplain network connectivity differed in both space and time according to this study (Amoros and Bornette, 2002; Hein et al., 2004; Reckendorfer et al., 2013; Weigelhoefer et al., 2015), and these help to shape and contribute to a myriad of benefits from floodplains. In this study, both betweenness and harmonic centrality were considered and as well the probability of connectivity index.

CHAPTER 6. CONCLUSIONS AND RECOMMENDATION

As expected, the combined influence of connectivity and local environmental conditions was greater and enhanced during high flow conditions than their independent contributions to the hydrochemistry of the floodplain water bodies. Lasting residual effects from connectivity were observed even in the mean and low flow months ie September and October. Strong directional exchange and large distance transport of materials impacted the floodplain hydrochemistry during the high flow month and undirected short distance transport exchanges of material became most pronounced during the mean flow (September) and low flow conditions in October.

From the cluster analyses, we observed laterally large spatial gradient for most of the parameters like DOM, phytoplankton and phytobenthos chlorophyll-a biomass, PIM and POM, CDOM, DOC, except for the nutrients and ions where the clusters were spatially clumped that could explain ground water pathway in the network and exchange processes between the water bodies. The inconsistent trend for most variables was unlikely as it was not only the network connectivity influencing the floodplain hydrochemistry but also environmental conditions from the temporal analyses using the variation partitioning. Floodplain hydrochemistry after the flood pulse was expected to shift from mainly autochthonous to allochthonous driven due to high river inputs and pattern dependent on hydrological conditions (exchange under very high flow conditions, mean and low water conditions) driven by fluctuating Danube River discharge. The findings also suggested that especially for the dissolved organic matter that intractable materials were prevalent from allochthonous origins and cannot easily be degraded/ removed from the system due to high humification index observed for most waterbodies mainly the unique Grundwasser Tümpel Lobau and Fadenbach bei Orth water bodies.

From the detailed analyses for the October 2021 sampling date, we expected lower nutrients (phosphorus and nitrogen forms) concentration, but higher sediment organic content, pelagic algal photosynthesis rate, phytoplankton, and phytobenthos chlorophyll-*a* concentrations, dissolved organic carbon, and dissolved organic matter in the backwater systems. Higher nutrient concentrations were found to be in the Danube main channel, water bodies that had had a surface connection to the Danube during the 3 hydrological stages and basically having shorter distance away from the main channel. The study was based on concepts and methods from landscape ecology to disentangle and apply these in understanding the hydro-chemical conditions of the Danube floodplain network dynamics, integrating these aquatic ecosystems into a meta-ecosystem approach. Landscape ecology ideas were incorporated into the riverine

network to better explain spatiotemporal exchanges between interconnected floodplain aquatic ecosystems and their adjacent river (The Danube). This progress has improved our understanding of how temporal and spatial scale variations in network connectivity and environmental conditions of floodplain water bodies influence hydrochemistry throughout this Danube floodplain.

We recommend for future studies to take the next step further to disentangle these meta-ecosystems to better understand the interconnectedness of such floodplain networks which depend on not only fluvial dynamics like the network connectivity but also the inherent local environmental conditions. More approaches to management of these systems not as one entity but application of meta-ecosystem approaches. During the disconnected stage, heterogeneity in floodplain hydrology was shown to rise considerably, restoring fluvial dynamics is very necessary. The approaches have a demonstrated beneficial impact on the regulatory ecosystem services provided by this floodplain, with a significant increase in nutrient retention. This allochthonous regulated system can help to enhance water quality by retaining imported materials and nutrients from the Danube main river.

Previous research has shown that restoring a regular surface water connection to the Danube River will boost the floodplain's nitrate removal capacities and lower greenhouse gas emissions like N₂O. If no action is done, the floodplain will become more dominated by disconnected lentic water body forms more susceptible to eutrophication. Reconnecting parts of a floodplain system that are already closer to the main channel, by bringing various stakeholders including the national park authority, nature conservation NGOs, and neighboring government states propose measures that are in line with the restoration of network connectivity as well as conservation targets of the national park to increase the number of water bodies with permanent surface water connections from just one, the Spittelaeur Arm that was also recently renatured to many more especially with shorter distances to the Danube, as the DANP is part of the Natura 2000 network, and a large flood retention area during peak flow among other biodiversity benefits.

CHAPTER 7. REFERENCES

- Allali, K., Bricaud, A., and Claustre, H. (1997). Spatial variations in the chlorophyll-specific absorption coefficients of phytoplankton and photosynthetically active pigments in the equatorial Pacific. *Journal of Geophysical Research: Oceans*, 102(C6), 12413-12423.
- Amoros, C., and Bornette, G. (2002). Connectivity and biocomplexity in water bodies of riverine floodplains. *Freshwater Biology*, 47(4), 761-776.
- APHA (1998) Standard Methods for the Examination of Water and Wastewater, 20th edn. American Public Health Association, Washington, DC
- APHA AWWA, W. E. F. (2005). Standard methods for the examination of water and wastewater. *APHA WEF AWWA*.
- Arnold, C., Bachmann, O., and Schnitzler, A. (2017). Insights into the Vitis complex in the Danube floodplain (Austria). *Ecology and Evolution*, 7(19), 7796-7806.
- Baker, A. (2002). Spectrophotometric discrimination of river dissolved organic matter. *Hydrological Processes*, 16(16), 3203-3213.
- Barrat, A., Barthélemy, M., and Vespignani, A. (2005). The effects of spatial constraints on the evolution of weighted complex networks. *Journal of Statistical Mechanics: Theory and Experiment*, 2005(05), P05003.
- Barthélemy, M. (2011). Spatial networks. *Physics Reports*, 499(1-3), 1-101.
- Birdwell, J. E., and Engel, A. S. (2010). Characterization of dissolved organic matter in cave and spring waters using UV-Vis absorbance and fluorescence spectroscopy. *Organic Geochemistry*, 41(3), 270-280.
- Bishop-Taylor, R., Tulbure, M. G., and Broich, M. (2015). Surface water network structure, landscape resistance to movement, and flooding are vital for maintaining ecological connectivity across Australia's largest river basin. *Landscape Ecology*, 30(10), 2045-2065.
- Bishop-Taylor, R., Tulbure, M. G., and Broich, M. (2018). Evaluating static and dynamic landscape connectivity modelling using a 25-year remote sensing time series. *Landscape ecology*, 33(4), 625-640.
- Bondar-Kunze, E., Preiner, S., Schiemer, F., Weigelhofer, G., and Hein, T. (2009). Effect of enhanced water exchange on ecosystem functions in backwaters of an urban floodplain. *Aquatic Sciences*, 71(4), 437-447.

