Stickstoffkreisläufe in renaturierten und degradierte Auen von Flüssen

Nitrogen cycling in restored and disturbed riverine floodplains

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"Think left and think right and think low and think high.
Oh, the things you can think up if only you try!"
- Dr. Seuss

"All life is an experiment.
The more experiments you make the better."
-Ralph Waldo Emerson

Kurzfassung

Steigender Nutzungsdruck auf Flusslandschaften führte zur Einengung aktiver Auen, was wiederum zum Verlust von Ökosystemleistungen dieser natürlichen Übergangsbereiche führte. Die bisherigen Bemühungen zur Reaktivierung dieser Gebiete beschränkten sich überwiegend auf die hydrologische Wiederanbindung dieser Flächen an die Hauptläufe von Flüssen. Dadurch konnten oftmals wichtige Habitate wie etwa Laichplätze für Fische wieder hergestellt werden. Die aus der Wiederanbindung resultierenden, biogeochemischen Veränderungen wurden jedoch meist wenig bis gar nicht beachtet. Aus diesem Grund befasst sich diese Arbeit mit den Auswirkungen von groß angelegten Renaturierungsprojekten auf die biogeochemischen Kreisläufe in zwei Überschwemmungsgebieten entlang der Donau bei Wien. Im Speziellen wurde dabei der Stickstoffkreislauf untersucht, da Überschwemmungsgebiete einerseits das Potential haben, Nitrat aus dem Wasser zu entfernen, andererseits aber auch Lachgas, ein effizientes Treibhausgas, ausstoßen können.

Das wichtigste Ergebnis dieses Projekts war der Beweis, dass Renaturierung und Wiederanbindung von Auen den Stickstoffkreislauf beeinflusst und wichtige Faktoren für den Umsatz sowie das Verhältnis von produziertem N_2O zu N_2 verändert. Es konnte bewiesen werden, dass Renaturierung durch Erhöhung der Überschwemmungsfrequenz die Effizienz der biogeochemischen Kreisläufe steigert. Die N_2O Emissionen verringern sich dadurch im Vergleich zu nicht angebundenen Überschwemmungsgebieten. Generell hat dieses Projekt das Verständnis für die Funktionen diverser Subsysteme in Überschwemmungsgebieten sowie die Rolle der gesamten Transformationskapazität und der biogeochemischen Wechselwirkungen in Überschwemmungssystemen verbessert. Durch ein im Rahmen dieses Projekts entwickeltes Modell konnte Aktivitäten auf Landschaftsebene prognostiziert werden, die Bereiche hoher Aktivität in häufig von der Donau überfluteten Bereichen identifizieren konnte. In einer Serie von Laborexperimenten konnten die spezifischen Bedingungen, welche zur Reduktion der N_2O Ausgasung führen, identifiziert werden.

Abschließend lässt sich feststellen, dass dieses Projekt das Verständnis für Managementmaßnahmen von Überschwemmungsgebieten maßgeblich verbessert hat. Es konnten darüber hinaus Vorschläge für Restaurierungsmaßnahmen gemacht werden, welche in Bezug auf die Umwandlung von Nährstoffen in Auen deutlich effizienter sind und das Potential haben, den Nährstofftransport auf Einzugsgebietsebene zu beeinflussen.

Summary

Increasing pressure on rivers results in the decoupling of the naturally occurring floodplains, resulting in a loss of the ecosystem services provided by these transition zones. Efforts to restore floodplains by reconnecting them to their source rivers have primarily focused on reestablishing the unique habitats found in floodplains (i.e. fish spawning sites). However, the resulting biogeochemical changes are not well documented. The purpose of this study was to understand the effects of this large-scale change to the biogeochemical cycling of two floodplain systems in the Danube River Basin. Nitrogen cycling was chosen due to the capacity of floodplains to remove nitrate from the river and to produce nitrous oxide, a harmful greenhouse gas.

The most important finding of this project demonstrated how floodplain restoration alters the nitrate removal pathways and ultimately N_2O and N_2 emission. I have shown that restoration, by increasing the frequency of inundation, improves biogeochemical cycling efficiency and reduce N_2O emissions from denitrification compared to decoupled floodplains. Generally, this project improved understanding of the function of different subsystems within the floodplain landscape as well as the role of overall transformation capacity and biogeochemical interplay within floodplain systems. Using the produced modeling tool, patterns of high activity in areas which were frequently inundated by the Danube River were identified. A series of laboratory experiments elucidated the specific changes which resulting in a reduction of N_2O production.

Overall, this project furthered the understanding of nitrogen cycling in floodplains and suggested restoration efforts which are more effective at transforming nutrients within the riverine landscape which affects the nutrient transport at the catchment scale.

Introduction

Floodplains: Why the kidneys matter

Floodplains are the ecosystem service centers of river ecosystems, acting as biogeochemical hot spots of nutrient cycling and carbon processing. As key sites of nutrient transformation, floodplains act as a sinks and prevent river eutrophication (Richardson 2004) and the accumulation of toxic compounds such as nitrite and heavy metals in their sediments. In terms of carbon cycling, floodplains play a major role in the recycling and removal of soluble organic carbon released from terrestrial ecosystems (Battin et al. 2008). River floodplains are recognized as important storage sites for sediments and associated nutrients mobilized from upstream catchments during floods (He and Walling 1997, Forshay and Stanley 2005). The transfer and storage of materials in floodplains are largely under the control of the connectivity pattern within the river landscape as well as of the magnitude, frequency and duration of floods (Racchetti et al. 2010). The local morphology, i.e. width and location within the floodplain, of these areas together with the main channel's flow regime, govern the overall retention capacity of individual water bodies within the floodplain, especially during flooding (Heiler et al. 1995, Hein et al. 2004). Additionally, the intensity of exchange between surface and subsurface waters contributes significantly to the nutrient retention capacity (Hill et al. 2000a).

In short floodplains are functional retention areas (Carling 1992), which control and maintain river water quality (Olde-Venterink et al. 2003, Banach et al. 2009a, Banach et al. 2009b, James 2010). Collectively, these factors create a mosaic of geomorphologic surfaces that influence the spatial pattern and successional development of riparian vegetation (Salo et al. 1986, Roberts and Ludwig 1991, Hein et al. 2005). In dynamically connected retention areas, the pattern of surface and sub-surface flow provides the basis for intensive and less limited nitrogen cycling.

There are increasing external environmental pressures on river water quality from agricultural runoff and other non-point sources such as atmospheric nitrogen inputs which increase the nitrogen load entering floodplains. In addition to the environmental stresses imposed on the floodplains, these systems have been exposed to several severe structural impacts, altering their character fundamentally (Tockner et al. 2010). More than 70% of the floodplain along the Danube and its major tributaries has been lost as a consequence of anthropogenic activity (Sommerwerk et al. 2009). Reduction in the number, area, and exchange conditions of inundation

areas has significantly decreased the nutrient and organic matter retention capacity along the river corridor, with major consequences for the both the riverine and coastal ecosystems (Schmidt 2001b). Restoration of large floodplains via surface water reconnection provides an opportunity to observe the effects of changing nitrogen and carbon pools on nitrogen cycling.

Controls on denitrification and alternative N pathways in floodplains

Nitrogen cycling is comprised of both oxic and anoxic pathways, but in this study the anoxic pathways of nitrate removal were investigated in detail. Denitrification, a particular form of microbial respiration, is a process controlled by O_2, NO_3, and C availability (Knowles 1982) which reduces nitrate (NO_3^-) to nitrite (NO_2^-), nitric oxide (NO), nitrous oxide (N_2O), and ultimately to dinitrogen (N_2) (Zumft 1997). Incomplete denitrification results in the production of N_2O, a greenhouse gas with 300-times the warming potential of CO_2 and a precursor molecule for ozone-depleting NO radicals in the stratosphere (Dickinson and Cicerone 1986, Bates et al. 2008).

Although nitrate loading is a significant problem, studies have shown that most of the anthropogenic nitrogen is removed before reaching the oceans, indicating that the riparian ecosystems are capable of removing large quantities of nitrogen (Howarth et al. 1988, Alexander et al. 2000, Peterson et al. 2001). Analysis of biogeochemical budgets indicates that river networks can remove 37–76% of the total N-input, mainly via denitrification, with a sizeable contribution by high-order river sections (Seitzinger et al. 2002a, Seitzinger et al. 2002b). With rates ranging from 0 to 345 μmol N m^{-2} h^{-1}, rivers systems are estimated to contribute approx. 1Tg N y^{-1} to the global N_2O emissions (Seitzinger 1988). Up to 80% of denitrification is estimated to occur in soils and freshwater systems (Galloway et al. 2008). Yet, despite the ability to remove large amounts of nitrate, increasing loads have been shown to increase the N_2O emissions in both field and laboratory experiments (Barnard et al. 2005, Verhoeven et al. 2006).

Other pathways of nitrate removal can be just as important as denitrification within anoxic sediments (Burgin and Hamilton 2007). Dissimilatory nitrate reduction to ammonia (DNRA) has the same environmental requirements as denitrification (anoxia, high nitrate and carbon substrate availability), but rather than a removal pathway, bio-reactive nitrogen is conserved and nitrate transformed into a more bio-available form (ammonium). Although DNRA has been reported as a significant pathway in marine and terrestrial systems accounting for 15-75% of nitrate removal

(An and Gardner 2002, Morley and Baggs 2010), it may be a minor route of nitrate removal in wetland systems (Matheson et al. 2002, Scott et al. 2008b). With restoration, the ratio of denitrification: DNRA may change along with the changing morphology and substrate availability (Fazzolari et al. 1998). Anammox, the anaerobic oxidation of ammonium coupled to nitrite reduction with N_2 as the end product, is present throughout the marine system, but its presence in floodplains is not well documented (Jetten 2001). Few studies have measured this pathway of nitrate removal in freshwater systems, let alone in riverine floodplains (Zhu et al. 2010).

Floodplains incorporate a range of active zones, both spatially from in-channel to terrestrial and temporally from constantly to rarely connected areas (Schiemer et al. 2001, Weilhoefer et al. 2008). The distance to the main channel and the regularity of surface connectivity, i.e. flooding, determine the duration and frequency of nutrient pulses to these retention areas throughout the year (Scott et al. 2008a, Scott et al. 2009, Fellows et al. 2011). The delivery patterns of carbon and nutrient inputs and the associated biogeochemical processes along river ecosystems are strongly related to surface connectivity (Preiner et al. 2008). While the input of nutrients, sediment and organic matter occurs mainly via surface flow from upstream, significant amounts of these materials are deposited during floods.

Flood pulsing

Biogeochemical processes, especially for nitrogen, are sensitive to the redox status of the soil. The area of water-substrate interface (i.e., water-sediment or wetland-upland length of contact) is positively correlated to the efficiency of nitrogen retention and use in river ecosystems. The frequency, duration, timing and intensity of floods directly affect nitrogen cycling in alluvial soils by controlling the duration of oxic and anoxic phases (Baker and Vervier 2004). Flooding duration is controlled by local topography (Benke et al. 2000); low areas are flooded more often and longer than higher ones, producing variations in biogeochemical patterns at the meter scale (Pinay et al. 1989, Pinay et al. 1999). Any change in natural water regimes will affect the biogeochemistry of riparian zones and floodplains as well as their ability to cycle and mitigate nutrient fluxes originating from upstream and upslope. Environmental disturbances (i.e. flooding) have been shown to have a major impact on biogeochemical cycling in wetlands by increasing the substrate availability and stimulate bacterial activity (Burns and Ryder 2001, Song et al.

2010). Flood pulses control organic carbon transformations and processes in floodplains and can trigger an increase of bacterial enzyme activity (Wantzen et al. 2008). The constant adaptation to changing hydrology and nutrient inputs occurring within in the floodplains create a variety of processes occurring at different scales and interfaces (Ward 1998, Orr et al. 2007, James 2010, Song et al. 2010).

Flooding events, as opposed to rainfall events, have the potential to provide substantial quantities of substrate for nitrogen and carbon cycling. Ultimately the end products of nitrogen cycling in riparian soils are controlled by the moisture regime, with important implications for floodplain productivity and management (Cavanaugh et al. 2006).

Implications for restoration and management

Numerous anthropogenic activities have led to river ecosystem fragmentation and habitat destruction, disrupting the structures and functions of these lotic ecosystems (e.g. Friedl and Wüest 2002). Within the Danube River Basin, about 80 % of all former floodplains have been lost as a consequence of river impoundments (WWF 1999). Reduced inundation areas have significantly decreased the nutrient and organic matter retention capacity along the river ecosystem, even altering coastal ecosystems (Schmidt 2001a). The deterioration of the functioning of river ecosystems has led to several rehabilitation and restoration measures in the last decade. Most have aimed at increasing the spatial heterogeneity of these ecosystems (Henry et al. 2002). Yet, a more integrated approach including restoration of landscape dynamics and key ecosystem processes such as carbon and nutrient retention is necessary (Pedroli et al. 2002, Hohensinner et al. 2004, Hernandez and Mitsch 2006, Hein et al. 2009).

Restoration by increasing surface water connectivity changes the abundance and diversity of the process facilitators - the microbial and phytobenthic communities (Rysgaard 1993, Cabezas et al. 2008), which will drive the biogeochemical processes. By altering the frequency, duration, period of occurrence, and variability of water levels, the water regime or surface water connectivity can directly affect nitrogen cycling in alluvial sediments and the sediment – water interface by controlling the duration of oxic and anoxic phases and thereby altering nitrification and denitrification rates (Groffman and Tiedje 1988, Hefting et al. 2004). The effects of altered water regime on the nitrogen cycling of river systems have been demonstrated at local scales (Hedin 1990, Hill et al. 2000b, Pinay et al. 2002, Alewell et al. 2008). The main challenge for scientists

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is to evaluate the effects of these changes at larger landscape-level scales and transfer this knowledge to decision makers and natural resource managers (Lamers et al. 2006).

Questions

This dissertation was based around the following questions and associated hypotheses:

1. Which environmental changes affect the users of NO_3 and what are their thresholds?
    1.1. The local conditions within the floodplain provide the specific "spot" characteristics necessary for denitrification (i.e. fine sediment, low oxygen conditions, sediment pH) while the Danube River is the main source of nitrate and dissolved organic matter.

2. What is the fate of NO_3 entering a restored and un-restored floodplain?
    2.1. Restoration via surface water reconnection would change the local conditions within the floodplain by increasing substrate input and reducing water retention times in the system. These changes were hypothesized to increase the overall rate of anoxic nitrate removal occurring in the restored floodplain compared to the degraded floodplain.
    2.2. Denitrification would be the dominant pathway of nitrate removal in floodplains. DNRA would be of secondary importance, but occurring mainly in disconnected areas. Anammox is not hypothesized to be of any importance.

3. When the concentration of NO3 entering the system through a flood pulse increases dramatically and suddenly (i.e. a pulse), what is its effect on these processes?
    3.1. Initially following the NO_3 pulse; there will be an increase in the denitrification rate and thus, the production of N_2O & N_2. However, because denitrifiers will preferentially use NO_3 instead of N_2O as a substrate, the concentration of N_2O will increase faster than that of N_2 after a period of time.

Methods

Site description

Two floodplain segments in the Danube River system were used to determine the effectively of floodplain connectivity as a stimulant for denitrification in different classes and types of connectivity. By comparing these floodplains on the micro-scale, it was possible to understand the impacts of restoration on the most basic level. With this knowledge, the ecological improvement of the floodplain was estimated.

The two floodplains, Lobau and Orth, are within the boundaries of the Alluvial Zone National Park, located downstream of the city of Vienna, Austria. In this area, the Danube River is a 9th order river with a drainage basin of 104 000 km^2. The flow regime has an alpine character with variable and stochastic patterns (regulated low discharge = 915 m^3s^{-1}, mean discharge = 1930 m^3s^{-1}, annual flood discharge = 5300m^3s^{-1}, 30 year max. flood discharge = 9340 m^3s^{-1}). Following the major regulation scheme in 1875, the Danube River was confined between flood protection dams, thus the main channel was disconnected from the adjacent floodplains (Chovanec et al. 2000). Restoration projects began in 1997 with the goal of reconnecting several floodplains to the main channel of the Danube (Hein et al. 1999, Schiemer et al. 1999a).

The Lobau floodplain covers an area of approximately 23 km². As no significant restoration measures have been undertaken within the Lobau floodplain, it is not integrated within riverine flow and in this study, considered as an altered and degraded floodplain. Aside from ground-surface water exchange and a controlled small water intake, the primary water exchange with the main channel takes place through an artificial 5m wide breach in the flood levee in the Lobau's south-eastern end. Positioned at river km 1908, the opening in the flood protection dam allows limited surface water connection between the main river and the Lobau at discharge above 1500 m^3s^{-1} (approx. 235 days $year^{-1}$). As the floodplain is connected at a downstream opening, floodwaters flow in an upstream direction into the side arms. When flood waters recede, the water discharges from the Lobau through the same opening back into the main channel of the Danube River. Due to the "bath tub" characteristic of the floodplain, flood waters move slowly into the backwater areas. The effective, active connections with sites in the floodplain to the Danube River have been significantly reduced, with highest connection occurring at the downstream portion of the floodplain.

In contrast, the reconnected and restored floodplain Orth, located downstream of the Lobau floodplain covering approximately 5.5 km², is characterized by very diverse flow conditions. Some side arms in this system have through-flow conditions just above riverine summer mean flow (2230 m^3s^{-1}), while others are connected only at much higher flow conditions. As part of the Danube River Restoration Project (Schiemer et al. 1999b), most of the historical retention structures present in the Orth floodplain have been removed, increasing the side-arm discharge significantly, as well as the duration of surface water connection to the main channel, i.e. connection duration (Tritthart et al. 2009). The three openings with the same width and depth as the floodplain channels (one at river km 1906.5 and two at river km 1905) and one outlet (river km 1902) connect parts of this side-arm system to the main river at discharges of 4400 m^3s^{-1} (approx. 7 days $year^{-1}$), 1500 m^3s^{-1} (approx. 235 days $year^{-1}$), and less than 900 m^3s^{-1} (approx. 365 days $year^{-1}$), respectively. The Orth floodplain is dominated by a channel-like system with high, steep, eroded banks. With the removal of the riverside embankments and controlled management, the Danube River is given the space to reshape the landscape in the Orth floodplain.

Overall study design

This study was comprised of three major parts, starting at the plot-scale, followed by the landscape scale, and finally the underlying micro-scale. In order to address Hypothesis 1.1 & 2.1, a field campaign was undertaken at the plot scale. Sites were selected in the side arms of the Lobau and Orth floodplains to encompass varying flowing and morphological characteristics based on the connectivity model created by Tritthart et al. (2009). Water and in-channel sediment sampling occurred during the growing seasons under periods of stable hydrological conditions when the Danube River was not experiencing a flood event. Potential microbial processing (substrate induced respiration and denitrification enzyme activity) was used to compare sites under controlled and unlimited nutrient conditions, and to furthermore assess the potential maximum rates of the in-situ microbial community. A detailed description of all the methods can be found in Welti et al. (2012b). Using the field campaign, a conceptual model using elucidating the landscape controls on potential microbial processing was created.

Based on the previous conceptual model, a modeling tool was developed to scale the plot measurements up to the landscape scale. Hydrological model simulations were coupled with

biogeochemical measurements in different sediment and water body types in order to address Hypothesis 2.1. The modeling tool combined steady-state hydrodynamic simulations with long-term discharge hydrographs to calculate water depths as well as statistical probabilities and event durations points connected to the Danube River (Tritthart et al. 2011, Welti et al. 2011).

In order to address the explicit pathways of nitrate removal (Hypotheses 2.2 & 3.1) two experiments were established in order to separate the effects of riverine nitrate input (Experiment 1) and changes in DOM composition (Experiment 2). Labeled ^{15}N-NO_3 was used to trace the pathways of removal through the water column and sediment. Detailed descriptions of the sampling and analysis can be found in Welti et al. (2012a).

Conclusions

The main conclusions, as reported in the supporting papers, can be summarized as follows:

1. Surface water connection, mediated by morphology regulates the potential denitrification rate and the ratio of N_2O to N_2 emissions.

   1.1. Re-establishment of surface water connection of a site resulted in changing the controls on sediment microbial respiration and denitrification, eventually impacting potential microbial activities

   1.2. Floodplain restoration would result in a series of morphological changes (ex. temperature, dissolved oxygen, and macrophyte distribution) resulting in an increase of substrate availability and ultimately more efficient N and C cycling, with an overall reduction of potential N_2O emissions.

2. The model outputs suggest that floodplains subject to frequent inundations can effectively and efficiently use inputs from the main river channel, resulting in complete denitrification and increased respiration.

   2.1. Increasing variability (i.e. inundation) in the floodplain would increase the efficiency of N biogeochemical cycling and especially denitrification

   2.2. Restoration measures should be aimed at increasing the hydrologic exchange patterns between different landscape elements (i.e. frequent inundation) in order to exploit the cycling capacity of a floodplain

3. Addition of riverine derived organic matter lowered the N_2O:N_2 ratio in the isolated site, whereas addition of floodplain derived organic matter increased the N_2O:N_2 ratio in the restored site.

   3.1. Demonstrated that increasing floodplain hydrological connection to the main river channel increases nitrogen retention and decreases nitrous oxide emissions.

   3.2. Prolonged connection to the river may increase the denitrification efficiency; however, surface water connections solely during floods will not increase the overall, long term denitrification efficiency as these sites do not respond quickly to an increase of NO_3.

Summary of Publications

1) Welti, N., E. Bondar-Kunze, G. Singer, M. Tritthart, S. Zechmeister-Boltstern, T. Hein, and G. Pinay. 2012. Large-Scale Controls on Potential Respiration and Denitrification in Riverine Floodplains. Ecological Engineering. in press.

The purpose of this paper is to evaluate the characteristics of surface water connection between side arms and the main river channel in a former braided river section and the role and degree of connectivity (i.e. duration of surface water connection) on the sediment biogeochemistry.

The primary objective of this study was to determine how changes in the physical gradients (i.e. physical elements in the landscape) related to the water delivery and discharge regime can affect the nitrogen and carbon cycles in floodplain ecosystems. More specifically, the aim of this paper is to determine how floodplain restoration, by increasing hydraulic exchange conditions between a large river main channel and its backwaters affects sediment and water quality as well as potential denitrification and respiration. The role of hydrology and local geomorphology on potential microbial processing in sediments of two river side channels was examined.

Potential microbial respiration (SIR) and denitrification (DEA) were measured over 2 years and compared between an un-restored floodplain of the Danube River with a restored floodplain of this river. The un-restored floodplain had higher autochthonous organic carbon contents in the sediments, which lead to higher SIR, DEA and emissions relative to the restored side arm system. In addition, these processes were highest in the least connected sites. Results suggest that surface water connection highly influences potential respiration. Surface water connection, mediated by morphology regulated the potential denitrification rate and the ratio of nitrous oxide (N_2O) to N_2 emissions, demonstrating the positive effects of restoration (increasing the surface water connectivity) in floodplain systems.

2) Tritthart, M., N. Welti, E. Bondar-Kunze, G. Pinay, T. Hein, and H. Habersack. 2011. Modelling highly variable environmental factors to assess potential microbial respiration in complex floodplain landscapes. Environmental Modelling & Software. 26:1097-1111.

The purpose of this paper was to create a modeling framework which combines hydrological models with measured biogeochemical data to predict floodplain connectivity and the related output pattern of sediment respiration. The predictive model integrates hydrology and morphology and is based on morphological input derived from LiDAR, bathymetric and terrestrial surveys, a long-term hydrograph of the Danube River, and biogeochemical and physical characteristics of sediment samples taken in the field.

The framework was comprised of three modules where data processing occurred; i) a hydrodynamic module to compute surface water elevations for characteristic river discharges; ii) a connectivity module, linking the previous module with a long-term hydrograph and performing an automatic event classification to yield connectivity properties; iii) an output simulation module which calculated the potential microbial respiration based on the best fit of the hydrological and morphological properties.

The duration of average connection or disconnection were found to be dependent on the morphology of the study area and the long-term hydrologic conditions. The Lobau floodplain was dominated by geomorphology due to the presence of retention structures, whereas the Orth floodplain was governed by hydrology. With respect to the relative changes of potential microbial respiration, lower discharges in the Danube River resulted in similarly low potential CO_2 output irrespective of floodplain morphology. Generally, areas of high activity were identified in areas with large water depths.

3) Welti, N., E. Bondar-Kunze, M. Tritthart, G. Pinay, and T. Hein. 2011. Nitrogen dynamics in complex river floodplain systems: effects of restoration. River Systems. DOI 10.1127/1868-5749/2011/0047

The purpose of this this paper was to use a hydromorphological model to assess areas of high potential denitrification rates and nitrous oxide release in a frequently and an infrequently connected floodplain system of the Danube River under different river discharge conditions

Hot spots of potential microbial respiration were found in areas of lower connectivity, if connected during higher discharges and areas of high water depths (Tritthart et al 2011). This original model was further expanded to include denitrification measurements. Based on the second model's projections, the decoupled floodplain was predicted to have more areas of high potential denitrification during mean and elevated discharges, but with more sites dominated by incomplete denitrification, resulting in higher N_2O emission. In the restored floodplain, frequently inundated, it was predicted that lower rates of denitrification would occur at lower river discharge levels, but with complete denitrification, resulting in N_2 production rather than N_2O. Both models suggest that floodplain subject to frequent inundations can more effectively and efficiently use inputs from the main river channel.

4) Welti, N., E. Bondar-Kunze, M. Mair, P. Lachouni, P. Bonin, W. Wanek, G. Pinay, and T. Hein. 2012. Mimicking floodplain reconnections and disconnections using ^{15}N mesocosm incubations. Biogeosciences. in preparation.

The purpose of this paper was to elucidate the effect of nitrate delivery and dissolved organic matter (DOM) quality on nitrate metabolism in floodplains.

A mesocosm experiment was set up using the isotope pairing technique and analyzed the effects of large, intact sediment cores under controlled conditions. Effects of changing nitrate additions and different dissolved organic carbon sources (assessed by fluorescence measurements) in two different sites were analyzed. The nitrate delivery regime and dissolved carbon content where changed to mimic disconnection and reconnection schemes. Using ^{15}N isotope techniques, the actual rates of denitrification, dissimilatory reduction of nitrate to ammonia, and anammox were measured. Restored sites had higher rates of denitrification dominated by N_2 production. Overall, floodplain disconnection promoted N_2O production, while reconnection promoted complete denitrification, resulting in a higher proportion of N_2 production. Dissolved organic carbon originating from the Danube River at medium flows, while lower in concentration, was higher in quality. The quality of dissolved organic quality changed within a flood event throughout the floodplains. Thus, the timing and discharge conditions of organic carbon input from the river main channel have an important implication for nitrogen cycling processes in the floodplain.

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Large-Scale Controls on Potential Respiration and Denitrification in Riverine Floodplains

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ABSTRACT

Restoration measures of deteriorated river ecosystems generally aim at increasing the spatial heterogeneity and connectivity of these systems in order to increase biodiversity and ecosystem stability. While this is believed to benefit overall ecological integrity, consequences of such restoration projects on biogeochemical processes per se (i.e. ecosystem functioning) in fluvial systems are rarely considered. We address these issues by evaluating the characteristics of surface water connection between side arms and the main river channel in a former braided river section and the role and degree of connectivity (i.e. duration of surface water connection) on the sediment biogeochemistry. We hypothesized that potential respiration and denitrification would be controlled by the degree of hydrological connectivity, which was increased after floodplain restoration. We measured potential microbial respiration (SIR) and denitrification (DEA) and compared a degraded floodplain section of the Danube River with a reconnected and restored floodplain in the same river section. Re-establishing surface water connection altered the controls on sediment microbial respiration and denitrification ultimately impacting potential microbial activities. Meta-variables were created to characterize the effects of hydrology, morphology, and the available carbon and nutrient pools on potential microbial processing. Mantel statistics and path analysis were performed and demonstrate a hierarchy where the effects of hydrology on the available substrates and microbial processing are mediated by the morphology of the floodplain. In addition, these processes are highest in the least connected sites. Surface water connection, mediated by morphology regulates the potential denitrification rate and the ratio of N_2O to N_2 emissions, demonstrating the effects of restoration in floodplain systems.

Key words: Floodplain restoration – Connectivity – Substrate induced respiration – Denitrification enzyme activity - Danube River - Path analysis

1 INTRODUCTION

At the catchment scale, rivers transport nutrients and organic matter from terrestrial and aquatic sources to coastal areas (Bennett et al. 2001; Seitzinger et al. 2002; Townsend-Small et al. 2005), produce and degrade organic matter during transport (del Giorgio and Pace 2008; Hedges et al. 2000), and constitute an important element in the global carbon cycle (Cole et al. 2007; Battin et al. 2009). Riverine landscapes, where biological and physical activities (ex: primary production and sedimentation) occur, constitute biogeochemical hot spots, in particular for nitrogen cycling (Fischer et al. 2005; Forshay and Stanley 2005; Hynes 1975; McClain et al. 2003; Naiman and Decamps 1997; Ren et al. 2000).

At the landscape scale, two fundamental principles regulate the cycling and transfer of carbon and nutrients in river ecosystems, particularly in large river floodplains (Pinay et al. 2002). The first principle relates to delivery patterns of carbon and nutrients into floodplain ecosystems. In floodplains of most large regulated rivers, inputs of sediment, nutrients, and organic matter occur primarily via surface flow (i.e. flooding), although groundwater transport and atmospheric deposition can also contribute high amounts of nutrients (Durisch-Kaiser et al. 2008; Tockner et al. 2000). River floodplains are recognized as important storage sites for sediments and associated nutrients mobilized from upstream catchments during floods (Forshay and Stanley 2005; He and Walling 1997). In addition to the magnitude, frequency and duration of floods, the transfer and storage of materials in floodplains is largely under the control of the surface water connectivity pattern within the riverine landscape (Brunet et al. 1994; Van der Lee et al. 2004; Burt 2005; Pinay et al. 2007). The second basic principle describes the geomorphological characteristics of floodplains which are defined, in this study, as the present morphology and the processes that shape it (ex. water-substrate contact, water-sediment interface). This is generally positively correlated to the efficiency of nutrient

retention and use in river ecosystems, and these positive relationships can occur both in the main channel itself and in the riparian and floodplain zones (Jones and Holmes 1996; Lefebvre et al. 2004; Pinay et al. 2009). Increasing the length or the duration of contact between water and substrates increases the biological use and thereby the total amount of nutrients cycled through the system (Sjodin et al. 1997), although this cycling capacity can be affected by the load itself (Mulholland et al. 2008). Similarly, the role of water levels, especially floods and flow pulses (Tockner et al. 2000), is important in determining the area available for water-substrate interactions. By changes in the frequency, duration, period of occurrence, and variability of water levels, the water regime or surface water connectivity can directly affect nitrogen cycling in alluvial sediments and the sediment – water interface by controlling the duration of oxic and anoxic phases and thereby altering nitrification and denitrification rates (Groffman and Tiedje 1988; Hefting et al. 2004). These factors create a mosaic of geomorphologic features that influence the spatial pattern and successional development of riparian vegetation (Hein et al. 2005; Roberts and Ludwig 1991; Salo et al. 1986) which in turn largely supports consumer biomass (Zeug and Winemiller 2008).

River systems can be strongly affected by natural disturbances or anthropogenic perturbations, such as dams, drainage, dredging, deforestation of riparian zones, and embankments. The two previously mentioned principles can be used to understand the mechanisms of how anthropogenic changes alter the biogeochemistry of riparian and instream zones as well as their ability to mediate nutrient fluxes originating from upstream (Bernot and Dodds 2005). In order to mitigate anthropogenic disturbance, river restoration and rehabilitation projects have been undertaken. Most projects have been aimed at increasing the spatial heterogeneity of these ecosystems in order to support higher habitat and biological diversity (Henry et al. 2002). Yet, a more integrated approach including restoration of vital ecological processes,

such as nitrogen cycling and retention, is necessary to recognize the biogeochemical role of floodplains (Hein et al. 2004; Hohensinner et al. 2004; Pedroli et al. 2002). Although nitrogen dynamics in floodplains have been well studied (Spink et al. 1998; Steiger and Gurnell 2003), restoration strategies specifically aimed at reducing nitrogen loads have been, until recently, limited to small streams (Cabezas and Comín 2010; Craig et al. 2008). The effects of altered water regime on the nitrogen cycling of river systems have been demonstrated at local scales (Hedin 1990; Hill et al. 2000; Pinay et al. 1995; Triska et al. 1993). The main challenge is now to evaluate the effects of these changes at larger landscape-level scales (Lamers et al. 2006).

The primary objective of this study was to determine how changes in the physical gradients (i.e. physical elements in the landscape) related to the water delivery and discharge regime can affect the nitrogen and carbon cycles in floodplain ecosystems. More specifically, the aim of our study is to determine how floodplain restoration, by increasing hydraulic exchange conditions between a large river main channel and its backwaters affects sediment and water quality as well as potential denitrification and respiration. We tested to what extent three major restoration variables can control sediment characteristics, water quality, and microbial activities: i) the type of connection to the main river channel (degraded or reconnected), ii) the average annual duration of connection and iii) the water age prior to sampling.

In this study, we examined the role of hydrology and local geomorphology on potential microbial processing in sediments of two river side channels. A restored and a degraded side arm system along a 10-km floodplain section of the Danube River downstream of Vienna, Austria were examined in this study. The two selected systems differed by the type of connection to the main river channel – disconnected and restored via reconnection (Lobau and

Orth, respectively). These two floodplain systems, while spatially close, vary greatly in their hydrology and geomorphology. Restoration via surface water reconnection changed the local conditions within the floodplain, by increasing substrate input and reducing water retention times in the system. These changes were hypothesized to increase the microbial processing occurring in a restored floodplain when compared to a degraded floodplain. Within these two floodplain systems we selected sites which differed by their average annual duration of connection and the water age before sampling. This gradient was selected in order to cover a representation of the different floodplain characteristics as they are influenced by hydrology (i.e. substrate availability, morphology, flow patterns). Potential microbial processing (substrate induced respiration and denitrification enzyme activity) was used to compare sites under controlled and unlimited nutrient conditions, and to furthermore assess the potential maximum rates of the in-situ microbial community.

2 MATERIALS AND METHODS

2.1 Sites description

Two floodplain segments of the Danube River were studied: the Lower Lobau and Orth (Figure 1). Both floodplains are located within the boundaries of the Alluvial Zone National Park, downstream the city of Vienna, Austria. In this area, the Danube River is a 9th order river with a drainage basin of 104 000 km^2. The flow regime has an alpine character with variable and stochastic patterns (regulated low discharge: 915 m^{3}s^{-1}, mean discharge: 1930 m^{3}s^{-1}, annual flood discharge: 5300 m^{3}s^{-1}, 30 year flood discharge: 9340 m^{3}s^{-1}). Following the major regulation scheme in 1875, the Danube River was confined between flood protection dams, thus the main channel was disconnected from the adjacent floodplains (Chovanec et al. 2000). Restoration projects began in 1997 with the goal of reconnecting

several floodplains to the main channel of the Danube (Hein et al. 2004; Schiemer et al. 1999).