- Borcard, D., Gillet, F., and Legendre, P. (2018). Spatial analysis of ecological data. In *Numerical ecology with R* (pp. 299-367). Springer, Cham.
- Borcard, D., Legendre, P., and Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, 73(3), 1045-1055.
- Calabrese, J. M., and Fagan, W. F. (2004). A comparison-shopper's guide to connectivity metrics. *Frontiers in Ecology and the Environment*, 2(10), 529-536.
- Castillo, M. M. (2020). Suspended sediment, nutrients, and chlorophyll in tropical floodplain lakes with different patterns of hydrological connectivity. *Limnologia*, 82, 125767.
- Coble, P. G. (1996). Characterization of marine and terrestrial DOM in seawater using excitation-emission matrix spectroscopy. *Marine chemistry*, 51(4), 325-346.
- Coble, P. G. (2007). Marine optical biogeochemistry: the chemistry of ocean color. *Chemical reviews*, 107(2), 402-418.
- Côté, B., and Platt, T. (1983). Day-to-day variations in the spring-summer photosynthetic parameters of coastal marine phytoplankton. *Limnology and Oceanography*, 28(2), 320-344.
- Crandall, R. M., Hayes, C. R., and Ackland, E. N. (2003). Application of the intermediate disturbance hypothesis to flooding. *Community Ecology*, 4(2), 225-232.
- Csardi, G., and Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, complex systems*, 1695(5), 1-9.
- Dawidek, J., and Ferencz, B. (2014). Water balance of selected floodplain lake basins in the Middle Bug River valley. *Hydrology and Earth System Sciences*, 18(4), 1457-1465.
- de Andrade, R. L., and Rêgo, L. C. (2019). P-Means centrality. *Communications in Nonlinear Science and Numerical Simulation*, 68, 41-55.
- Dezső, J., Lóczy, D., Salem, A. M., and Nagy, G. (2019). Floodplain connectivity. In *The Drava River* (pp. 215-230). Springer, Cham.
- Dolph, C. L., Hansen, A. T., and Finlay, J. C. (2017). Flow-related dynamics in suspended algal biomass and its contribution to suspended particulate matter in an agricultural river network of the Minnesota River Basin, USA. *Hydrobiologia*, 785(1), 127-147.

- Eilers, P. H. C., and Peeters, J. C. H. (1988). A model for the relationship between light intensity and the rate of photosynthesis in phytoplankton. *Ecological modelling*, 42(3-4), 199-215.
- Erős, T., and Lowe, W. H. (2019). The landscape ecology of rivers: from patch-based to spatial network analyses. *Current Landscape Ecology Reports*, 4(4), 103-112.
- Erős, T., Olden, J. D., Schick, R. S., Schmera, D., and Fortin, M. J. (2012). Characterizing connectivity relationships in freshwaters using patch-based graphs. *Landscape ecology*, 27(2), 303-317.
- Estrada, E., and Bodin, Ö. (2008). Using network centrality measures to manage landscape connectivity. *Ecological Applications*, 18(7), 1810-1825.
- European Union, Copernicus Land Monitoring Service 2018, European Environment Agency (EEA)
- Fellman, J. B., Hood, E., and Spencer, R. G. (2010). Fluorescence spectroscopy opens new windows into dissolved organic matter dynamics in freshwater ecosystems: A review. *Limnology and oceanography*, 55(6), 2452-2462.
- Fletcher, R., and Fortin, M. J. (2018). Introduction to Spatial Ecology and Its Relevance for Conservation. In *Spatial Ecology and Conservation Modeling* (pp. 1-13). Springer, Cham.
- Forshay, K. J., and Stanley, E. H. (2005). Rapid nitrate loss and denitrification in a temperate river floodplain. *Biogeochemistry*, 75(1), 43-64.
- Fortin, M. J., James, P. M., MacKenzie, A., Melles, S. J., and Rayfield, B. (2012). Spatial statistics, spatial regression, and graph theory in ecology. *Spatial Statistics*, 1, 100-109.
- Funk, A., Martínez-López, J., Borgwardt, F., Trauner, D., Bagstad, K. J., Balbi, S., ... and Hein, T. (2019). Identification of conservation and restoration priority areas in the Danube River based on the multi-functionality of river-floodplain systems. *Science of the Total Environment*, 654, 763-777.
- Gabriel, H., Blaschke, A. P., Taschke, R., and Mayr, E. (2014). "Water connection (New) Danube–Lower Lobau (Nationalpark Donauauen)," in Water Quantity Report for Surface Water, Municipal Department MA45, (Vienna: Vienna Waters).