The Lobau floodplain covers an area of approximately 23 km². As no significant restoration measures have been undertaken within the Lobau floodplain, it is not integrated within riverine flow and in this study, considered as an altered and degraded floodplain. Aside from ground-surface water exchange and a controlled small water intake, the primary water exchange with the main channel takes place through an artificial 5m wide breach in the flood levee in the Lobau's south-eastern end (Figure 1). Positioned at river km 1908, the opening in the flood protection dam allows limited surface water connection between the main river and the Lobau at discharge above 1500 m^3s^{-1} (approx. 235 days $year^{-1}$). As the floodplain is connected at a downstream opening, floodwaters flow in an upstream direction into the side arms. When flood waters recede, the water discharges from the Lobau through the same opening back into the main channel of the Danube River. Due to the "bath tub" characteristic of the floodplain, flood waters move slowly into the backwater areas. The effective, active connections with sites in the floodplain to the Danube River have been significantly reduced, with highest connection occurring at the downstream portion of the floodplain. Three major retention structures with culverts prevent the side arms from becoming completely dry during low flow periods, resulting in shallow lake-like conditions. The riparian forests are dominated by hardwood forests and agricultural relics; natural floodplain vegetation covers only a minimal portion of the floodplain itself (Burger and Dogan-Bacher 1999). *Phragmites sp* is generally present at all sites along the terrestrial aquatic boundary. As a heavily used recreational area, the Lobau is managed and maintained to provide access for bicyclists as well as larger trucks throughout, which use the paved roads to transport materials.

In contrast, the reconnected and restored floodplain Orth, located downstream of the Lobau floodplain covering approximately 5.5 km² (Figure 1), is characterized by very diverse flow conditions. Some side arms in this system have through-flow conditions just above riverine summer mean flow (2230 m^3s^{-1}), while others are connected only at much higher flow conditions. As part of the Danube River Restoration Project (Schiemer et al. 1999), most of the historical retention structures present in the Orth floodplain have been removed, increasing the side-arm discharge significantly, as well as the duration of surface water connection to the main channel, i.e. connection duration (Tritthart et al. 2009). The three openings with the same width and depth as the floodplain channels (one at river km 1906.5 and two at river km 1905) and one outlet (river km 1902) connect parts of this side-arm system to the main river at discharges of 4400 m^3s^{-1} (approx. 7 days $year^{-1}$) , 1500 m^3s^{-1} (approx. 235 days $year^{-1}$) , and less than 900 m^3s^{-1} (approx. 365 days $year^{-1}$), respectively. The Orth floodplain is dominated by a channel-like system with high, steep, eroded banks. High amounts of gravel and woody debris are transported within the restored channels, creating dynamic gravel beds and log jams in the channels. Due to the restoration efforts, this floodplain is not actively managed for recreational purposes and is perceived as a "wild" floodplain. With the removal of the riverside embankments and controlled management, the Danube River is given the space to reshape the landscape in the Orth floodplain. Sites within both floodplains are not only connected during flooding situations, but during a wide range of discharge levels, as previously noted.

2.2 Hydrology

Based on the results of a hydrodynamic model in the Orth floodplain (Tritthart et al. 2009) and a simplified hydrostatic flooding model in the Lobau (Tritthart et al. 2011), a hydrological connectivity model was developed prior to field sampling. The current morphology of the

floodplains was used in combination with a long-term hydrograph. A number of steady-state water surface calculations together with a long-term hydrograph (30 years) (Figure 2) were used in order to estimate both statistically averaged and event-based connectivity parameters: duration of connection, duration of disconnection, and frequency of connection (Tritthart et al. 2009). The average duration of disconnection described the duration (days) between connection events. From this model, the water age of the surface water (in days) was calculated for each site at the time of sampling. The water age, which has been corrected for a minimum velocity of 0.2 ms^{-1} required for particles to pass through the system without settling, described the age of the water as it passed through the sampling point (Hein et al. 2004). To calculate water age in the Lobau where bidirectional flow occurred, it was important to consider the flow direction: the water age was assumed to be zero throughout the rising limb of the hydrograph; once the peak of the hydrograph passed and the flow reverses to outflow conditions, no nutrients from the river could enter the system on a surface pathway; thus the water age was calculated from that point onwards.

The two first variables, i.e. type of connection and average annual duration of connection, were used for side arm restoration schemes, as they were defined and assessed for the technical descriptions of the measures. The third variable, i.e. the water age, is defined as the retention time of the surface water in the side arm system.

2.3 Field sampling

Fourteen sites were selected in the side arms of the Lobau and Orth floodplains, using the connectivity model, described in section 2.2 to encompass varying flowing and morphological characteristics. Ten sites were selected in 2006 and four additional sites were sampled in 2007 (Figure 1). In both years, water and in-channel sediment sampling occurred during the

growing seasons under periods of stable hydrological conditions (but not stagnant), when the Danube River was not experiencing a flood event. Triplicate sediment samples of 5-10 cm depth were taken randomly using a PVC corer (internal diameter 5 cm) in deep and shallow macrophyte-free areas within the floodplain side arm channel of each sampling site. Each triplicate sample was a homogenized mixture of 3-5 sediment cores from one location which were mixed to provide a representative sample of the sampling location. To estimate the amount of macrophytes and terrestrial leaf litter, sites were ranked on a 0-5 scale following Udy et al. (2006), with 0 when neither macrophytes nor leaf litter were present and 5 with 100 % coverage within a 10m² area. Water samples were taken at the same time using 5L containers. All samples were kept cool (< 10°C) while in transport back to the lab. Water and activity samples were analyzed within 24h of sampling. Sediment samples were stored frozen at -20°C until analyzed for their nutrient content. Electrical conductivity, dissolved oxygen (%), pH, and temperature of the surface water were measured using an HQ40d sonde (Hach Lange, Düsseldorf, Germany) at the time of sampling.

2.4 Sediment and water characteristics

Dry weight of the soil samples was determined by oven-drying sediments at 70°C to constant mass. Organic N and C concentration and isotope abundances were acidified (1M HCl) to remove inorganic C and measured with an elemental analyzer (EA 1110, CE Instruments, Milan, Italy) connected to an isotope ratio mass spectrometry IRMS (DeltaPLUS, Finnigan MAT, Bremen, Germany). Dried sediments were size fractioned using a sieve tower. Sediment D_{50} was calculated from the sediment particulate size. Organic matter content of the sediment fractions was determined as weight loss by ignition (LOI %) of dry sediment at 450°C for 4 hours. Nitrogen concentrations in the sediment were analyzed for $N-NH_4^+$, $N-NO_3^-$, and $N-NO_2^-$ using standard colorimetric methods (APHA 1998) for a continuous flow

analyzer (CFA, Systea Analytical Technology). Phosphorus fractions of inorganic P (HCl extraction), organic P (HNO_3 combustion), and soluble reactive P (H_2O extraction) were determined using a continuous flow analyzer (CFA, Systea Analytical Technology) (Ruban et al. 2001). From each site, a 50ml water sample was taken and filtered through a GF/F (Whatman) filter to analyze P-PO_4 N-NH_4, N-NO_3, and N-NO_2 using a continuous flow analyzer (CFA, Systea Analytical Technology) and standard colorimetric methods (APHA 1998).

2.5 Potential respiration and denitrification

Potential denitrification enzyme activity (DEA) was measured according to Smith and Tiedje (1979). Ten grams (fresh weight) subsets of sediment samples were weighed into 100ml serum flasks, which were made anoxic by flushing the flask atmosphere with N_2. The flask contents were incubated with 10% (v/v) acetylene to allow the accumulation of denitrified nitrogen as N_2O, after adding 1 mg C g^{-1} sediment (added as glucose) and 0.2 mg N g^{-1} sediment (added as KNO_3). Denitrification rates were calculated as the rate of N accumulated as N_2O in the headspace after 4 h in dark at 25 °C and analyzed by gas chromatography with ^{63}Ni electron capture detector (HP 5890II GC). DEA was also measured under the same conditions but without acetylene to determine the proportion of N denitrified as N_2O during the assay (DEA_{N2O}) and analyzed by gas chromatography to quantify N_2O concentrations (AGILENT 6890N, Santa Clara, U.S.A., connected to an automatic sample-injection system (DANIHSS 86.50, Headspace-sampler, Cologno Monzese, Italy).

Substrate induced respiration (SIR) was measured according to Beare et al. (1990) by incubating 10 g fresh weight of sediment with 2 mg glucose-C g^{-1} sediment in a 100ml serum flask. SIR was calculated as the accumulation of CO_2–C in the flask during incubation after

4 h incubation at 25 °C in the dark per gram of sediment (DW) and per hour, using the gas chromatograph Agilent 6890N.

2.6 Statistics

All measured processes and sediment characteristics (chemical and physical) were compared between floodplains using Mann Whitney U tests with the SPSS software package.

We considered local physical gradients, nutrient availability, and carbon availability as explanatory links between hydrology and ecosystem processes (i.e., potential respiration and potential denitrification). Each of these quantities can be regarded as a meta-variable which is described by a set of explicitly measured and correlated variables. In fact, we expressed each meta-variable as a matrix of pairwise dissimilarities between two sampling sites. This approach efficiently integrates information from the various variables needed to account for the complexity of our study system. We then used Mantel and partial Mantel (controlling for effects of hydrology) statistics to test for associations between these meta-variables. Further, we used causal modeling on dissimilarity matrices (i.e., path analysis based on Mantel statistics treated as correlation coefficients) to relate the various meta-variables in the hypothesized causal framework (Legendre and Legendre 1998). All tests and path analysis were performed for both areas. Mantel statistics do not have to be large, i.e. close to 1 or -1, to be statistically significant. Significance of path coefficients was assessed by randomizing all involved matrices using 10^4 permutations, building randomized distributions for each path coefficient, and computing probabilities for observed path coefficients with the percentile method (Manly 2006). All calculations were done in R 2.9. (R-Development-Core-Team 2010), using the packages vegan (Oksanen et al 2010) and sem (Fox et al 2010).

3 RESULTS

3.1 Hydrological and physical conditions

The two sampling years were hydrologically different (Figure 3). In 2006, three flood events in April, June and August exceeded the level of an annual flood; of these, April and August floods were characterized by a statistical return period of 1 in 10 years, respectively. In 2007, however, the annual flood level was exceeded only once (in September) reaching a statistical return period of approximately 1 in 15 years. With this one annual flood event and average discharge, 2007 was similar to the long term discharge pattern (Figure 2). In both the degraded (Lobau) and restored (Orth) side arms, the average connection ($p=0.068$) was not significantly different between the two years (Table 1); however, the duration of disconnection was significantly shorter in the restored section ($p<0.05$).

3.2 Comparison of the side arm systems with different connection types

Sediment N and P pools varied between the two side arm systems (Table 1). Significant differences were observed between the two systems in the water column and sediment for $N-NH_4$, $N-NO_3$, and $N-NO_2$ (water only). Concentrations of $N-NO_3$, $N-NO_2$, and $N-NH_4$ in the sediment were higher in the Orth floodplain than in the Lobau floodplain (Table 1). The same trend was observed in the water column, except for $N-NH_4$ which was significantly higher in the Lobau floodplain. Similarly, concentrations of SRP in the sediment were lower in the Orth side arms, although not significantly (Table 1). The sediment C: N ratio was significantly higher in the Orth floodplain (Table 1). Significantly lower water temperatures and higher dissolved oxygen concentrations were observed in the Orth side arms than in the Lobau (Table 1). The average grain size and mean surface water pH were significantly different

between the two floodplain systems. No significant difference was observed for mean electrical conductivity between the systems.

Parameters related to the quality of the sediment organic matter and microbial activities presented significant differences between the two floodplains types (Figure 4). The percentage of organic matter (Figure 4A) in the sediment was significantly higher in the degraded system, than in the restored floodplain. Organic matter content of the sediment did not only differ significantly between sites in terms of concentration, but also in terms of quality. Indeed, the $\delta^{13}C$ of the organic matter content was significantly lower in the Lobau than in Orth (Figure 4B), while the $\delta^{15}N$ signature was significantly higher (Figure 4C). In the degraded section, higher and more variable rates of SIR in the sediment were measured (mean 1678.5 mg CO_2 m^{-2}h^{-1}) compared to the restored system (mean 471.6 mg CO_2 m^{-2}h$^-$) (Figure 4D). Similarly, average rates of sediment DEA presented higher average rates and higher variance (F = 34.903, p<0.01) in the degraded system (mean 48.70 mg N-N_2O m^{-2}h^{-1}) compared to those in the restored system (mean 6.23 mg N-N_2O m^{-2}h^{-1}) (Figure 4E). The range of the ratios of DEA: DEA$_{N2O}$ was also larger in the degraded floodplain (mean 0.48) than in the restored floodplain (mean 0.26) (Figure 4F).

3.3 Influence of connectivity-related parameters

A weak, but significant trend was observed for sediment organic matter concentration, SIR, DEA, and DEA: DEA$_{N2O}$ decreasing as a function of average duration of connection (Figure 5A, D, E, & F), while $\delta^{13}C$ and $\delta^{15}N$ decreased slightly to an average of -25‰ and +2‰ respectively, although not significant (Figure 5B & C). When considering these variables (sediment organic matter content, $\delta^{13}C$, $\delta^{15}N$, SIR, DEA, DEA: DEA$_{N2O}$) in relation to the water age the patterns change (Figure 6). Although the same weakly decreasing trend for

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sediment organic matter content was observed with increasing water age, $\delta^{13}C$ increased significantly, albeit weakly, with increasing water age and $\delta^{15}N$ began to show a weakly significant decreasing trend (Figure 6A, B, & C). No significant relationships were found for the remaining variables (Figure 6D, E & F).

3.4 Environmental control of potential microbial processing

The weak linear relationships between the singular connectivity parameters and sediment characteristics and potential microbial activity and the high co-correlation between individual variables led to the creation of multivariable matrices (Table 2). Most of the links in the suggested causal framework were described by multivariate datasets. Information content of these various complex datasets with heterogeneous as well as co-linear variables was condensed to a limited number of dissimilarity matrices by computing Euclidean distances between all sampling sites based on standardized variables selected to describe the meta-variables: Hydrology, Physical Gradients, carbon sources (Carbon), nutrient concentrations (Nutrients) and potential processes (Output) (DEA and SIR, respectively) (Table 2).

Mantel statistics could identify a direct effect of Hydrology on the Output (as DEA) (Mantel $r = 0.079$, $P<0.001$, Figure 4) and on SIR (Mantel $r = 0.186$, $P<0.001$, Table 3) as well as on the physical characteristics of the floodplain ($r = 0.503$), the sediment N and P pools ($r = 0.224$) and the C sources ($r = 0.141$), all at $P<0.001$ (Table 3). Partial Mantel tests controlling for the effect of hydrology showed a significant influence from the floodplain physical characteristic on the C sources ($r = 0.170$), SIR ($r = 0.147$) and DEA ($r = 0.122$), all at $P<0.001$ (Table 3). Path analysis (Figure 7) based on Mantel statistics computed among meta-variables suggested a strong influence of hydrology on physical gradients, which furthermore influence DEA and the ratio of DEA_{N2O}: DEA. Both, nutrients and carbon were

shown to be controlled by a similar, but weaker pathway, yet neither nutrients nor carbon participated in the determination of DEA. Path analysis based on Mantel statistics using SIR as the output variable (Table 3) suggested the same pathway of influence of hydrology on physical gradients which influenced SIR (Figure 8). However, a weaker direct link was calculated where hydrology directly influences SIR.

4 DISCUSSION

4.1 Restored versus degraded connection to the main river channel

Restored surface water connection entailed fast flowing water (mean flowing velocities > 1m s^{-1}) in the side arms during floods with larger grain size sediment deposits, whereas the degraded and decoupled surface connection to the main channel river channel entailed gradual flooding with low flow velocity, thus depositing fine sediments in the downstream areas of the floodplain (Reckendorfer and Hein 2006). Due to these differences in flow, restored connection led to lower water temperature and higher dissolved oxygen concentration (Table 1). The higher organic matter content measured in the degraded system (Lobau) (Figure 4A) most probably originated from autogenic sources, i.e. the riparian forest and macrophytes present in the area. The importance of autogenic organic carbon in the degraded side arm system was supported by the lower δ^{13}C value of organic matter in the sediments at Lobau sites with short connection periods (Figure 4B). The higher δ^{13}C values measured in restored sites together with their very high variability, independent of the average connection time (Figure 5B), suggested that organic matter in these restored sites was mostly controlled by riverine transported organic matter and had potentially a more recalcitrant nature (Hein et al. 2003; Aspetsberger et al. 2002). Sustained higher potential microbial activity in the sediment was confirmed by higher SIR and DEA (Figure 4D & 4E), similar to results presented from the restored Baraboo River floodplains (Orr et al. 2007). Higher

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observed SIR and DEA in degraded floodplain sediments implied that such systems could potentially remove more carbon and nitrogen. However, the actual rates may be substrate limited due to a lack of inputs from the Danube River - the main source of substrates. Similar patterns between geomorphological distributions and potential denitrification have been shown between riverine and backwater sites in the Upper Mississippi, where backwater areas exhibited higher DEA than riverine sites despite receiving less nitrate inputs from the Mississippi (Richardson 2004).

A higher $\delta^{15}N$ and total organic N (NO_3 and NH_4) in the sediments from the degraded floodplain (Figure 4C) supports our result pointing to higher DEA in degraded systems. In the absence of organic pollution such as manure or waste water, the dominant process contributing to higher $\delta^{15}N$ could be a consequence of faster N cycling and higher denitrification activity, which fractionates between the two N isotopes and preferentially removes the lighter isotope from the sediment. Since $\delta^{15}N$ was not measured from NO_3 or NH_4 separately, it can only be considered as a mixture of present organic N pools. Positive shifts have been shown to represent higher nitrogen cycling in lacustrine and marine systems (Lehmann et al. 2004; Teranes and Bernasconi 2000). This trend is only representative when comparing the two ecosystems as neither the duration of connection nor the water age can explain the observed patterns.

The average ratio of potential N_2O to N_2 emission (DEA: DEA_{N2O}) was similar in both systems; yet, in the degraded system larger variation of this ratio as well as higher rates of potential emissions (DEA) were measured. Therefore, the degraded system could support higher potential denitrification dominated by N_2O emissions (Figure 4). The domination of N_2O in the degraded site could be due to the high NH_4 concentrations measured in the

sediment. When NO_3 is limiting, the last step of denitrification ($N_2O \rightarrow N_2$) will be limited as this is the most energy dependent step (Morely and Baggs 2010). In systems where the microbial community is conditioned for low NO_3 concentrations, incomplete denitrification may be the dominant pathway. This tendency towards incomplete denitrification has major implications for the greenhouse gas balance of the system. Higher rates of denitrification resulting in N_2O production mean that during floods the degraded site is a source of N_2O whereas the restored site would be able to transform the excess NO_3 to N_2, resulting in a net gain of ecosystem services. As the degraded floodplain is 23 km^2, a reduction of N_2O emissions following restoration would be of a considerable magnitude (Verhoeven et al 2000).