- Genty, B., Briantais, J. M., and Baker, N. R. (1989). The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochimica et Biophysica Acta (BBA)-General Subjects*, 990(1), 87-92.
- Gmitrowicz-Iwan, J., Ligęza, S., Pranagal, J., Smal, H., and Olenderek, H. (2020). Small Floodplain Reservoirs in the Face of Climate Change—Sink or Source of Nutrients? *Water*, 12(12), 3423.
- Gordon, B. A., Dorothy, O., and Lenhart, C. F. (2020). Nutrient retention in ecologically functional floodplains: A review. *Water*, 12(10), 2762.
- Gounand, I., Harvey, E., Little, C. J., and Altermatt, F. (2018). Meta-ecosystems 2.0: rooting the theory into the field. *Trends in Ecology & Evolution*, 33(1), 36-46. <https://doi.org/10.1016/j.tree.2017.10.006>
- Habersack, H., Schober, B., and Hauer, C. (2015). Floodplain evaluation matrix (FEM): An interdisciplinary method for evaluating river floodplains in the context of integrated flood risk management. *Natural Hazards*, 75(1), 5-32.
- Hager, H., and Schume, H. (2001). The floodplain forests along the Austrian Danube. *The floodplain forests in Europe. Current situation and perspectives. European Forest Institute Research Report*, 10, 83-100.
- Hansen, H. P., and Koroleff, F. (1999). Determination of nutrients. In 'Methods of Seawater Analysis. (Eds K. Grasshoff, K. Kremling, and M. Ehrhardt.) pp. 159–228.
- Hastings, A. (2012). Temporally varying resources amplify the importance of resource input in ecological populations. *Biology Letters*, 8(6), 1067-1069.
- Heiler, G., Hein, T., Schiemer, F., and Bornette, G. (1995). Hydrological connectivity and flood pulses as the central aspects for the integrity of a river-floodplain system. *Regulated Rivers: Research & Management*, 11(3-4), 351-361.
- Hein, T., Baranyi, C., Herndl, G. J., Wanek, W., and Schiemer, F. (2003). Allochthonous and autochthonous particulate organic matter in floodplains of the River Danube: the importance of hydrological connectivity. *Freshwater biology*, 48(2), 220-232.
- Hein, T., Baranyi, C., Reckendorfer, W., and Schiemer, F. (2004). The impact of surface water exchange on the nutrient and particle dynamics in side-arms along the River Danube, Austria. *Science of the Total Environment*, 328(1-3), 207-218.

- Hein, T., Heiler, G., Pennetzdorfer, D., Riedler, P., Schagerl, M., and Schiemer, F. (1999). The Danube restoration project: functional aspects and planktonic productivity in the floodplain system. *Regulated Rivers: Research & Management: An International Journal Devoted to River Research and Management*, 15(1-3), 259-270.
- Hein, T., Schwarz, U., Habersack, H., Nichersu, I., Preiner, S., Willby, N., and Weigelhofer, G. (2016). Current status and restoration options for floodplains along the Danube River. *Science of the Total Environment*, 543, 778-790.
- Heinz Walz GmbH, (2003). Phytoplankton Analyzer PHYTO-PAM and Phyto-Win Software V 1.45 System Components and Principles of Operation, 2. Edition: July 2003
- Höfle, R., Dullinger, S., and Essl, F. (2014). Different factors affect the local distribution, persistence, and spread of alien tree species in floodplain forests. *Basic and Applied Ecology*, 15(5), 426-434.
- Hohensinner, S., and Drescher, A. (2008). Historical change of European floodplains: the Danube River in Austria. *The Floodplain Forests of temperate zone of Europe, Lesnická práce, Prague*.
- Hopkins, K. G., Noe, G. B., Franco, F., Pindilli, E. J., Gordon, S., Metes, M. J., ... and Hogan, D. M. (2018). A method to quantify and value floodplain sediment and nutrient retention ecosystem services. *Journal of environmental management*, 220, 65-76. <https://doi.org/10.1016/j.jenvman.2018.05.013>
- House, W. A. (2003). Geochemical cycling of phosphorus in rivers. *Applied geochemistry*, 18(5), 739-748. <https://igraph.org/>
- Hudson, N., Baker, A., and Reynolds, D. (2007). Fluorescence analysis of dissolved organic matter in natural, waste, and polluted waters—a review. *River research and applications*, 23(6), 631-649.
- Huguet, A., Vacher, L., Relexans, S., Saubusse, S., Froidefond, J. M., and Parlanti, E. (2009). Properties of fluorescent dissolved organic matter in the Gironde Estuary. *Organic Geochemistry*, 40(6), 706-719.
- Humphries, P., Keckeis, H., and Finlayson, B. (2014). The river wave concept: integrating river ecosystem models. *BioScience*, 64(10), 870-882.

- ICPDR website, Danube Basin-Austria. <https://www.icpdr.org/main/danube-basin/austria>
- ICPDR website, Danube River Basin Management Plan (2015), <https://www.icpdr.org/main/activities-projects/river-basin-management-plan-update-2015>
- ISO 15681-2:2003 (2003) Water quality. Determination of orthophosphate and total phosphorus contents by flow analysis (FIA and CFA). Part 2: Method by continuous flow analysis (CFA). Geneva
- ISO 7887. (2011). Water Quality–Examination and Determination of Colour. *International Organization for Standardization, Geneva, Switzerland.*
- Junk WJ, Wantzen KM (2004). The flood pulse concept: new aspects, approaches, and applications - an update. In: Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume II. Welcomme RL and Petr T, Eds., FAO Regional Office for Asia and the Pacific, Bangkok, Thailand, RAP Publication 2004/17 pp 117–149
- Junk, W. J., Bayley, P. B., and Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. *Canadian special publication of fisheries and aquatic sciences*, 106(1), 110-127.
- Katutis, K., and Rudzianskaitė, A. (2015). The fluctuation of calcium and magnesium concentrations in the floodwater in the Nemunas and Miniija lowlands. *Zemdirbyste-Agriculture*, 102(3).
- Kirschner, A. K., Riegl, B., and Velimirov, B. (2001). Degradation of emergent and submerged macrophytes in an oxbow lake of an embanked backwater system: implications for the terrestrialization process. *International Review of Hydrobiology: A Journal Covering all Aspects of Limnology and Marine Biology*, 86(4-5), 555-571.
- Kühl, M., Glud, R. N., Borum, J., Roberts, R., and Rysgaard, S. (2001). Photosynthetic performance of surface-associated algae below sea ice as measured with a pulse amplitude-modulated (PAM) fluorometer and O₂ microsensors. *Marine ecology progress series*, 223, 1-14.
- Lamers, L. P. M., Loeb, R. A. M. A., Antheunisse, A. M., Miletto, M., Lucassen, E. C. H. E. T., Boxman, A. W., ... and Roelofs, J. G. M. (2006). Biogeochemical constraints on the