4.2 Geomorphologic controls

A detailed analysis of the relationship between average annual duration of connection of the side arms to the sediment organic matter quantity and potential microbial activities revealed a decrease of these variables with an increase of connection, both in terms of average value and variability (Figure 5). Interestingly, this pattern was stronger for the degraded side arm system (filled circles). In the restored side arm system (open circles), the percentage of organic carbon remained low regardless the average duration of connection. The high variability in percentage of organic carbon (Figure 5A) at sites with short duration of connection in Lobau could be interpreted as stronger influence of local environmental conditions (e.g., the type and density of riparian and instream vegetation) at these backwater sites with prolonged periods of disconnection. The higher variability of organic matter quantity was associated with a higher variability of potential respiration (SIR), but not DEA, especially in mostly disconnected sites (less than 5 days of connection per year; Figure 5D). High rates (SIR only) and variability of SIR and DEA were significantly related to the duration of connection (Figure 5D & E). The

differences in overall hydrology changed the sediment environmental conditions, which in turn could cause shifts in the microbial community composition (Gutknecht et al. 2006). This study could not determine whether this high variability of response in long term disconnected sites was the result of a genetically different microbial community or simply a difference in density.

Altering the flow patterns entering the side arms not only changed the physical area (morphology) of the system, but also changed the delivery patterns of carbon and nutrients. The inherent hydrologic and morphologic heterogeneity of the two floodplains makes it difficult to use singular linear relationships to describe large-scale controls on potential microbial processing. The path analysis revealed that Hydrology factors directly affected SIR and nutrient content in sediments (Figure 7B). Yet, more importantly, the hydrology strongly influenced the side arm physical characteristics, which in turn, significantly controlled the available carbon and nutrient sources (Figure 7A & B). This demonstrated that flood regime was not the only variable which controlled biogeochemical processing; the overall morphology of the floodplain system was influencing these biogeochemical processes, too. This supported Boyer et al. (2006) who argued that hydrological and physical characteristics were a major controlling factor in N cycling in aquatic systems. By restoring surface water connections, the river can change the morphology of the floodplain which will further influence the local substrate availability for respiration and denitrification (Amoros 2001). Even though the path analysis did not point to a direct relationship between the available nutrient and carbon pools and DEA, there will be a change in the available substrates following restoration as suggested in the observed changes along the connectivity gradients presented (Figures 4 - 6). The absence of this link in the path diagrams is most likely due to

the method of measurement used. DEA and SIR are just estimates of the potential activity and are measured under saturated conditions, thus separating the *in situ* nutrient conditions.

Due to the network of factors influencing each other, our results did not single out one main variable that drives the link between morphology and microbial processing. Using one single parameter to explain a biogeochemical reaction that is the result of several variables underestimates the complexity and heterogeneity of floodplains and the effects of restoration. The absence of a clear relationship between sediment characteristics and potential microbial activities on the one hand, and the water age before sampling on the other hand (Figure 6 & 7A), supports the idea that it is the combination of the type of connection and morphological characteristics which are the main drivers of sediment quality and consequently, microbial processes. Modeling of potential respiration at the same site suggested that sites of high activity were found in areas of lower connectivity if connected during higher discharges and areas of high water depth (Tritthart et al. 2011). The results suggest that the local morphology coupled with the hydrologic regime at the landscape scale create the conditions necessary for microbial processing. Restoration of floodplains via surface water reconnection would return the necessary substrate inputs to the system. Frequent and constant riverine connections could increase denitrification efficiency, as suggested by the reduced N_2:N_2O ratios in the restored floodplain. Alteration of vegetation patterns (ex. appearance of floating vegetation in less connected areas; increased leaf litter in gouged channels) caused by changes in hydrology and morphology may also drive sediment quality changes and ultimately impact the conditions for microbial processing.

5 CONCLUSION

Large river floodplain restorations often imply reconnection of preexisting side arms to the main channel by partial removal of embankments or levees. Most of these reconnection schemes are aimed at enhancing biodiversity by creating a more dynamic hydrological regime in the floodplain. In this study we evaluated the importance of restoring the connection of side arms to their main river channel (i.e. increasing annual average duration of connection and decreasing water age) on sediment biogeochemical characteristics and their effects on potential microbial activities. The path diagram illustrated a hierarchical structure that suggested that the morphology of a specific site mediates the influence of the main source water (riverine inputs) for DEA and the carbon and nutrient conditions in the sediment. By re-establishing surface water connection of a site, the controls on sediment microbial respiration and denitrification were changed, eventually impacting potential microbial activities. Floodplain restoration would result in a series of morphological changes (ex. temperature, dissolved oxygen, and macrophyte distribution) resulting in an increase of substrate availability and ultimately more efficient N and C cycling, with an overall reduction of potential N_2O emissions. Further quantification of these links between the type and duration of connection between side arms and main channel, including the hyporheic zone, measurable at large scale, and microbial processes, measurable at micro-scale, should allow quantifying the effects of floodplain restoration on nutrient cycling in the river systems.

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Table 1

Floodplain	N	Duration Connection	Duration Disconnection *	Depth	Temperature *	pH *	Conductivity	Sediment D_{50} *	DO *	Leaf Litter	Macrophytes *
		Days	Days	mm	°C		µs cm^{-1}	mm	mg l^{-1}	Rank	Rank
Degraded	78	10.31 (10.34)	107.89 (211.71)	1.52 (0.93)	15 (5)	7.5 (0.49)	491 (65)	0.32 (0.84)	7.62 (2.5)	3 (1.5)	3 (1.4)
Restored	57	10.05 (5.32)	58.02 (80.72)	1.02 (0.70)	10.87 (4.32)	7.70 (0.34)	517 (130)	0.30 (0.93)	10.05 (2.74)	3 (0.7)	1 (1.1)

Floodplain	N	N-NO$_3$ *	N-NO$_3$ *	N-NO$_2$	N-NO$_2$ *	N-NH$_4$ *	N-NH$_4$ *	P$_{tot}$	SRP	SRP	C:N *
		mg kg dry sediment^{-1}	µg L^{-1}	mg kg dry sediment^{-1}	µg L^{-1}	mg kg dry sediment^{-1}	µg L^{-1}	mg kg dry sediment^{-1}	µg L^{-1}	mg kg dry sediment$^-$	
Degraded	78	4.8 (7.4)	299 (287.1)	0.4 (0.7)	3.7 (2.8)	208.2 (390.4)	26.0 (15.2)	773.1 (1174.6)	6 (8.0)	1.4 (2.0)	10.4 (2.1)
Restored	57	6.7 (4.5)	766 (658.8)	0.2 (0.2)	8.0 (7.6)	41.3 (56.1)	69.0 (114.1)	506.8 (285.8)	5 (5.2)	0.7 (0.5)	17.3 (6.6)

Table 2

Physical	Hydrology	Nutrients	Carbon	Output	Output
Mean Depth Water Body (m)	Duration of Connection (days)	N pools in sediment and water $(N\text{-}NO_3^-, N\text{-}NH_4^+, N\text{-}NO_2^-)$ (mg kg dry sediment^{-1} & mg l^{-1}, respectively)	Organic material in sediment (%)	DEA (mg N m^{-2} h^{-1})	SIR (mg CO$_2$ m^{-2} h^{-1})
Water Temperature (°C)	Duration of Disconnection (days)	P pools in sediment and water (PO_4^+, P_{tot}, SRP) (mg kg dry sediment^{-1} & mg l^{-1}, respectively)	$\delta^{13}C$ in sediment	Ratio DEA$_{N2O}$:DEA	
Conductivity (μS/m)	Connection (days year^{-1})	C:N in sediment	Present Macrophytes (rank)		
Sediment Size (D50) (mm)	Water Age (days)	$\delta^{15}N$ in sediment	Litter Coverage (rank)		
Dissolved Oxygen (%)					
pH					

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Table 3

	Physical gradients	Nutrients	Carbon	DEA	SIR
Hydrology	**0.503** **P<0.001**	**0.224** **P<0.001**	**0.141** **P<0.001**	**0.079** **P<0.05**	**0.187** **P<0.001**
Physical gradients		**0.085** **P<0.001**	**0.217** **P<0.01**	**0.145** **P<0.001**	**0.219** **P<0.001**
Nutrients	0.085 P=0.05		**0.398** **P<0.001**	-0.054 P=0.80	-0.066 P=0.89
Carbon	**0.170** **P<0.01**	**0.380** **P<0.001**		0.055 P=0.13	-0.059 P=0.91
DEA	**0.122** **P<0.01**	-0.07 P=0.91	0.04 P=0.19		
SIR	**0.147** **P<0.01**	-0.114 P=0.99	-0.088 P=0.99		

Figure 1: Map of the Lobau (degraded) and Orth (restored) floodplains, located downstream from Vienna, Austria. Sampling sites are marked with stars and openings to the Danube River marked with arrows and their respective river km. Flow direction of the Danube River marked with dashed arrows.

Figure 2: Thirty year (1977-2007) hydrograph for the Danube River. Horizontal lines represent connection discharges for the different connection points (upper line annual flood 5300 m^3s^{-1}, mid line summer mean low flow 2230 m^3s^{-1}, lower line 1500 m^3s^{-1}). (Data source: via donau and the Austrian Federal Ministry for Agriculture, Forestry, Environment and Water)

Figure 3: Hydrograph of the Danube River from January 2006 to January 2008, encompassing the study period. Discharges are presented as hourly mean values. Horizontal lines represent connection discharges for the different connection points (upper line annual flood 5300 m^3s^{-1}, mid line summer mean low flow 2230 m^3s^{-1}, lower line connection threshold for Lobau floodplain 1500 m^3s^{-1}) (Data source: via donau and the Austrian Federal Ministry for Agriculture, Forestry, Environment and Water)

Figure 4: Comparison of average percentage of sediment organic carbon content (A), $\delta^{13}C$ (B), $\delta^{15}N$ (C), SIR (D), DEA (E) and ratio of potential N_2O to N_2 emission (F) between the degraded system (n= 65) and the restored system (n= 34) floodplain systems. Box lines indicate upper and lower quartiles. Whiskers extend to the 95th and 5th percentiles. Mann Whitney U values between the sites and their significance are noted on each figure.

Figure 5: Average percentage of sediment organic carbon content (A), $\delta^{13}C$ (B), $\delta^{15}N$ (C), SIR (D), DEA (E), and ratio of potential N_2O to N_2 emission (F) as a function of mean annual duration of connection with the main Danube River channel. Filled circles represent degraded sites (n=65) while open circles represent restored sites (n=34). The r² and significance (*p*) for the linear function is noted on each figure.

Figure 6: Average percentage of sediment organic carbon content (A), $\delta^{13}C$ (B), $\delta^{15}N$ (C), SIR (D), DEA (E), and ratio of potential N_2O to N_2 emission (F) as a function of the water age in the study sites. Filled circles represent degraded sites (n=65) while open circles represent restored sites (n=34). The r² and significance (*p*) for the linear function is noted on each figure.

Figure 7: Path diagram depicting relationships among meta-variables described by dissimilarity matrices. Path coefficients are computed from Mantel statistics. Data of both floodplains Lobau and Orth were used simultaneously with A) DEA and $N_2O:N_2 + N_2O$ or B) SIR as the output meta-variable. For significant path coefficients, line width is proportional to the magnitude of the presented path coefficient. P values are presented as p<0.05*, p<0.01**, p<0.001***.
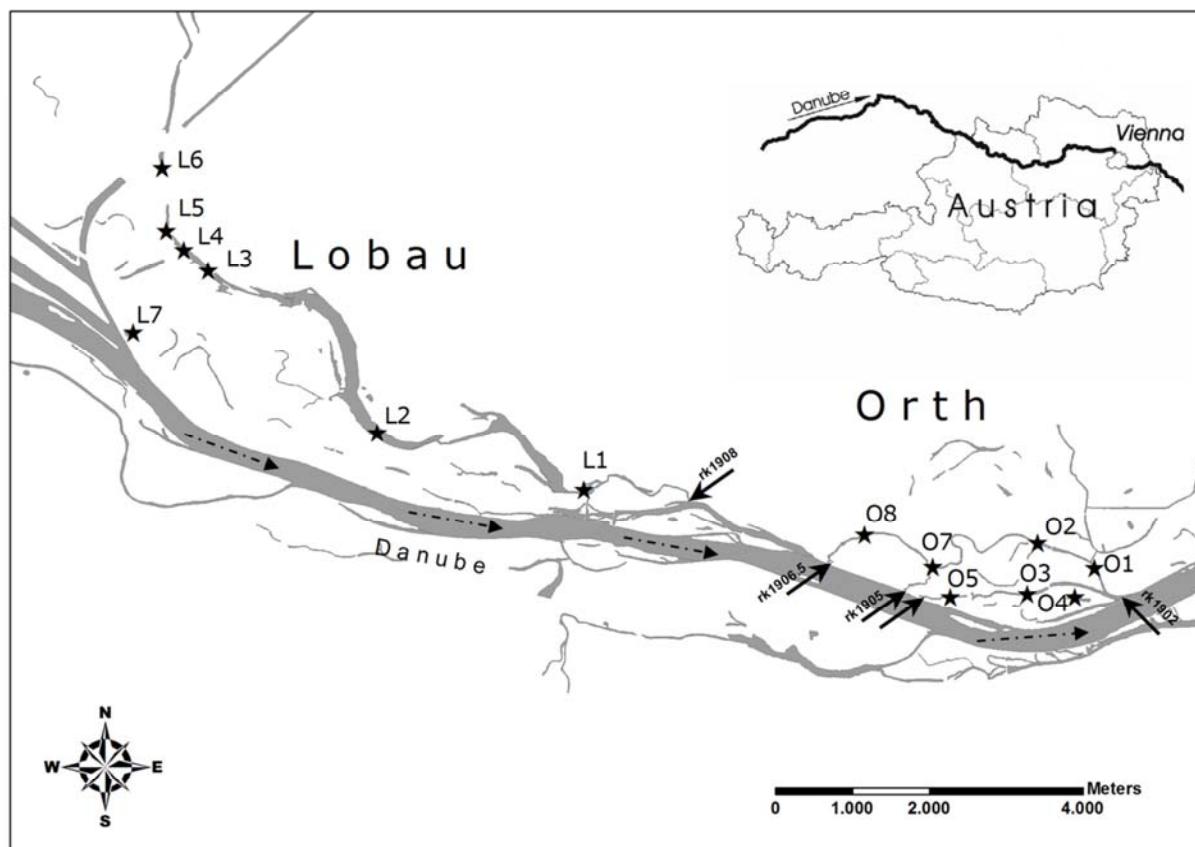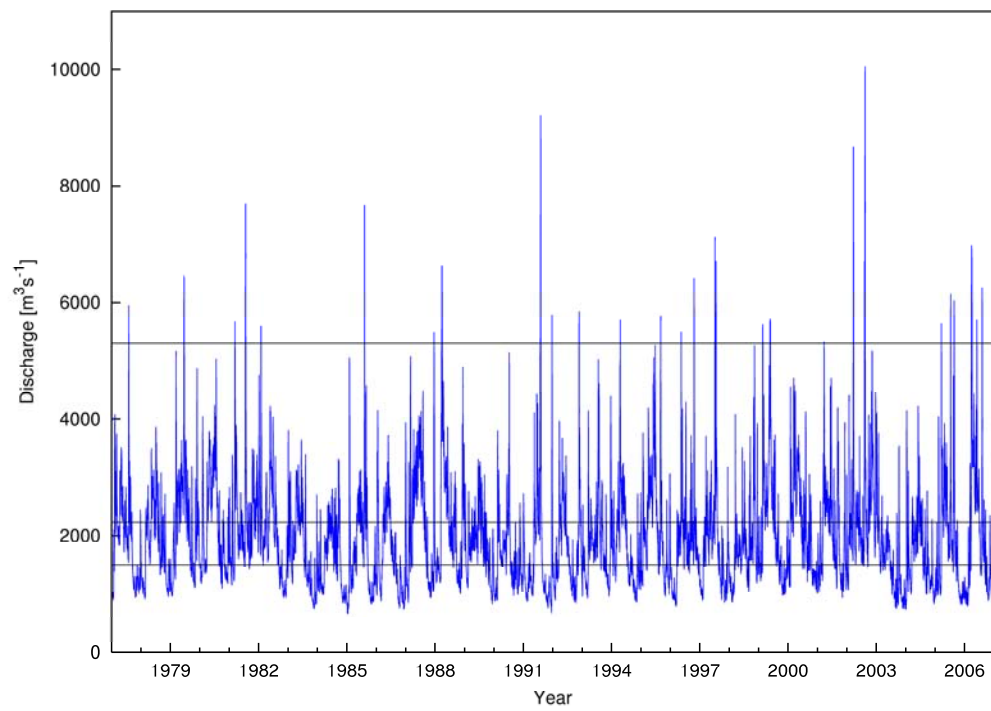
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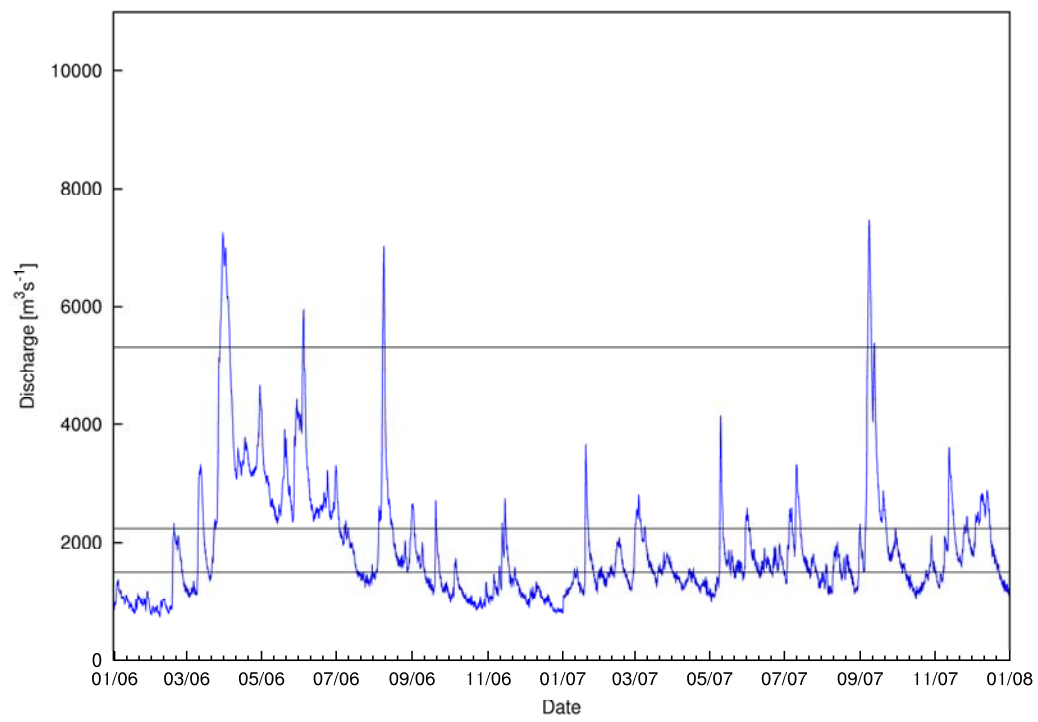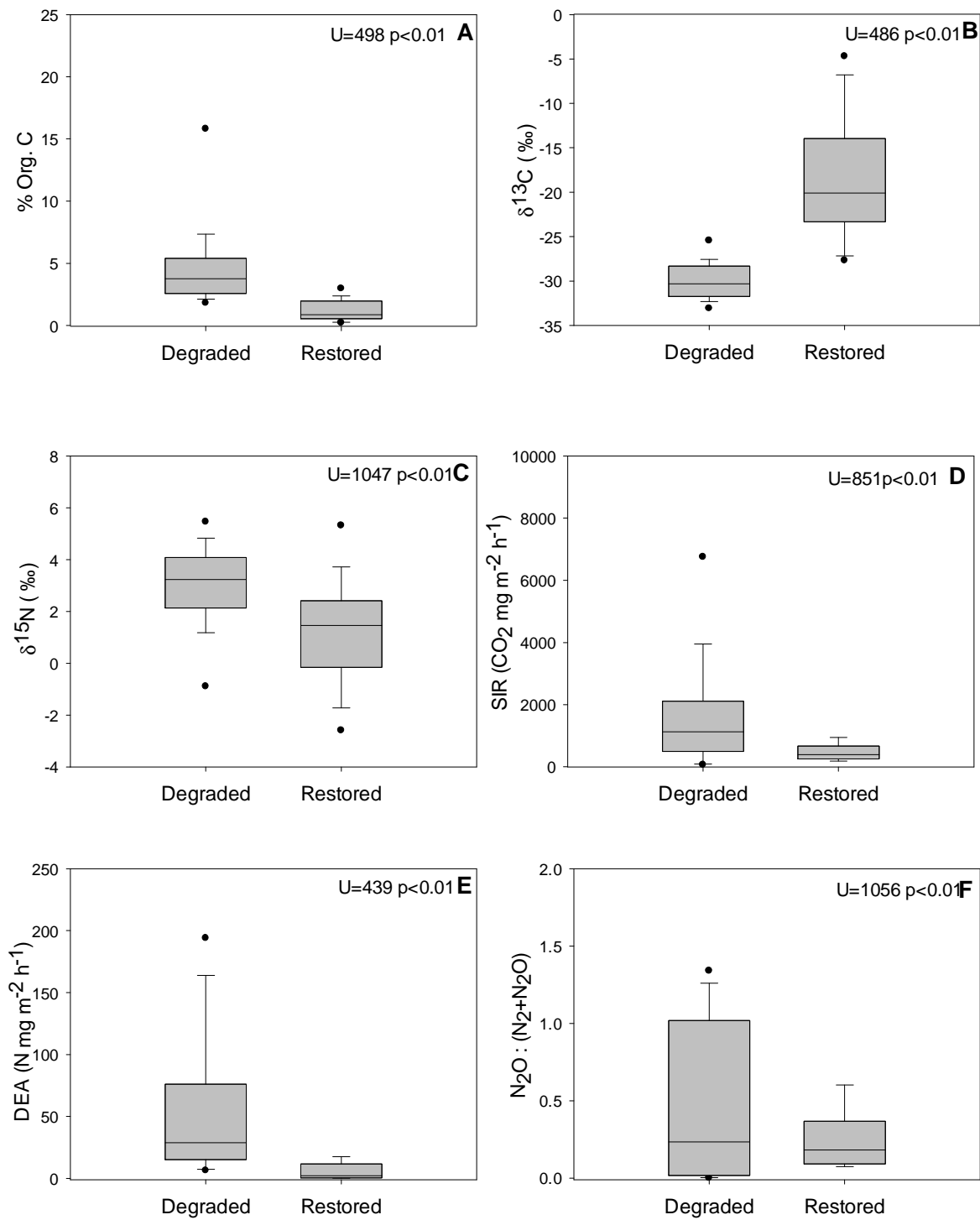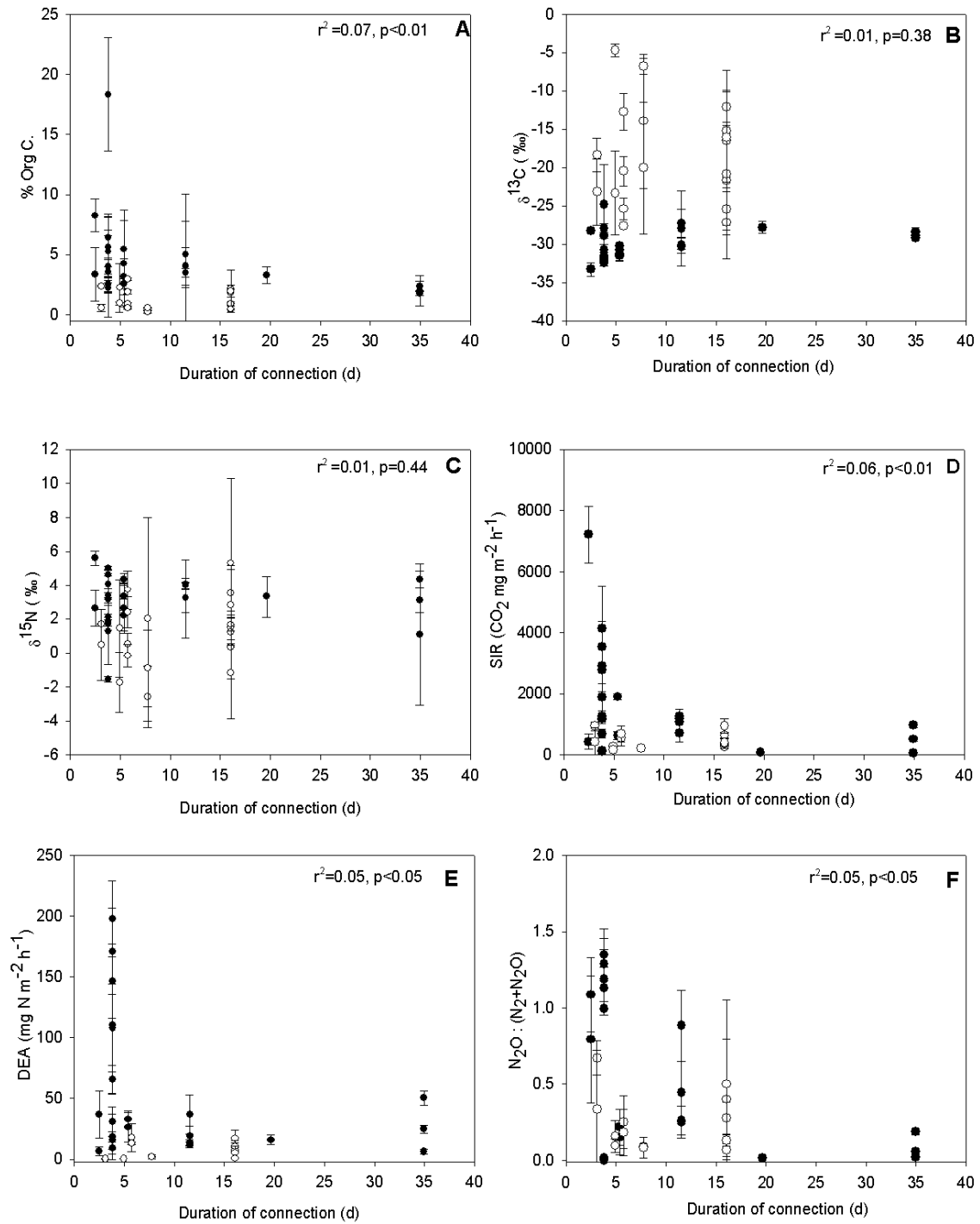
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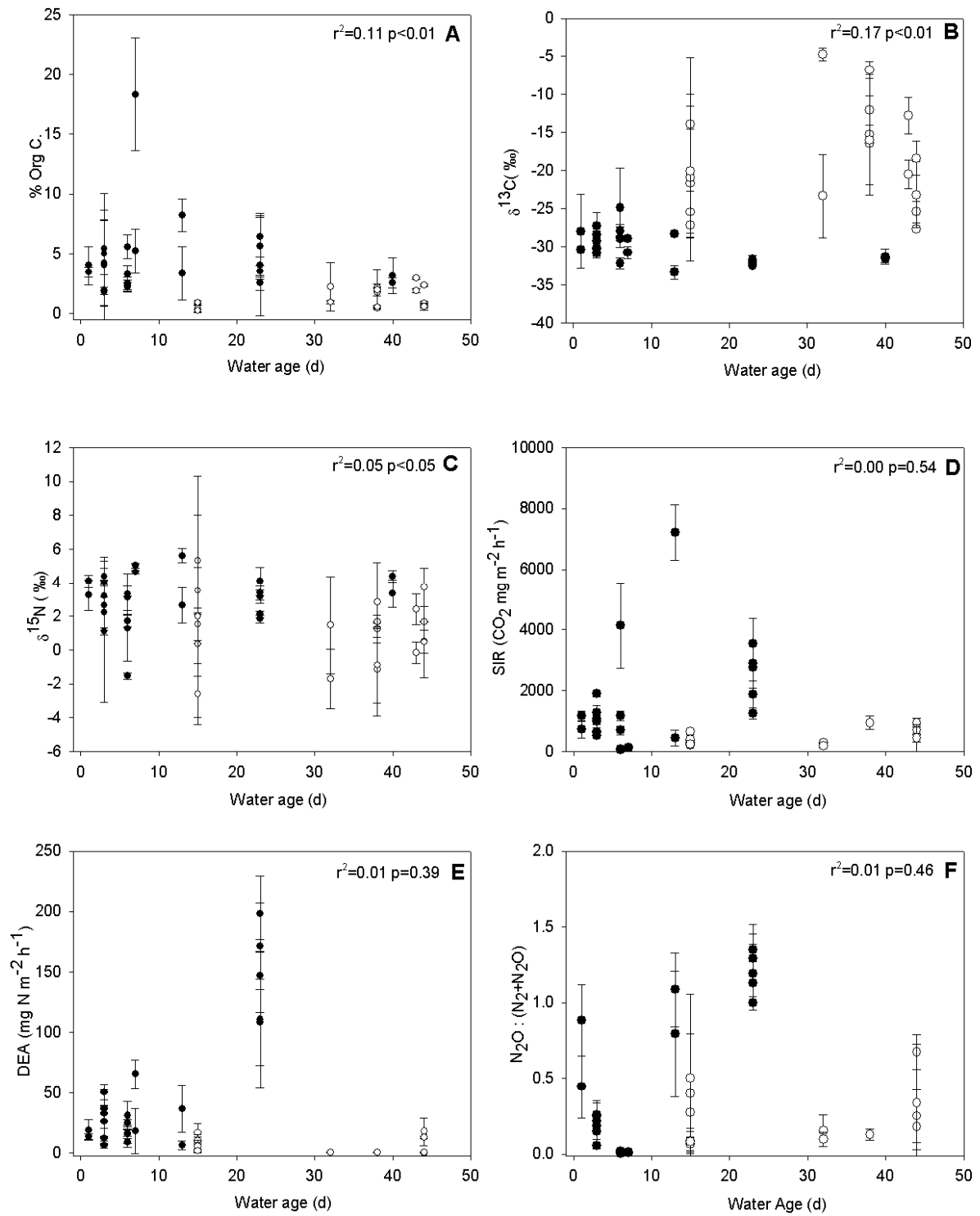
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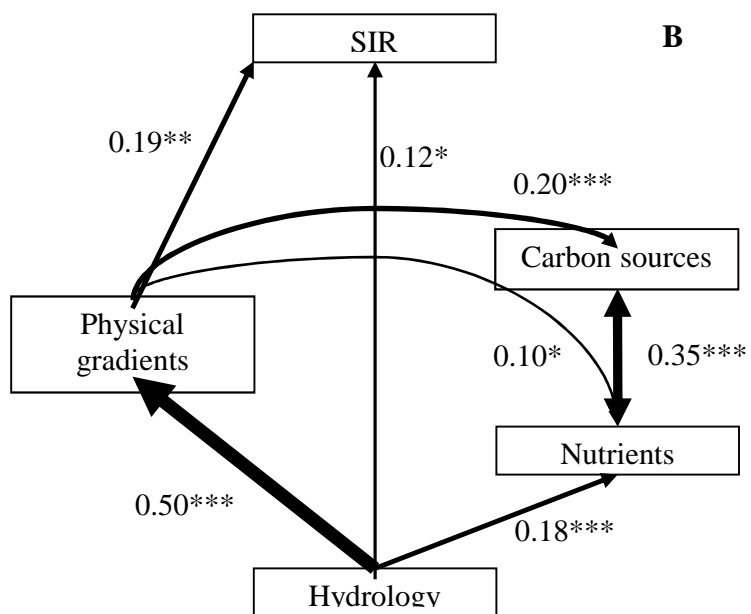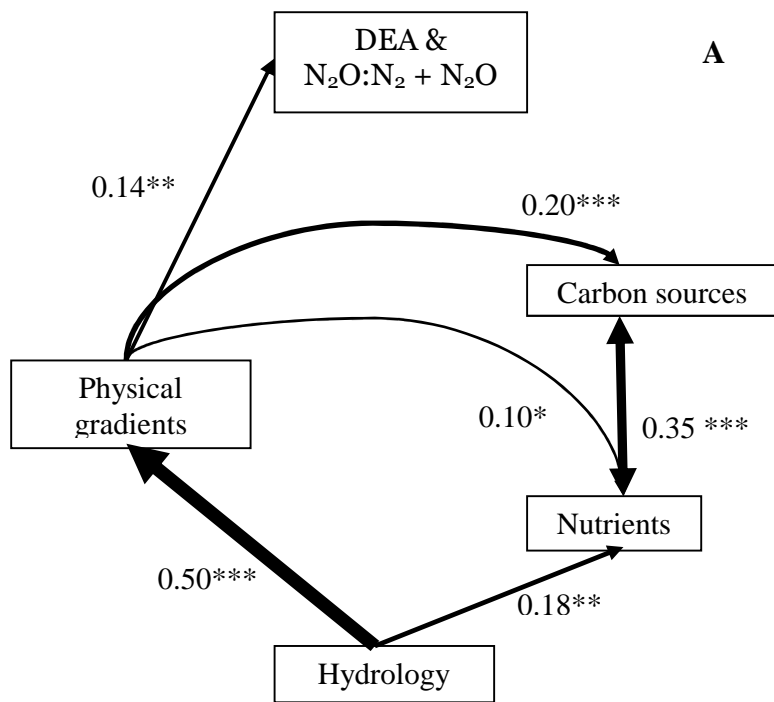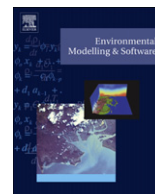
Figure 5: Welti et al.

Figure 6: Welti et al.

Figure 7: Welti et al.

Modelling highly variable environmental factors to assess potential microbial respiration in complex floodplain landscapes

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ABSTRACT

The hydrological exchange conditions strongly determine the biogeochemical dynamics in river systems. More specifically, the connectivity of surface waters between main channels and floodplains is directly controlling the delivery of organic matter and nutrients into the floodplains, where biogeochemical processes recycle them with high rates of activity. Hence, an in-depth understanding of the connectivity patterns between main channel and floodplains is important for the modelling of potential gas emissions in floodplain landscapes. A modelling framework that combines steady-state hydrodynamic simulations with long-term discharge hydrographs was developed to calculate water depths as well as statistical probabilities and event durations for every node of a computation mesh being connected to the main river. The modelling framework was applied to two study sites in the floodplains of the Austrian Danube River, East of Vienna. Validation of modelled flood events showed good agreement with gauge readings. Together with measured sediment properties, results of the validated connectivity model were used as basis for a predictive model yielding patterns of potential microbial respiration based on the best fit between characteristics of a number of sampling sites and the corresponding modelled parameters. Hot spots of potential microbial respiration were found in areas of lower connectivity if connected during higher discharges and areas of high water depths.