- ecological rehabilitation of wetland vegetation in river floodplains. *Hydrobiologia*, 565(1), 165-186.
- Lasne, E., Lek, S., and Laffaille, P. (2007). Patterns in fish assemblages in the Loire floodplain: the role of hydrological connectivity and implications for conservation. *Biological Conservation*, 139(3-4), 258-268.
- Lawaetz, A. J., and Stedmon, C. A. (2009). Fluorescence intensity calibration using the Raman scatter peak of water. *Applied spectroscopy*, 63(8), 936-940.
- Li, Y., Zhang, Q., Cai, Y., Tan, Z., Wu, H., Liu, X., and Yao, J. (2019). Hydrodynamic investigation of surface hydrological connectivity and its effects on the water quality of seasonal lakes: insights from a complex floodplain setting (Poyang Lake, China). *Science of the Total Environment*, 660, 245-259.
- Loreau, M., Mouquet, N., and Holt, R. D. (2003). Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters*, 6(8), 673-679.
- Mănoiu, V. M., and Crăciun, A. I. (2021). Danube River Water Quality Trends: A Qualitative Review Based on the Open Access Web of Science Database. *Ecohydrology & Hydrobiology*.
- Marra, W. A., Kleinhans, M. G., and Addink, E. A. (2014). Network concepts to describe channel importance and change in multichannel systems: test results for the Jamuna River, Bangladesh. *Earth Surface Processes and Landforms*, 39(6), 766-778.
- Massicotte, P. (2019). eemR: tools for pre-processing emission-excitation-matrix (EEM) fluorescence data. *R package version*, 1(1).
- Mayora, G., Devercelli, M., and Frau, D. (2016). Spatial variability of chromophoric dissolved organic matter in a large floodplain river: control factors and relations with phytoplankton during a low water period. *Ecohydrology*, 9(3), 487-497.
- Mayora, G., Devercelli, M., and Giri, F. (2013). Spatial variability of chlorophyll-a and abiotic variables in a river–floodplain system during different hydrological phases. *Hydrobiologia*, 717(1), 51-63.
- Mayora, G., Scarabotti, P., Schneider, B., Alvarenga, P., and Marchese, M. (2020). Multiscale environmental heterogeneity in a large river-floodplain system. *Journal of South American Earth Sciences*, 100, 102546.

- Mayora, G., Schneider, B., & Rossi, A. (2018). Turbidity and dissolved organic matter as significant predictors of spatio-temporal dynamics of phosphorus in a large river-floodplain system. *River Research and Applications*, 34(7), 629-639.
- Mayora, G., Schneider, B., and Rossi, A. (2018). Turbidity and dissolved organic matter as significant predictors of spatio-temporal dynamics of phosphorus in a large river-floodplain system. *River Research and Applications*, 34(7), 629-639.
- Mazzoleni, M., Mård, J., Rusca, M., Odongo, V., Lindersson, S., and Di Baldassarre, G. (2021). Floodplains in the Anthropocene: A Global Analysis of the Interplay Between Human Population, Built Environment, and Flood Severity. *Water Resources Research*, 57(2), e2020WR027744.
- McKnight, D. M., Boyer, E. W., Westerhoff, P. K., Doran, P. T., Kulbe, T., and Andersen, D. T. (2001). Spectrofluorometric characterization of dissolved organic matter for indication of precursor organic material and aromaticity. *Limnology and Oceanography*, 46(1), 38-48.
- Millennium ecosystem assessment, M. E. A. (2005). *Ecosystems and human well-being* (Vol. 5). Washington, DC: Island Press.
- Murphy, K. R., Stedmon, C. A., Wenig, P., and Bro, R. (2014). OpenFluor—an online spectral library of auto-fluorescence by organic compounds in the environment. *Analytical Methods*, 6(3), 658-661.
- Natho, S., Tschikof, M., Bondar-Kunze, E., and Hein, T. (2020). Modeling the effect of enhanced lateral connectivity on nutrient retention capacity in large river floodplains: How much connected floodplain do we need? *Frontiers in Environmental Science*, 8, 74.
- Noe, G. B., and Hupp, C. R. (2007). Seasonal variation in nutrient retention during inundation of a short-hydroperiod floodplain. *River Research and Applications*, 23(10), 1088-1101.
- Ohno, T. (2002). Fluorescence inner-filtering correction for determining the humification index of dissolved organic matter. *Environmental science & technology*, 36(4), 742-746.