1. Introduction

River systems can be viewed as open ecosystems dynamically linked along the river network and within the riverine landscape at the catchment scale. The water exchange conditions and the linkage to the hydrological regime at the local (i.e. reach) scales determine matter transport, cycling and transformation (Tockner et al., 2000). Within riverine landscapes, riparian wetlands and floodplains are key areas for biogeochemical cycling, where the hydrological dynamics affect the temporal variability and spatial heterogeneity (Amoros and Bornette, 2002; Cook, 2007). The constant adaptation to changing hydrology and nutrient inputs occurring within in the floodplains create a variety of processes occurring at different scales and interfaces (Ward et al., 1999). As a result, these riverine

landscape features, where physical sedimentation and biological activities occur, act as biogeochemical hot spots, in particular for carbon and nitrogen cycling (McClain et al., 2003). Consequently, this variability at the local scale has been shown to impact global elemental cycles (Seitzinger et al., 2006; Battin et al., 2009). Especially, the roles of river networks and within rivers, the role of different landscape elements such as floodplains, have been recently discussed for their contribution to global estimates of carbon cycling (Battin et al., 2009).

The delivery patterns of carbon and nutrient inputs and carbon dioxide emission along river ecosystems are strongly related to surface connectivity (Hein et al., 2004; Preiner et al., 2008). While the input of nutrients, sediment and organic matter occurs mainly via surface flow from upstream, significant amounts of these materials are deposited during floods. The transfer and storage of materials in floodplains are largely under the control of the connectivity pattern within the river landscape as well as of the magnitude, frequency and duration of floods (Pinay et al., 2002; Richardson et al.,

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2004). In dynamically connected retention areas, the pattern of surface and sub-surface flow provides the basis for intensive microbial processing, in particular the frequency, duration, timing and intensity of floods directly affect carbon turnover in sediments and alluvial soils (Pinay et al., 1995, 2000, 2007).

As a result of flood protection engineering, riverine floodplains in urban or agricultural areas are often decoupled from the main river, thus changing their connectivity patterns and nutrient cycling regimes. Restoration by reconnection is an attempt to recreate the nutrient processing potential of floodplains (Klocker et al., 2009). However, created and restored sites, due to homogenous sediment characteristics and changing hydrological regimes, may not return to the full potential of undisturbed, heterogeneous systems (Bruland et al., 2006; Orr et al., 2007).

Understanding changing environmental conditions and predicting the resulting effects requires integrated modelling of river systems (e.g. Arheimer et al., 2004; Poole et al., 2004; Laursen and Seitzinger, 2005; Hollander et al., 2006; Johnson et al., 2007; Metcalf et al., 2010). It is necessary to integrate the understanding of river ecosystems, nutrient dynamics and microbial processing, while considering the possible effects of restoration in order to evaluate the impact of restoration. While hydrological models have been widely applied for traditional engineering solutions in water management, the use as tools for river restoration is a recent development, which has been used to answer habitat requirements, hydrodynamics, changes in biodiversity and nutrient transformation (Trepel and Palmeri, 2002; Jones et al., 2006; Liu et al., 2008; Groffman et al., 2009).

However, modelling of the actual underlying processes has shown to be particularly challenging. In Zeng et al. (2006), a process-based biogeochemical model was applied to study nutrient cycling in a small impoundment. Kondolf et al. (2006) proposed the use of process-based conceptual models in order to facilitate ecological restoration. A catchment-scale modelling study of surface water——groundwater interaction and nitrate attenuation in riparian zones was presented by Rassam et al. (2008) using various water quality model components. Despite these process-based approaches a modelling framework determining in high spatial detail the environmental factors responsible for biogeochemical processes, eventually allowing an assessment on the landscape scale, has not been available so far.

This paper presents such a modelling framework and its underlying modules that aim at predicting spatially detailed system connectivity and related output patterns of potential microbial sediment respiration leading to CO_2 emissions in complex floodplain landscapes. The predictive model integrates hydrology and morphology. It is based on morphological input derived from LiDAR, bathymetric and terrestrial surveys, a long-term hydrograph of the main river, and biogeochemical and physical characteristics of sediment samples taken in the field. In a first step, connectivity patterns and wetting/drying cycles of natural floodplain environments were determined for a computation mesh based on the output of 2-D steady-state hydrodynamic modelling combined with a long-term discharge hydrograph of 30 years using a gauge transformation technique. This allowed for an automatic analysis of flow events, eventually yielding statistically relevant statements regarding connectivity probabilities and the respective duration of connection and disconnection cycles for every mesh node within the computational domain. These properties were assigned to field samples according to the sampling location. In a final step, the model linked the properties of every computation node to those of the field samples employing a best-fit approach based on least square errors. The predictive power of the modelling approach was applied to two study sites located in the Alluvial Zone National Park of the Austrian Danube East of Vienna.

2. Modelling approach

The modelling framework relies on five fundamental prerequisites: (i) a high-quality digital elevation model of the study area, derived from LiDAR and combined with additional bathymetric and terrestrial measurements; (ii) a computation mesh representing the topography reasonably well, i.e. by applying local mesh refinement; (iii) water surface elevations for several characteristic river discharges derived from hydrodynamic modelling; (iv) a long-term discharge hydrograph, covering 30 years or more, for a gauge either within the computational domain or used as boundary condition for the hydrodynamic model; (v) a statistically relevant number of field sediment samples and their biogeochemical properties measured in the lab.

Within the modelling framework, data processing was performed in three modules (Fig. 1): (a) a hydrodynamics module, used for computing water surface elevations in the floodplain for characteristic river discharges; (b) a connectivity module, linking the output of the hydrodynamics module with a long-term hydrograph and performing an automatic event classification to yield connectivity properties of every computation node; (c) an output simulation module, calculating the potential microbial respiration for the entire mesh based on the best fit of hydrological and morphological properties at sampling sites.

2.1. Hydrodynamics and node-propagation module

Any hydrodynamic model capable of delivering steady-state water surface elevations for a 2-D domain is suitable for this module, which particularly includes all 2-D and 3-D numerical models. If the number of model boundary conditions is reduced to one — as in some backwaters or flood retention pools — the dynamic component could be dropped from the flow equations and a simple node-propagation technique could be applied to obtain the water surface elevations.

In the study presented here, the 2-D hydrodynamics code Current2D (Milbradt, 2002) was used to obtain water surfaces for characteristic discharges between low and high flow conditions. It solved the shallow water equations using stabilized finite elements on a triangular mesh. Turbulence was modelled by means of the Smagorinsky (1964) eddy-viscosity approach. In this approach, the molecular viscosity of water is augmented by an eddy viscosity, which is calculated from local derivatives of the velocity field and thus encounters for the spatially varying effect of turbulence in every element of the computation mesh. Time discretisation was conducted by an explicit Euler technique; in this method, the temporally varying flow field and water surface elevations are calculated for a large number of small time steps, requiring that every time step is completed before calculation of the variables for the next time step commences, since they depend on the previously determined values. In elements with a water depth of less than 0.1 m only a standard Galerkin approximation was performed, which means that a horizontal water surface was assumed and its level was approximated by the water levels of surrounding elements. Among other studies, the numerical model was successfully applied in an analysis of the large flood of 2002 in the Danube river basin (Tritthart and Milbradt, 2003).

In simulation domains (i.e., study sites) characterised by inflow and outflow through the same cross-section profile, resulting in only one boundary condition, a node-propagation technique was employed using the RSim-GUI graphical pre-processor of the RSim-3D hydrodynamic model (Tritthart and Gutknecht, 2007a,b): similar to a particle tracing approach (Tritthart et al., 2009), a given water surface elevation — or flood wave crest height — was propagated from a computation node to its dry neighbours provided sufficiently low bed elevation. This procedure was realised using
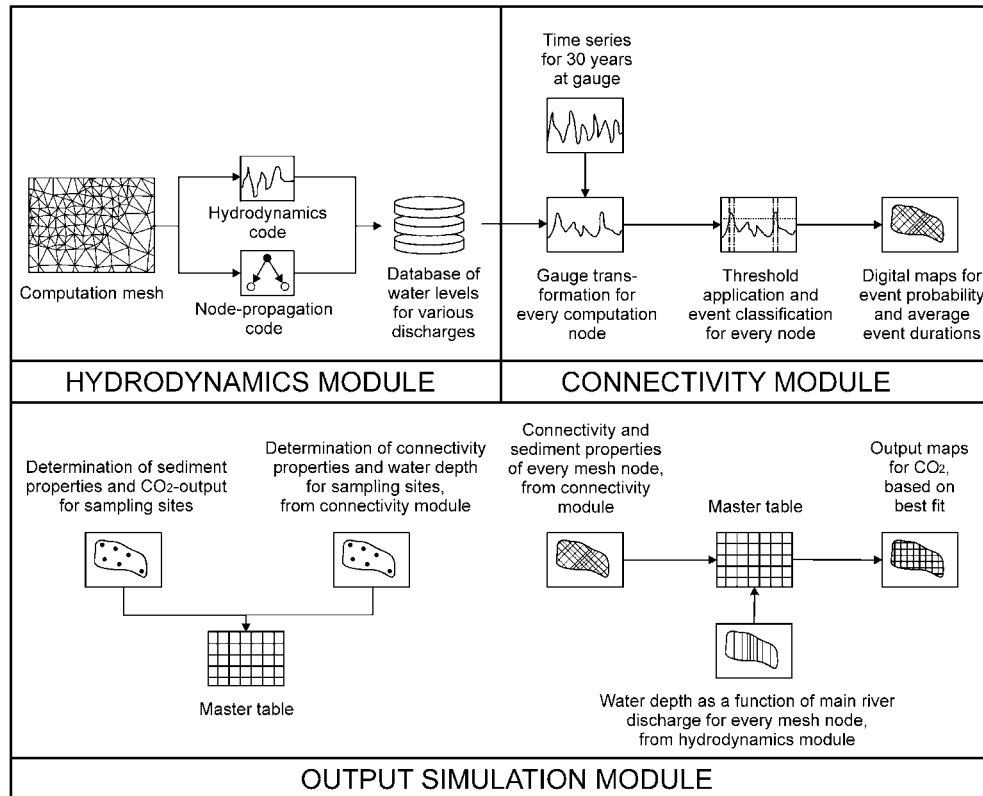
Fig. 1. Modules, components and flow chart of the modelling framework.

a binary tree data structure which guaranteed very fast execution time, particularly in comparison to a fully 2-D shallow water model. As only the final steady-state water surface was of interest, such a calculation without dynamic components did not introduce additional error.

The calculated water surfaces for every node and characteristic discharge were inserted into a database used by the connectivity and output simulation modules. In addition to these results of steady-state simulations, a minimum water surface was calculated for every node, corresponding to the lowest possible water level at this location. This minimum water surface was identical to the terrain elevation for nodes that could actually fall dry, while it corresponded to the horizontal pool water level in all regions within the computational domain that remained wet due to pool conditions in the hypothetical case of the main river falling completely dry. The minimum water surface was determined by computing a stepwise water-level drawdown from a high starting level, either by hydrodynamics or node-propagation: whenever the model predicted a node to be wet at a higher water surface elevation and dry at a lower water surface elevation, even though its elevation allowed it to be wet under these conditions, pool conditions were present for that node. In such a case, the corresponding pool water surface was found iteratively between the two elevations. The calculated minimum water surface elevations directly correspond to the threshold of connectivity for every node: whenever a node encounters a water surface elevation higher than the minimum water surface, it must necessarily be connected to the main river. All connectivity threshold elevations for every node were inserted into the database as well.

2.2. Connectivity module

Using the water surface elevations determined by the steady-state hydrodynamic simulations, a relationship between characteristic

discharges at a gauge and the corresponding water levels at each mesh node could be established (Fig. 2). A linear interpolation within the water level range encompassed by the characteristic discharges higher and lower than the discharge for the current time step within the discharge hydrograph was usually sufficient to yield the local water level. Water levels for runoff higher than the maximum simulated discharge were extrapolated based on the water surface gradient of the maximum simulated discharge (I_{max}). The same
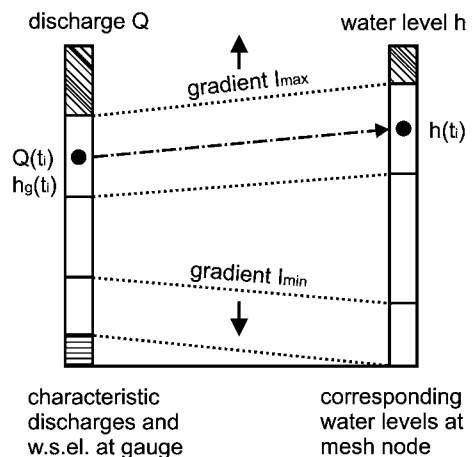
Fig. 2. Diagram representing the gauge transformations: based on steady-state numerical modelling of water surface elevations (w.s.el.) for characteristic discharges Q, the unknown water levels h for specific points in time t_i at arbitrary locations within the computational domain can be derived from known water surface elevations at the gauge h_g; maximum (I_{max}) and minimum gradients (I_{min}) for every location are applied for water levels above the highest or below the lowest modelled discharge, respectively.

technique was applied for the lowest simulated discharge and the corresponding gradient I_{min}.

This procedure, referred to as gauge transformation, was applied to a hydrograph covering a statistically relevant period; usually 30 years or longer. As result of this procedure a local, virtual hydrograph of water levels H was obtained for every computation node (Fig. 3). Applying the respective connectivity threshold H_0, calculated individually for each node within the hydrodynamics module, this stage hydrograph was then converted into a time series of binary information for each node, corresponding to a connected or disconnected state. Subsequently, by analysis of the binary state changes, the time series was broken down into events. This allowed calculating event duration T_{Ei} and interval between events T_{Ii}. However, while the connectivity threshold was a reasonably good limiting value for the calculation of event durations, smaller flow events may not have reached the respective computation node, due to levelling caused by retention effects during wave propagation which were not covered in the modelling approach. Therefore, an event was only counted at an individual node if its peak was sufficiently higher than the connection threshold H_0 for this node. This correction for hydrologic retention was realised by introducing a critical connection threshold H_C for each node. This threshold was obtained from: $H_C = H_0 + c$, where c is a system-wide constant which must be calibrated according to gauge readings but is usually small, i.e. in the range of 0.05 to 0.10 m.

After a statistical evaluation of frequency and duration of event occurrence, the resulting parameters were obtained: (i) probability of connection (connectivity); (ii) average connection duration; (iii) average disconnection duration. This statistical information was then stored for every computation node, and used for plotting maps of connectivity properties.

The connectivity module outlined here comprised a number of simplifications regarding the actual fluvial processes encountered during the exchange of mass between a river and its riparian zones. These simplifications are therefore only applicable under several premises:

1. *Negligible hysteresis effects in the study area.* Water levels were assumed to be equal for the same discharge during the ascending and descending limb of the flood hydrograph.
2. *No sharp increase or drop in water levels.* The approach was based on quasi-steady state hydrodynamic modelling results. Therefore, the temporal change in water levels must be smooth at any time.
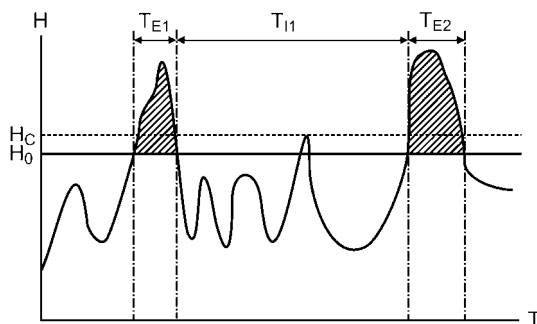
Fig. 3. Diagram representing the event analysis in the connectivity module: events are defined as sections of the hydrograph exceeding the connectivity threshold H_0 as derived from the computation of a minimum surface by numerical modelling of a water surface drawdown; in order to account for retention leading to levelling of comparably small peaks in the hydrograph, events are counted only if exceeding a critical water surface elevation H_C. Event duration is denoted by T_{Ei}, intervals between events by T_{Ii}.

3. *Comparably small size of the domain of interest or study reach.* The propagation time of flood waves through the computation domain must be of the same order/scale as the time resolution of the input hydrograph, as otherwise significant errors would be introduced.

If the abovementioned assumptions are not met, the hydrodynamic model must be run in unsteady mode for the entire duration of the input hydrograph instead. In such a case the node-propagation code cannot be used.

2.3. Output simulation module

The output simulation module connected the output of the hydrodynamics and connectivity modules with sediment properties in order to predict the potential biogeochemical output of the entire system. This was performed in a two-stage procedure (Fig. 1): (i) assemble the master table, which linked physical, biogeochemical and hydromorphological parameters of all samples taken; (ii) calculate the best fit for properties at an arbitrary mesh node as a function of main river discharge and corresponding water depths.

The output simulation module was based on the parameters given in Table 1, derived from the hydrodynamics module (Hy), the connectivity module (Co) or field sampling (Sa). Parameters 1 through 5 were input parameters, whereas parameter 6 was a model output parameter. For each of the input parameters, the minimum and maximum values were determined in order to allow for deriving dimensionless parameters through standardisation. For every computation node i and every row of the master table, corresponding to sampling point j, the residual $R_{i,j}$ was evaluated according to Equation (1),

$$R_{i,j} = W_H \left(\frac{H_i - H_j}{H_{max} - H_{min}} \right)^2 + W_{D50} \left(\frac{D_{50,i} - D_{50,j}}{D_{50,max} - D_{50,min}} \right)^2$$
$$+ W_{PC} \left(\frac{P_{C,i} - P_{C,j}}{P_{C,max} - P_{C,min}} \right)^2 + W_{TC} \left(\frac{T_{C,i} - T_{C,j}}{T_{C,max} - T_{C,min}} \right)^2$$
$$+ W_{TD} \left(\frac{T_{D,i} - T_{D,j}}{T_{D,max} - T_{D,min}} \right)^2 \tag{1}$$

where W_H, W_{D50}, W_{PC}, W_{TC} and W_{TD} were weighting factors of the parameters water depth, median sediment grain size, connectivity, average connection duration and average disconnection duration, respectively. The sampling point j featuring the minimal residual $R_{i,j}$ was assumed to be representative for the computation node i, and the corresponding output parameters for potential microbial respiration were set for the mesh node. Once the output for all nodes had been derived, output maps of the computation domain could be plotted.