- Opperman, J. J., Luster, R., McKenney, B. A., Roberts, M., and Meadows, A. W. (2010). Ecologically functional floodplains: connectivity, flow regime, and scale 1. *JAWRA Journal of the American Water Resources Association*, 46(2), 211-226.
- Parsons, M., Thoms, M. C., and Norris, R. H. (2004). Using hierarchy to select scales of measurement in multiscale studies of stream macroinvertebrate assemblages. *Journal of the North American Benthological Society*, 23(2), 157-170.
- Peršić, V., and Horvatić, J. (2011). Spatial distribution of nutrient limitation in the Danube River floodplain in relation to hydrological connectivity. *Wetlands*, 31(5), 933.
- Platt, T., Sathyendranath, S., Ulloa, O., Harrison, W. G., Hoepffner, N., and Goes, J. (1992). Nutrient control of phytoplankton photosynthesis in the Western North Atlantic. *Nature*, 356(6366), 229-231.
- Preiner, S., Bondar-Kunze, E., Pitzl, B., Weigelhofer, G., and Hein, T. (2020). Effect of Hydrological Connectivity on the Phosphorus Buffering Capacity of an Urban Floodplain. *Frontiers in Environmental Science*, 8, 147.
- Preiner, S., Drozdowski, I., Schagerl, M., Schiemer, F., and Hein, T. (2008). The significance of side-arm connectivity for carbon dynamics of the River Danube, Austria. *Freshwater Biology*, 53(2), 238-252.
- Pucher, M., Wünsch, U., Weigelhofer, G., Murphy, K., Hein, T., and Graeber, D. (2019). staRdom: versatile software for analyzing spectroscopic data of dissolved organic matter in R. *Water*, 11(11), 2366.
- Rebelo, L. M., Johnston, R., Hein, T., Weigelhofer, G., D'Haeyer, T., Kone, B., and Cools, J. (2013). Challenges to the integration of wetlands into IWRM: The case of the Inner Niger Delta (Mali) and the Lobau Floodplain (Austria). *Environmental science & policy*, 34, 58-68.
- Reckendorfer, W., Baranyi, C., Funk, A., and Schiemer, F. (2006). Floodplain restoration by reinforcing hydrological connectivity: Expected effects on aquatic mollusc communities. *Journal of Applied ecology*, 43(3), 474-484.
- Reckendorfer, W., Funk, A., Gschöpf, C., Hein, T., and Schiemer, F. (2013). Aquatic ecosystem functions of an isolated floodplain and their implications for flood retention and management. *Journal of Applied Ecology*, 50(1), 119-128.

- Riedler, P., Baranyi, C., Hein, T., Keckeis, S., and Schagerl, M. (2006). Abiotic and biotic control of phytoplankton development in dynamic side-arms of the River Danube. *Large Rivers*, 577-594.
- Robertson, A. I., Bunn, S. E., Boon, P. I., and Walker, K. F. (1999). Sources, sinks, and transformations of organic carbon in Australian floodplain rivers. *Marine and Freshwater Research*, 50(8), 813-829.
- Rochat, Y. (2009). *Closeness centrality extended to unconnected graphs: The harmonic centrality index* (No. CONF).
- Sankar, M. S., Dash, P., Singh, S., Lu, Y., Mercer, A. E., and Chen, S. (2019). Effect of photo-biodegradation and biodegradation on the biogeochemical cycling of dissolved organic matter across diverse surface water bodies. *Journal of Environmental Sciences*, 77, 130-147.
- Saura, S., and Pascual-Hortal, L. (2007). A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. *Landscape and urban planning*, 83(2-3), 91-103.
- Saura, S., and Rubio, L. (2010). A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography*, 33(3), 523-537.
- Saura, S., and Torné, J. (2009). Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. *Environmental modelling & software*, 24(1), 135-139.
- Schiemer, F., Baumgartner, C., and Tockner, K. (1999). Restoration of floodplain rivers: The 'Danube restoration project'. *River Research and Applications*, 15(1-3), 231-244.
- Schiemer, F., Hein, T., and Peduzzi, P. (2006). Hydrological control of system characteristics of floodplain lakes. *Ecohydrology & Hydrobiology*, 6(1-4), 7-18.
- Schinegger, R., Trautwein, C., Melcher, A., and Schmutz, S. (2012). Multiple human pressures and their spatial patterns in European running waters. *Water and Environment Journal*, 26(2), 261-273.
- Schreiber, U., Klughammer, C., and Kolbowski, J. (2011). High-end chlorophyll fluorescence analysis with the MULTI-COLOR-PAM. I. Various light qualities and their applications. *PAM Appl. Notes*, 1, 1-21.

- Seekell, D. A., Lapierre, J. F., Ask, J., Bergström, A. K., Deiningner, A., Rodríguez, P., and Karlsson, J. (2015). The influence of dissolved organic carbon on primary production in northern lakes. *Limnology and Oceanography*, 60(4), 1276-1285.
- Serôdio, J., Vieira, S., and Cruz, S. (2008). Photosynthetic activity, photoprotection and photoinhibition in intertidal microphytobenthos as studied in situ using variable chlorophyll fluorescence. *Continental Shelf Research*, 28(10-11), 1363-1375.
- Stanford, J. A., Lorang, M. S., and Hauer, F. R. (2005). The shifting habitat mosaic of river ecosystems. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, 29(1), 123-136.
- Staska, B., Essl, F., and Samimi, C. (2014). Density and age of invasive *Robinia pseudoacacia* modulate its impact on floodplain forests. *Basic and Applied Ecology*, 15(6), 551-558.
- Stedmon, C. A., and Markager, S. (2005). Resolving the variability in dissolved organic matter fluorescence in a temperate estuary and its catchment using PARAFAC analysis. *Limnology and oceanography*, 50(2), 686-697.
- Steinman, A. D., Lamberti, G. A., Leavitt, P. R., and Uzarski, D. G. (2017). Biomass and pigments of benthic algae. In *Methods in Stream Ecology, Volume 1* (pp. 223-241). Academic Press.
- Taylor, P. D., Fahrig, L., Henein, K., and Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, 571-573.
- The Donau River Information Services (DoRIS)
<https://www.doris.bmk.gv.at/fahrwasserinformation/pegelstaende-und-prognosen/jahresverlauf>
- Thomaz, S. M., Bini, L. M., and Bozelli, R. L. (2007). Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*, 579(1), 1-13.
- Thoms MC, Southwell M, and McGinness HM (2005). Floodplain-river ecosystems: Fragmentation and water resources development. *Geomorphology* 71:126-138
- Thoms, M. C., Parsons, M. E., and Foster, J. M. (2007). The use of multivariate statistics to elucidate patterns of floodplain sedimentation at different spatial scales. *Earth Surface Processes and Landforms*, 32(5), 672-686.