In the study presented here, the weighting factors were derived from a Mantel Test on the entire master table, yielding the

Table 1
Parameters of the output simulation module; Hy = hydrodynamics module, Co = connectivity module, Sa = field sampling.

Parameter #	Parameter description	Hy	Co	Sa
1	Water depth, H	m		
2	Median sediment grain size, D_{50}			mm
3	Connectivity, P_C		%	
4	Average connection duration, T_C		days	
5	Average disconnection duration, T_D		days	
6	Potential carbon dioxide (CO_2) output O_{CO2}			mg m^{-2} h^{-1}

Table 2
Metavariable dissimilarity (distance) matrices and underlying variables. All matrices are Euclidean distance matrices calculated on standardized variables (from Welti et al., submitted for publication).

Metavariable	Underlying variables			
Physical template	Depth of the water body (m)	Water temperature (°C), conductivity ($\mu S/m$) pH	Dissolved oxygen (%)	Sediment size (D50) (mm)
Hydrology	Duration of connection (days)	Duration of Disconnection (days)	Connection (days year^{-1})	Water age (days)
Processes	Substrate induced respiration (SIR) (mg CO_2 m^{-2} h^{-1})			

corresponding influence of the input on the output parameters (Table 2). In general, a Mantel Test is a statistical test of the correlation between two matrices. Welti et al. (submitted for publication) used Mantel Tests to explain the relationship between hydrology and geomorphology on potential denitrification and microbial respiration (substrate induced respiration), demonstrating the underlying hierarchy. Mantel statistics do not have to be large, i.e. close to 1 or -1, to be statistically significant. Significance of path coefficients was assessed by randomizing all involved matrices using 10^4 permutations, building randomized distributions for each path coefficient, and computing probabilities for observed path coefficients with the percentile method (Manly, 2006). All calculations were done in R 2.9. (R-Development-Core-Team, 2005), using the packages vegan (Oksanen et al., 2010) and sem (Fox et al., 2010). Mantel and partial Mantel (controlling for effects of hydrology) statistics were used to test for associations between metavariables, and causal modelling on dissimilarity matrices (i.e. path analysis using Mantel statistics treated as correlation coefficients) to relate the various metavariables in the hypothesized causal framework (Legendre and Legendre, 1998; King et al., 2005). These tests were based on matrices containing measured parameters describing floodplain morphology, hydrology, organic carbon sources and nutrient availability in the floodplain sediments during a two year study in the floodplain study sites. These links demonstrated to which extent the relationship between the floodplain hydrology and the potential respiration was mediated by the geomorphological context of the area. The weights for Equation (1) were derived from the Mantel Test results (Table 3) for the floodplain systems investigated, creating a general statistical model for potential microbial activity. The hydrology metavariable included the parameters connectivity, average connection duration and average disconnection duration; physical descriptors included sediment grain size, temperature and water depth (Table 2). As temperature was considered constant to remove the effects of seasonality, allowing for a generalised view on the output processes, the weights were derived from the associations between metavariables. Following the requirement that weights for parameters combined under the same metavariable must be equal to each other, this resulted in $W_H = W_{D50} = W_1$ and $W_{PC} = W_{TC} = W_{TD} = W_2$. As the

weights must sum up to unity, we obtained the conditional equation: $2W_1 + 3W_2 = 1$, or $W_2 = 0.333 (1-2W_1)$. Given that the metavariable association between the physical template and output processes was determined as 0.13, whereas the association between hydrology and output processes was calculated as 0.08 (Table 3), the ratio between W_2 and W_1 could be calculated: $W_2 = 0.08/0.13$ $W_1 = 0.615W_1$. Substituting this ratio for W_2 in the conditional equation resulted in the following coefficients: $W_H = 0.26$; $W_{D50} = 0.26$; $W_{PC} = 0.16$; $W_{TC} = 0.16$; $W_{TD} = 0.16$.
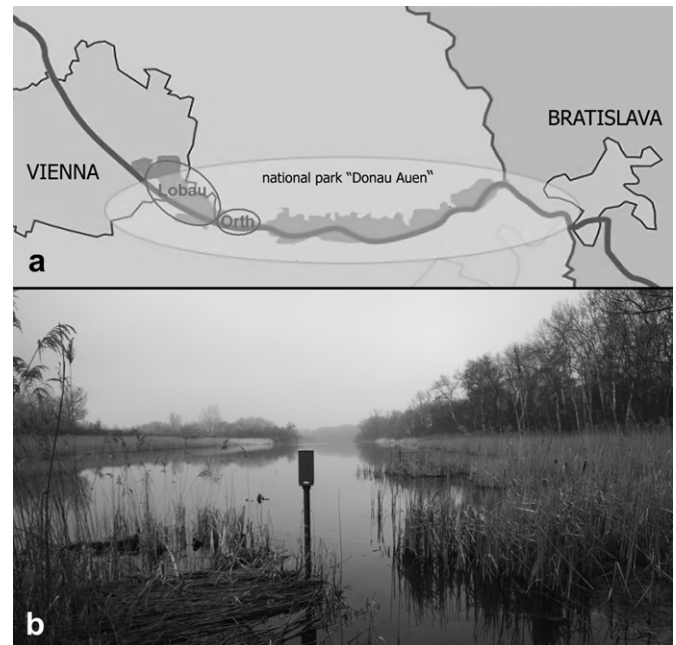
3. Study sites

Two study sites were selected: Lobau and Orth. Both are situated within the Alluvial Zone National Park at the Danube East of Vienna (Fig. 4a). This river reach is characterised by a mean discharge of 1930 m^3 s^{-1}, an annual flood discharge of 5300 m^3 s^{-1} (Table 4) and a strong seasonality controlled by the regime of its alpine catchment (Tockner et al., 1999). Before the major regulation scheme of 1875, the river stretch was originally an anabranched section consisting of a main stem and a channel-network of numerous small and large branches (Nanson and Knighton, 1996; Hohensinner et al., 2004). Ecological degradation of the river led to constrained side arm connectivity and loss of riverine habitats due to floodplain aggradation. Nowadays the river is under major restoration efforts which aim at improving the ecological status of the river (Habersack et al., 2007).

Table 3
Associations between metavariable dissimilarity matrices as expressed by Mantel statistics. Mantel (upper diagonal) and partial Mantel (lower diagonal) statistics (controlling for hydrology), significant values printed bold, P-values not corrected for multiple testing.

	Physical template	Nutrients	Organic carbon sources	Processes
Hydrology	**0.5** **P < 0.01**	**0.22** **P < 0.01**	**0.14** **P < 0.01**	**0.08** **P < 0.03**
Physical template		**0.18** **P < 0.01**	**0.22** **P < 0.01**	**0.13** **P < 0.01**
Nutrients	0.09 P = 0.05		**0.4** **P < 0.01**	−0.09 P = 0.99
Organic carbon sources	**0.17** **P < 0.002**	**0.38** **P < 0.001**		−0.01 P = 0.55
Processes	**0.11** **P < 0.007**	−0.11 P = 1	−0.02 P = 0.59	

Fig. 4. (a) Location of the study sites, i.e. Lobau and Orth within the Austrian national park "Donau Auen" between Vienna and Bratislava; (b) Photograph of a typical lake environment and gauge in the Lobau study area, near sampling site EW (see Fig. 5).

Table 4
Characteristic discharges of the Danube River East of Vienna.

| Identifier	Description	Discharge [$m^3 s^{-1}$]
RNQ	Regulated low flow	915
MQ	Mean flow	1930
HSQ	Highest navigable flow	5060
HQ_1	Annual flood	5300
HQ_{30}	30 year flood	9340
HQ_{100}	100 year flood	10,400

3.1. Lobau

The Lobau is a floodplain of the Danube River located on the left river bank downstream of Vienna. It covers an area of approximately 23 km². Except for groundwater-surface water exchange and a small upstream inflow, the primary water exchange with the main river takes place through an artificial breach in the flood levee encompassing the Lobau's southern side (Fig. 5a). Three major retention structures with culverts prevent the side arms to fall completely dry during low flow periods, resulting in reservoir-like conditions (Fig. 4b). Several gauging stations, most of them gauge boards, but some also equipped with automatic recorders, are present in the Lobau; however, time series of gauge readings without major data gaps are only available for gauges located in the reservoir-like sections constituting the main stem of the floodplain system. Time series of different gauges within each of these sections are highly intercorrelated. Hence, out of the gauges available, four have been selected — one per section in the main stem of the river system — to validate the model (Fig. 5a). Modelling of the Lobau was performed on a mesh comprised of approximately 150,000 nodes using the node-propagation module, based on hydrographs of a gauge in the Danube River located 250 m downstream of the inlet.

3.2. Orth

The side-arm system of Orth is located just downstream of the Lobau. It covers approximately 5.5 km² (Fig. 5b), and features very diverse flow characteristics. Some side arms are characterised by a through-flow at runoff just above estival mean flow, while others are connected at much higher flow conditions. Most of the historical retention structures present in this river system have been removed in recent years as the inlets of the side-arms have been improved by lowering the bank heights to 1 m above low water level, thus increasing the side-arm discharge significantly as well as the connection duration. There are four main inlets and one outlet connecting this sidearm system to the main river. Modelling of the Orth study area was conducted using 2-D hydrodynamic modelling on a mesh of approximately 55,000 nodes, including the main river itself. The computation mesh was refined along the side arms and
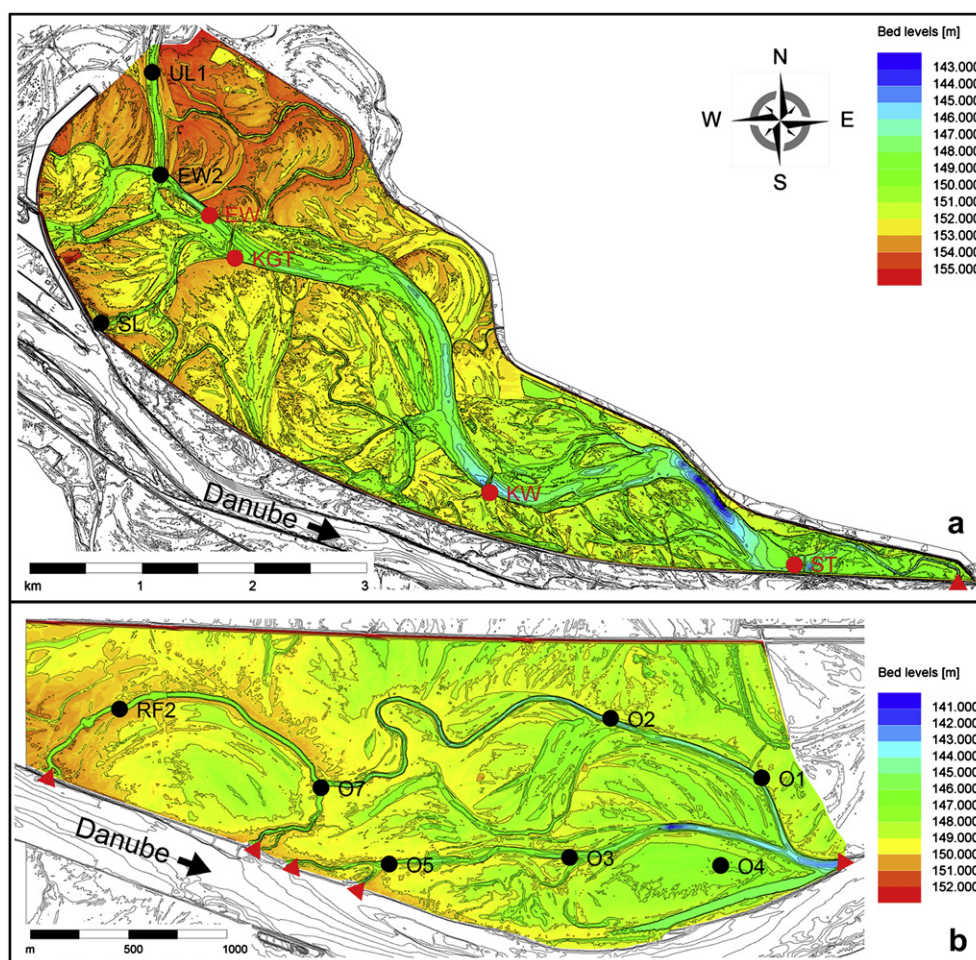
Fig. 5. Digital Elevation models of the study sites (a) Lobau and (b) Orth; shaded areas indicate the floodplain modelling domain. Inflow and outflow cross-sections are represented by triangles; aquatic sampling sites are marked by filled circles; sampling sites with associated gauge recordings used for validation are coloured in red (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

coarser in the floodplain regions. The model was calibrated on characteristic water levels of the Danube River in Austria (KWD) (Austrian Federal Waterways Authority, 1997), an official catalogue of water levels for characteristic discharges for every river kilometre obtained from gauges, hydrodynamic models and standard interpolation methods.

4. Field sampling and analyses

A total of 25 sampling sites of different flow and connectivity characteristics have been selected within the two side-arm systems. Sampling took place during three consecutive growing seasons (May–October) in 2006, 2007 and 2008; hence, the output rates modelled based on sampled data are valid only for the growing season. Triplicate sediment cores of 5-10 cm were taken using a PVC corer (inside diameter 5 cm) in deep and shallow aquatic areas of each of the 25 sampling sites. Among the 25 sites, 10 were terrestrial sites of 1 m^2 each, where 10 cm^2 triplicate samples in the top 5 cm soil layer were taken. Aquatic sampling occurred in 15 sites (Fig. 5) during different flow conditions and contrasting dry and wet periods. Grain size diameter D_{50}, organic carbon and nitrogen content of the sediment and potential respiration were determined in the laboratory.

Dried sediments obtained at each site were sieved through a sieve tower (20.00, 6.30, 2.00, 1.00, 0.50, 0.125, and 0.063 mm sieve sizes) to determine sediment size fractions and calculate D_{50}. From each sediment core, a 0.5 ml subsample of dried sediment was acidified with HCl to remove inorganic carbon and 1 to 2 mg of each sample were weighed into tin capsules and analysed for organic N and C concentration at the Department of Chemical Ecology and Ecosystem Research, University of Vienna.

Substrate induced respiration (SIR) was measured according to Beare et al. (1990). Three subsamples of 10 g of wet sediment were weighed into three 100 ml Schott glass flasks and closed with a silicon insert lid and received a 5 g C l^{-1} (as glucose) amendment. All flasks were incubated at room temperature in the dark for 4 h. A 10 ml gas sample was taken from each flask and injected into an evacuated 10 ml headspace glass vial. Gas samples were analysed using a gas chromatograph (Agilent 6890N coupled with an Agilent G1888 Headspace sampler) and the results calculated according to Bauernfeind (1996). Initial CO_2 concentrations were assumed to be zero, so the concentration after 4 h was the rate of SIR.

Substrate induced respiration (SIR) was measured in the laboratory within 2 days after sampling. These potential activities represent the state of enzyme pools present at the sampling time with no other limiting factor, and without de novo enzyme synthesis and cell multiplication. In the framework of our study, these potential activity measurements were more relevant than actual in situ rates (flux measurements) since (i) actual fluxes cannot be accurately measured under in vitro conditions and (ii) variations in actual activities can reflect short-term variations in environmental conditions (e.g. temperature, water content) whereas variations in potential activities reflect deeper modifications of the sediment microbial functioning such as a modification of the level of enzyme synthesis involved in the carbon degradation, a modification of the density and/or diversity of the microbial community responsible for a given biotransformation (Beare et al., 1990).

5. Validation study

A validation of the modelled stage hydrographs for sites within the Lobau study region calculated by the connectivity module was conducted by comparing the corresponding module output to gauge readings. The objective was to verify whether the assumptions on which the connectivity module is based are justified and to confirm validity of its implementation.
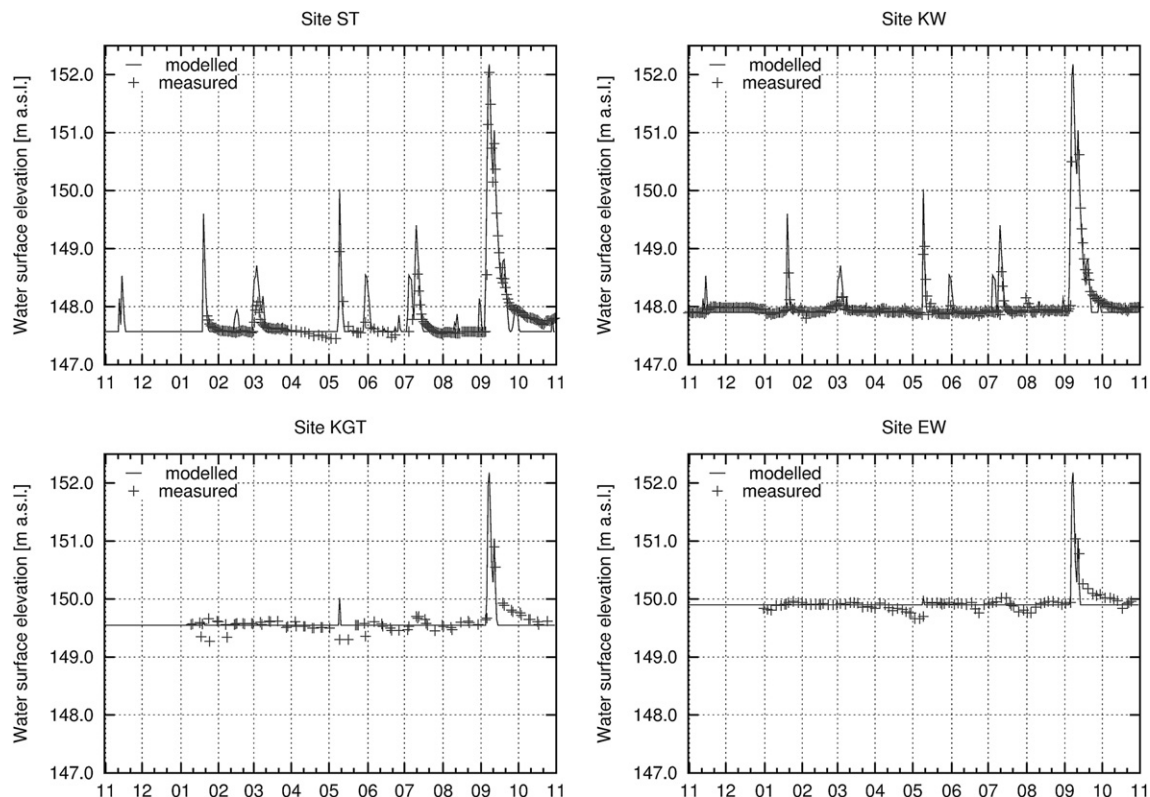

Fig. 6. Comparison of measured and modelled water surface elevations for the hydrological year 2007 (November 2006–October 2007) at four sites within the Lobau study area.