- Thorp, J. H., Thoms, M. C., and Delong, M. D. (2006). The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications*, 22(2), 123-147.
- Tockner K, Pennetzdorfer D, Reiner N, Schiemer F, and Ward JV (1999) Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). *Freshwater Biology* 41:521-535
- Tockner, K. (2021). Freshwaters: Global Distribution, Biodiversity, Ecosystem Services, and Human Pressures. In *Handbook of Water Resources Management: Discourses, Concepts, and Examples* (pp. 489-501). Springer, Cham.
- Tockner, K., and Stanford, J. A. (2002). Riverine flood plains: present state and future trends. *Environmental conservation*, 29(3), 308-330.
- Tockner, K., Lorang, M. S., and Stanford, J. A. (2010). River flood plains are model ecosystems to test general hydrogeomorphic and ecological concepts. *River research and applications*, 26(1), 76-86.
- Tockner, K., Malard, F., and Ward, J. V. (2000). An extension of the flood pulse concept. *Hydrological processes*, 14(16-17), 2861-2883.
- Tockner, K., Pennetzdorfer, D., Reiner, N., Schiemer, F., and Ward, J. V. (1999). Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). *Freshwater Biology*, 41(3), 521-535.
- Tockner, K., Pusch, M., Borchardt, D., and Lorang, M. S. (2010). Multiple stressors in coupled river-floodplain ecosystems. *Freshwater Biology*, 55, 135-151.
- Tockner, K., Uehlinger, U., and Robinson, C. T. (2009). *Rivers of Europe*. Academic Press.
- Urban, D. L., Minor, E. S., Treml, E. A., and Schick, R. S. (2009). Graph models of habitat mosaics. *Ecology Letters*, 12(3), 260-273.
- Uroy, L., Alignier, A., Mony, C., Foltête, J. C., and Ernoult, A. (2021). How to assess the temporal dynamics of landscape connectivity in ever-changing landscapes: a literature review. *Landscape Ecology*, 36(9), 2487-2504.
- Van Oijen, T., Veldhuis, M. J. W., Gorbunov, M. Y., Nishioka, J., Van Leeuwe, M. A., and De Baar, H. J. W. (2005). Enhanced carbohydrate production by Southern Ocean phytoplankton in response to in situ iron fertilization. *Marine chemistry*, 93(1), 33-52.

- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., and Cushing, C. E. (1980). The river continuum concept. *Canadian journal of fisheries and aquatic sciences*, 37(1), 130-137.
- Wang, P., Ma, J., Wang, X., and Tan, Q. (2020). Rising atmospheric CO₂ levels result in an earlier cyanobacterial bloom-maintenance phase with higher algal biomass. *Water Research*, 185, 116267.
- Ward, J. V., and Tockner, K. (2001). Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology (Print)*, 46(6), 807-819.
- WCL, C. P., WCL, R. P., Başıoğlu, D., Beklioğlu, M., UMF, H. L., and Mas, S. Standard Operating Protocol (SOP) on Water Chemistry.
- Weigelhofer, G., Hein, T., and Bondar-Kunze, E. (2018). Phosphorus and nitrogen dynamics in riverine systems: Human impacts and management options. *Riverine Ecosystem Management*, 187.
- Weigelhofer, G., Hein, T., Kucera-Hirzinger, V., Zornig, H., and Schiemer, F. (2011). Hydrological improvement of a former floodplain in an urban area: potential and limits. *Ecological Engineering*, 37(10), 1507-1514.
- Weigelhofer, G., Jirón, T. S., Yeh, T. C., Steniczka, G., and Pucher, M. (2020). Dissolved Organic Matter Quality and Biofilm Composition Affect Microbial Organic Matter Uptake in Stream Flumes. *Water*, 12(11), 3246.
- Weigelhofer, G., Preiner, S., Funk, A., Bondar-Kunze, E., and Hein, T. (2015). The hydrochemical response of small and shallow floodplain water bodies to temporary surface water connections with the main river. *Freshwater Biology*, 60(4), 781-793. <https://doi.org/10.1111/fwb.12532>
- Wetzel, R. G. (1992). Gradient-dominated ecosystems: sources and regulatory functions of dissolved organic matter in freshwater ecosystems. In *Dissolved organic matter in lacustrine ecosystems* (pp. 181-198). Springer, Dordrecht.
- Withers, P. J. A., and Jarvie, H. P. (2008). Delivery and cycling of phosphorus in rivers: a review. *Science of the total environment*, 400(1-3), 379-395.
- Wohl, E. (2021). An integrative conceptualization of floodplain storage. *Reviews of Geophysics*, 59(2), e2020RG000724.

Wu, J. (2013). Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton Park workshop. *Landscape ecology*, 28(1), 1-11.

APPENDIX 1

Table 12: One-way ANOVA result for hydro-chemical differences between the three months as described in results section 4.2.

Variable	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Total phosphorus	2	76806	38403	11.84	4.05e-05 ***
	66	214131	3244		
CDOM/Color	2	845	422.4	1.541	0.222
	66	18088	274.1		
PIM	2	0.003625	0.001813	5.793	0.00481 **
	66	0.020651	0.000313		
POM	2	0.262	0.1308	1.138	0.327
	66	7.588	0.115		
Phytoplankton Chl- <i>a</i>	2	3082	1540.8	5.591	0.00571 **
	66	18189	275.6		
Temperature	2	1396.6	698.3	129.9	<2e-16 ***
	66	354.7	5.4		
Conductivity	2	22411	11206	0.2	0.819
	66	3700661	56071		
BIX	3	0.0784	0.026132	4.499	0.00621 **
	66	0.3833	0.005808		
HIX	3	0.03332	0.011106	3.344	0.0243 *
	66	0.21923	0.003322		
FI	3	0.02638	0.008793	2.597	0.0517.
	66	0.22348	0.003386		
B	3	0.0484	0.01613	1.19	0.32
	66	0.8944	0.01355		
T	3	0.168	0.05606	1.02	0.39
	66	3.628	0.05498		
C	3	0.0608	0.02028	0.822	0.486
	66	1.6284	0.02467		

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Table 13: Cation and anion correlation with electrical conductivity during the low flow month.

		Correlations						
		EC (µs/cm)	Sodium (mg/L)	Potassium (mg/L)	Calcium (mg/L)	Magnesium (mg/L)	Chloride (mg/L)	Sulfate (mg/L)
EC (µs/cm)	Pearson Correlation	1	.898**	.207	.921**	.972**	.964**	.919**
	Sig. (2-tailed)		.000	.332	.000	.000	.000	.000
	N	24	24	24	24	24	24	24
Sodium (mg/L)	Pearson Correlation	.898**	1	-.084	.772**	.896**	.875**	.849**
	Sig. (2-tailed)	.000		.695	.000	.000	.000	.000
	N	24	24	24	24	24	24	24
Potassium (mg/L)	Pearson Correlation	.207	-.084	1	.397	.143	.091	-.026
	Sig. (2-tailed)	.332	.695		.055	.504	.674	.903
	N	24	24	24	24	24	24	24
Calcium (mg/L)	Pearson Correlation	.921**	.772**	.397	1	.891**	.881**	.848**
	Sig. (2-tailed)	.000	.000	.055		.000	.000	.000
	N	24	24	24	24	24	24	24
Magnesium (mg/L)	Pearson Correlation	.972**	.896**	.143	.891**	1	.985**	.952**
	Sig. (2-tailed)	.000	.000	.504	.000		.000	.000
	N	24	24	24	24	24	24	24
Chloride (mg/L)	Pearson Correlation	.964**	.875**	.091	.881**	.985**	1	.973**
	Sig. (2-tailed)	.000	.000	.674	.000	.000		.000
	N	24	24	24	24	24	24	24
Sulfate (mg/L)	Pearson Correlation	.919**	.849**	-.026	.848**	.952**	.973**	1
	Sig. (2-tailed)	.000	.000	.903	.000	.000	.000	
	N	24	24	24	24	24	24	24

** . Correlation is significant at the 0.01 level (2-tailed).

APPENDIX 2

Below are results that didn't yield significant differences with the One-way ANOVA in section 4.2, they are comparisons between the variables and between the months

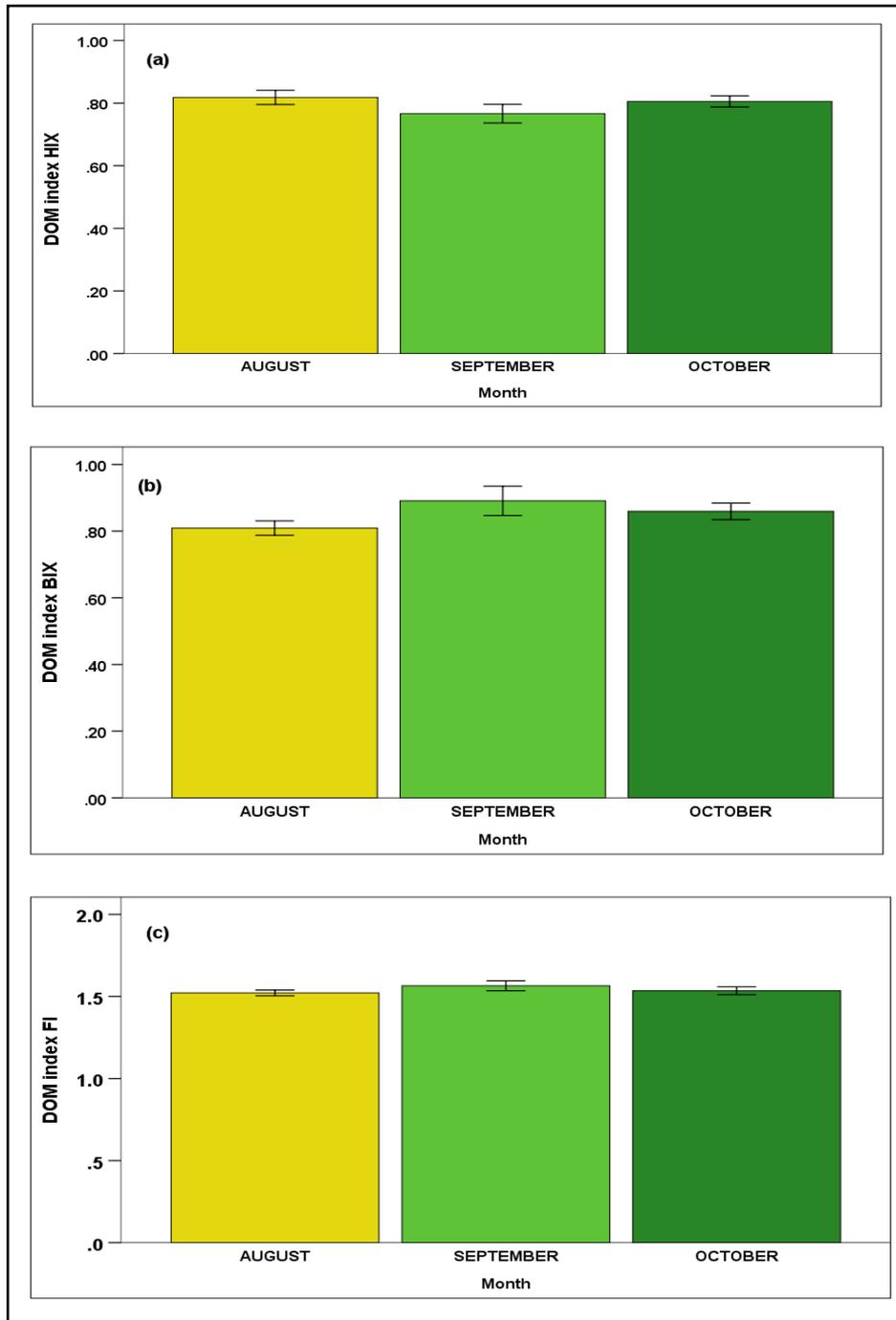


Figure 16: Temporal variation of DOM quality (a) humification index (HIX), (b) biological index (BIX), and (c) fluorescence index (FI) between the three months, bars represent means and standard error.

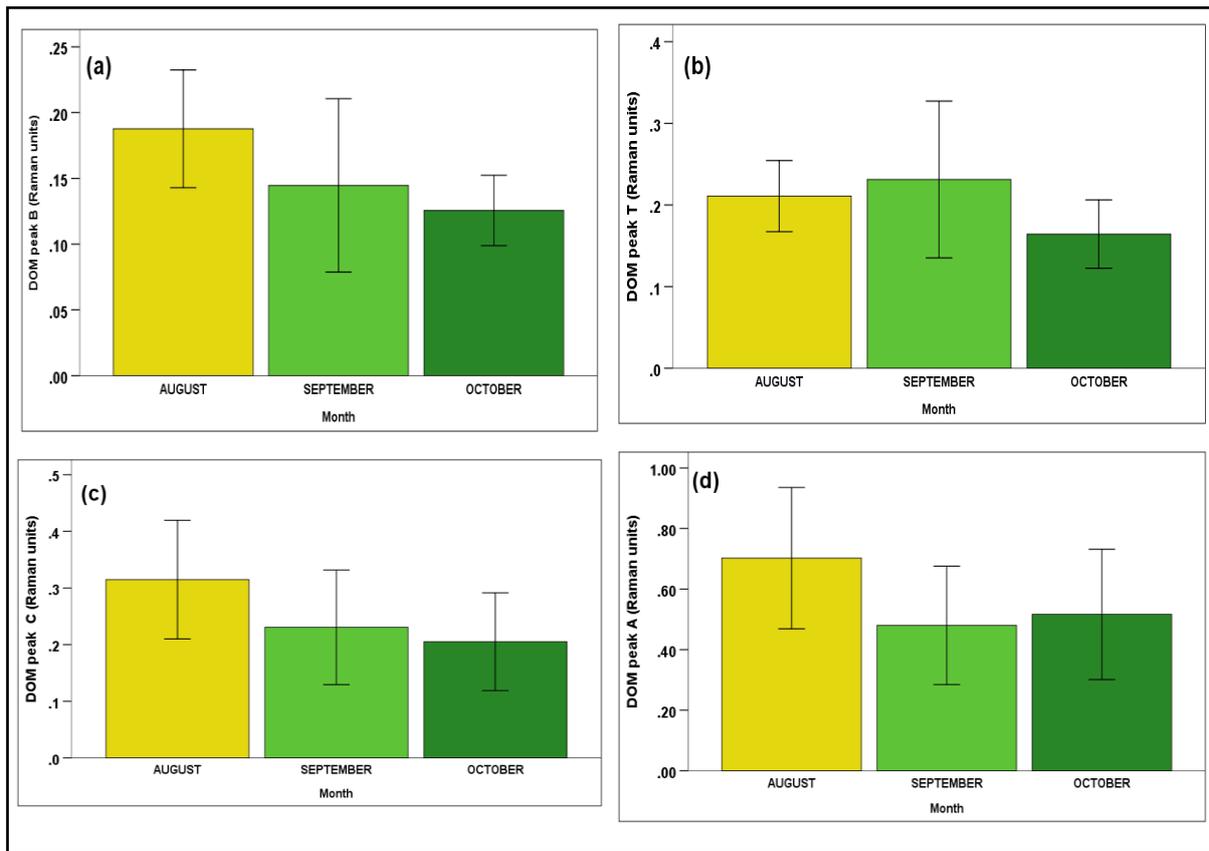


Figure 17: Temporal variation in DOM fluorescence peaks

(a) protein-like fluorescence peak attributed to tyrosine in the peak B region, (b) protein-like fluorescence peak in the tryptophan T region (c) terrestrial humic peak C indicator of allochthonous carbon in the water bodies, and (d) represents terrestrial and microbially derived humic substances represented by fluorescence peak A. (bars represent mean \pm standard error).

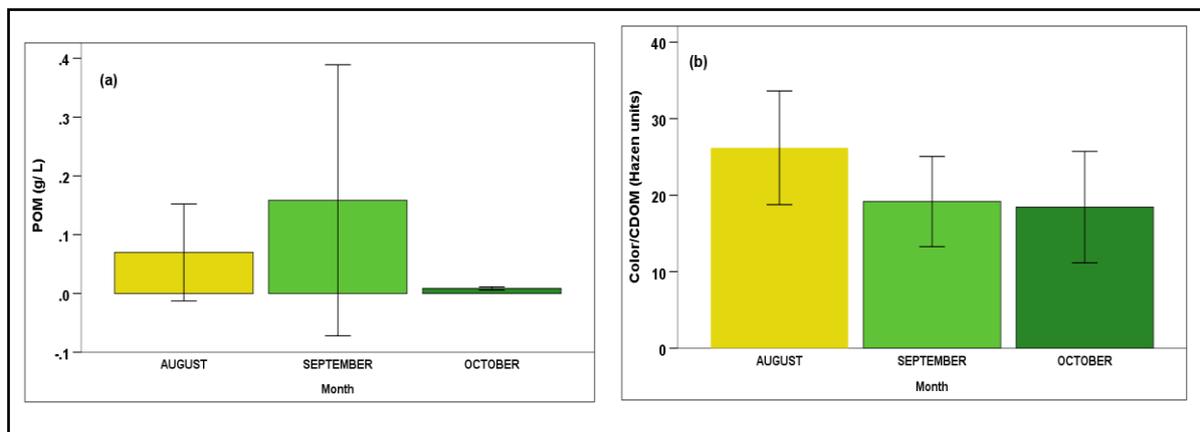


Figure 18: Temporal variation of (a) POM concentration and (b) CDOM concentration between the three months.