The period chosen for validation was the hydrologic year 2007, starting November 1, 2006 and ending October 31, 2007. This period was selected as it is the only hydrologic year for which data without major gaps were available at four different gauges. The corresponding sites are located in different reservoirs of the Lobau (Fig. 5a).

Fig. 6 depicts a comparison between modelled and measured hydrographs at all four sites. The diagrams indicate that the calculated minimum water surface − which is found if no flood event has taken place for significant time − represented adequately the measured data. It confirms that the concept of a minimum surface, the node-propagation technique applied to calculate it, as well as the underlying Digital Elevation Model was appropriate. The minimum surface was also not subject to large fluctuations, indicating that evaporation was not a major issue in these study sites to be considered in the modelling framework. In general, the timing of events was properly modelled, even though the magnitude was overestimated for some events at most sites. However, the nature of the gauge readings available, i.e. two manuals (KGT and EW) and two automatic (ST and KW) might not represent the reality of the water level during high flood events. Indeed, during flood events, gauges are often inaccessible for personnel while automatic gauge recorders may stop operating; therefore the peak of a flood wave may be missed. This fact was particularly evident for the flood event taking place during September 2007, when the highest water levels noted at site EW, near the upper end of the Lobau, exceeded those recorded at site KW, much closer to the inlet, which was contrary to

the pattern retention effects would cause. Moreover, the readings showed the correctly modelled peak of the event at site ST to decrease by 1.5 m within the distance of 2.5 km to site KW, which cannot be credited to retention alone. However, while the magnitude of the events in terms of water levels was sometimes overestimated, the event duration important for connectivity calculations was generally well predicted. Only for very large events, the duration of the falling limb of the hydrograph was underestimated by the model; however, in terms of functional connectivity with the main river, it was unlikely to see any river water input into the system during that period as the flow direction was inverted during that phase.

In order to obtain a quantitative indicator of model performance, the correlation between measured and simulated water surface elevations at all four gauges was calculated and is presented in Fig. 7. The analysis was performed on data covering the entire years of 2006 and 2007, after removing stage data corresponding to the respective pool surfaces, i.e. by only considering flood events exceeding these levels. The correlation diagram indicated a minor tendency towards overestimation of water surface elevations − and thus inundation areas and connectivity − for smaller flood events, whereas larger events were captured more precisely. Overall, the investigation yielded a correlation coefficient of $R^2 = 0.85$, which is similar to the values reported for hydrodynamic studies in literature (cf. Tritthart et al., 2009). Therefore the results of the validation study indicated that the model assumptions were justifiable and correct.
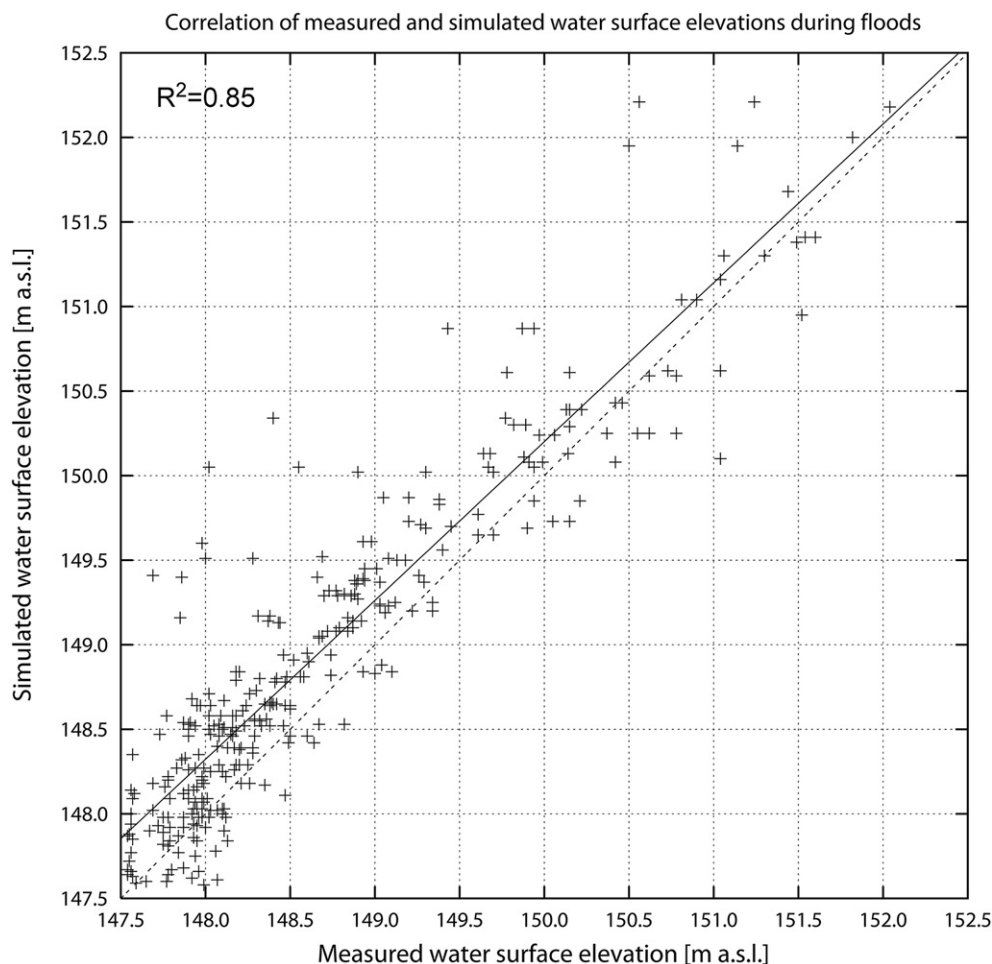

Fig. 7. Correlation between measured and simulated water surface elevations during flood events in the years 2006 and 2007 at four gauges within the Lobau study area; the dashed line signifies the line of perfect agreement; the continuous line is fitted to the data using a least-squares regression.

6. Results and discussion

6.1. Connectivity

Connectivity, average connection duration and average disconnection duration for both study regions are depicted in Fig. 8. In the Lobau study area, the region close to the exchange inlet/outlet was characterised by connection probabilities of well above 50% (Fig. 8a). However, the morphology of the floodplain and the presence of the retention structures reduced this parameter to 30% and even 10% in the regions of the study area characterised by higher terrain altitudes. In contrast, the connectivity for the Orth study area (Fig. 8b) followed a different pattern as this region was dominated by through-flow rather than backwater flow. Due to the absence of functional retention structures, only the natural morphological features presented an obstacle to the flow and therefore to connectivity. While the reach close to the outlet was permanently connected, side arms with more frequent through-flow conditions
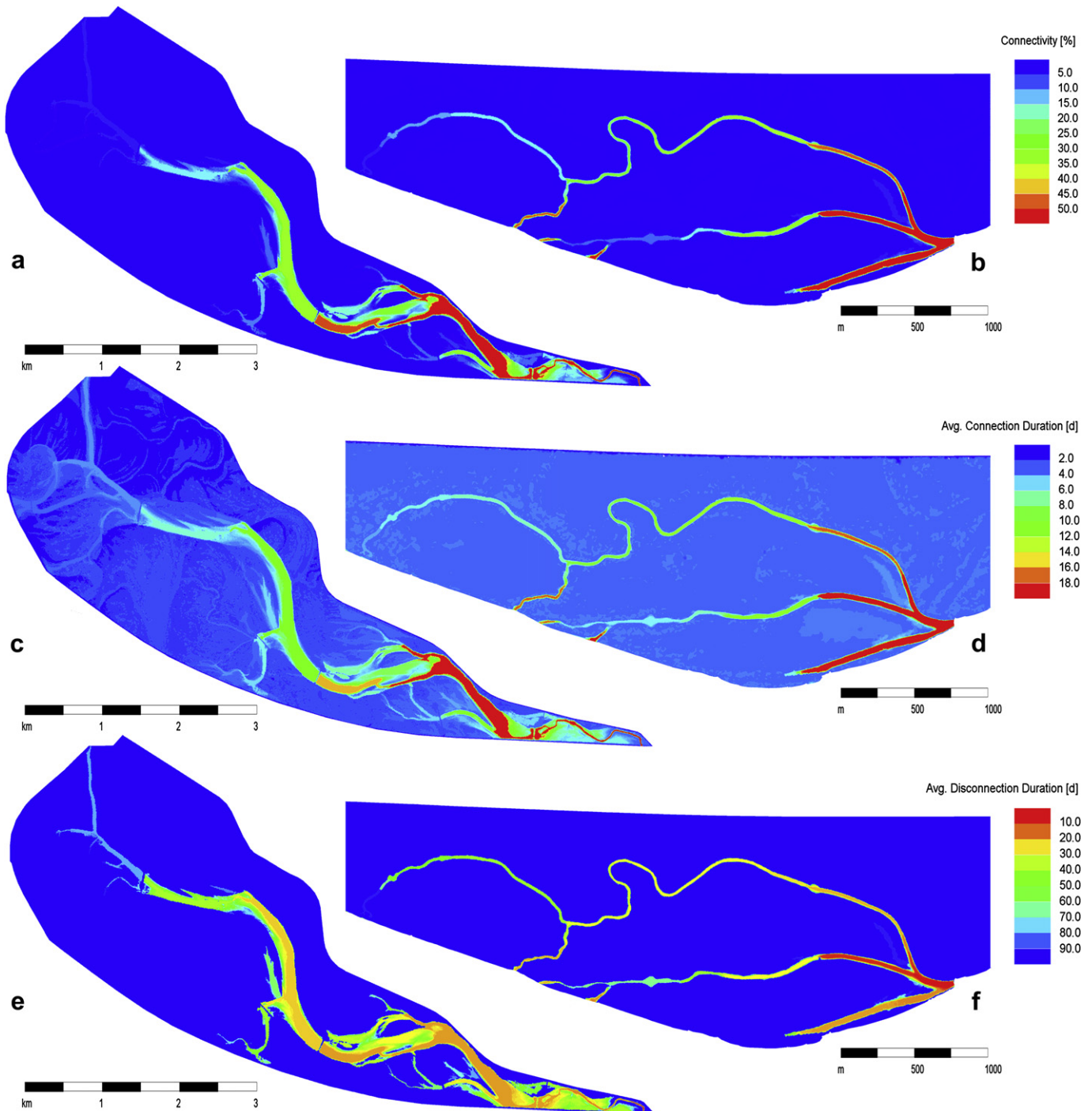
Fig. 8. Modelling results of the connectivity module: Connectivity map of the Lobau (a) and Orth (b) study areas; Map of average connection duration in the Lobau (c) and Orth (d) study areas; Map of average disconnection duration in the Lobau (e) and Orth (f) study areas.

featured connectivity probabilities of 30%; those dominated by backwater conditions were characterised by a connectivity of around 10%.

The duration of average connection or disconnection cycles were only dependent on the morphology of the study area and the long-term hydrologic conditions; hence they were independent from each other and from the connectivity probability. In the Lobau study area the average connection duration of the region close to the exchange cross-section was more than 30 consecutive days (Fig. 8c); Connection duration reduced to 6–10 days in the middle reach and less than 2 days in the upper section due to the retention structures. In Orth, side arms which were not permanently connected presented average connection durations between 4 and 18 days (Fig. 8d).

The average duration of disconnection was less than 10 consecutive days in the lower part of the Lobau, between 15 and 30 days in the middle section and almost 90 days in the upper reach (Fig. 8e). In the Orth study area (Fig. 8f), this parameter ranged between 20 and 60 days in most of the side arms, with a smaller reach dominated by backwater conditions characterised by up to 90 days of disconnection.

Histograms of the parameters connectivity, average connection duration and average disconnection duration, detailing the fractions of the total area occupied by classes of these parameters, are depicted in Fig. 9. Due to the distribution of terrain elevations, in both study areas a high proportion of around 90% of the total area were characterised by a low connectivity of less than 10% (Fig. 9a). However, while the Orth study area featured a more or less equal distribution of the remaining classes throughout the connectivity spectrum up to 50%,

the corresponding values for the Lobau were subject to larger fluctuations between classes in that range. These fluctuations resulted from the geomorphic control of the Lobau due to its anthropogenic partitioning into several reservoir-like sections. Moreover, the Orth study site also encompassed areas in the range of 50% up to permanent connectivity (100%), while such areas were virtually nonexistent in the Lobau, which is another indicator of its underlying geomorphic control. A similar pattern was visible for the average duration of connection (Fig. 9b): around 90% of the total area were connected only for short periods of up to four days; while the Lobau exhibited peaks for some of the remaining classes − corresponding to the reservoir-like sections − and did not feature areas of a longer connection duration than 20 days, the study site near Orth showed a more uniform distribution of areas spread over a larger class spectrum, which indicated predominantly hydrologic control. When analysing the average duration of disconnection (Fig. 9c), a remarkably high fraction of 68.8% of the area within the Lobau study site was characterised by statistical average disconnection times longer than 500 days, while only 13.5% were in this class for the side arm system near Orth. This histogram revealed also an interesting feature of the Orth study site, where low variability of the bank elevations throughout the side arms led to sudden widespread inundations (42.2% of the area) on average every 200 days; while this feature is clearly of geomorphic nature, the general control is hydrologic, as indicated by the class distribution in the remaining spectrum.

In the spatial distribution of the parameters connectivity, average connection duration and average disconnection duration the dominant influence of geomorphology − i.e. the conditioning
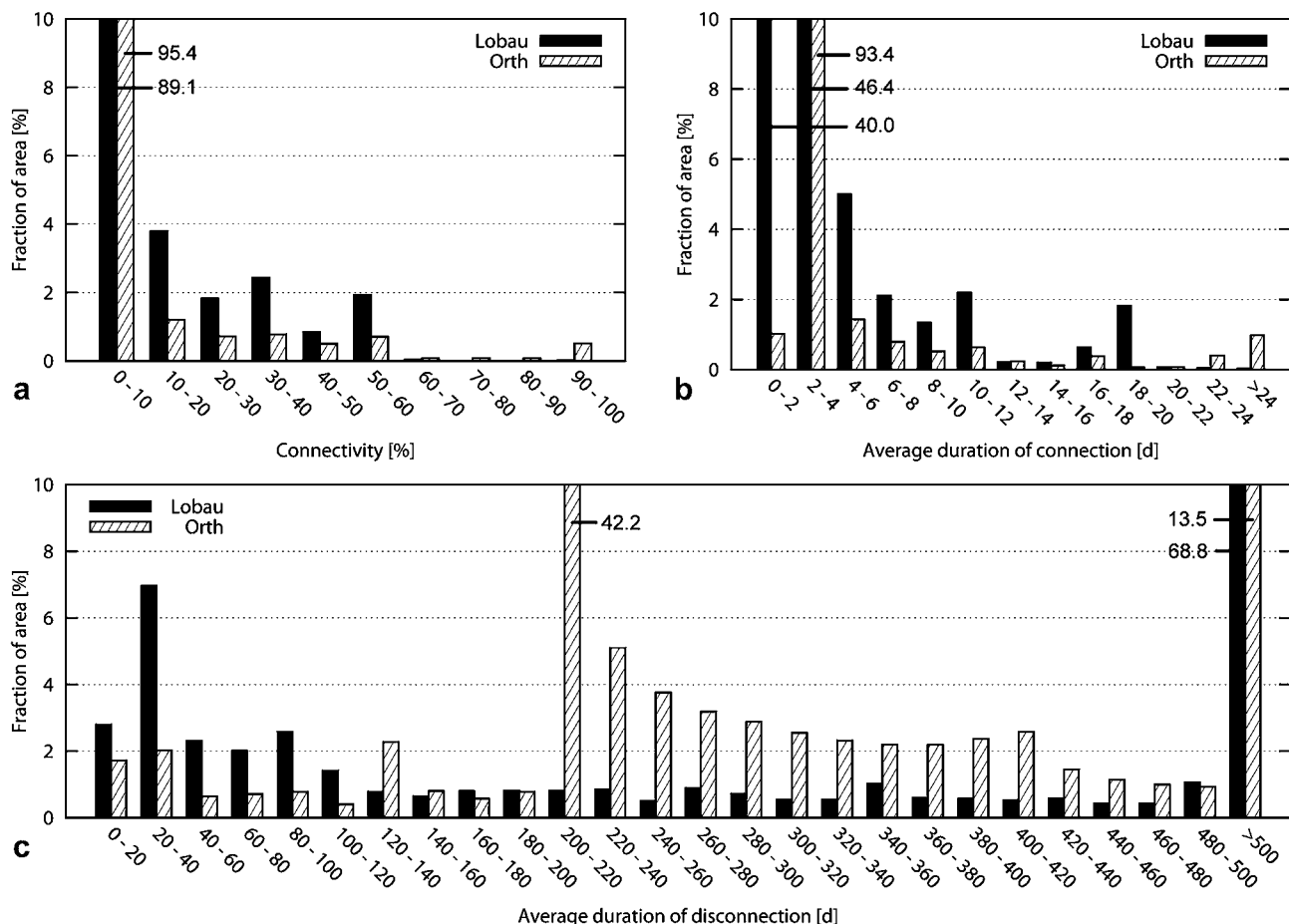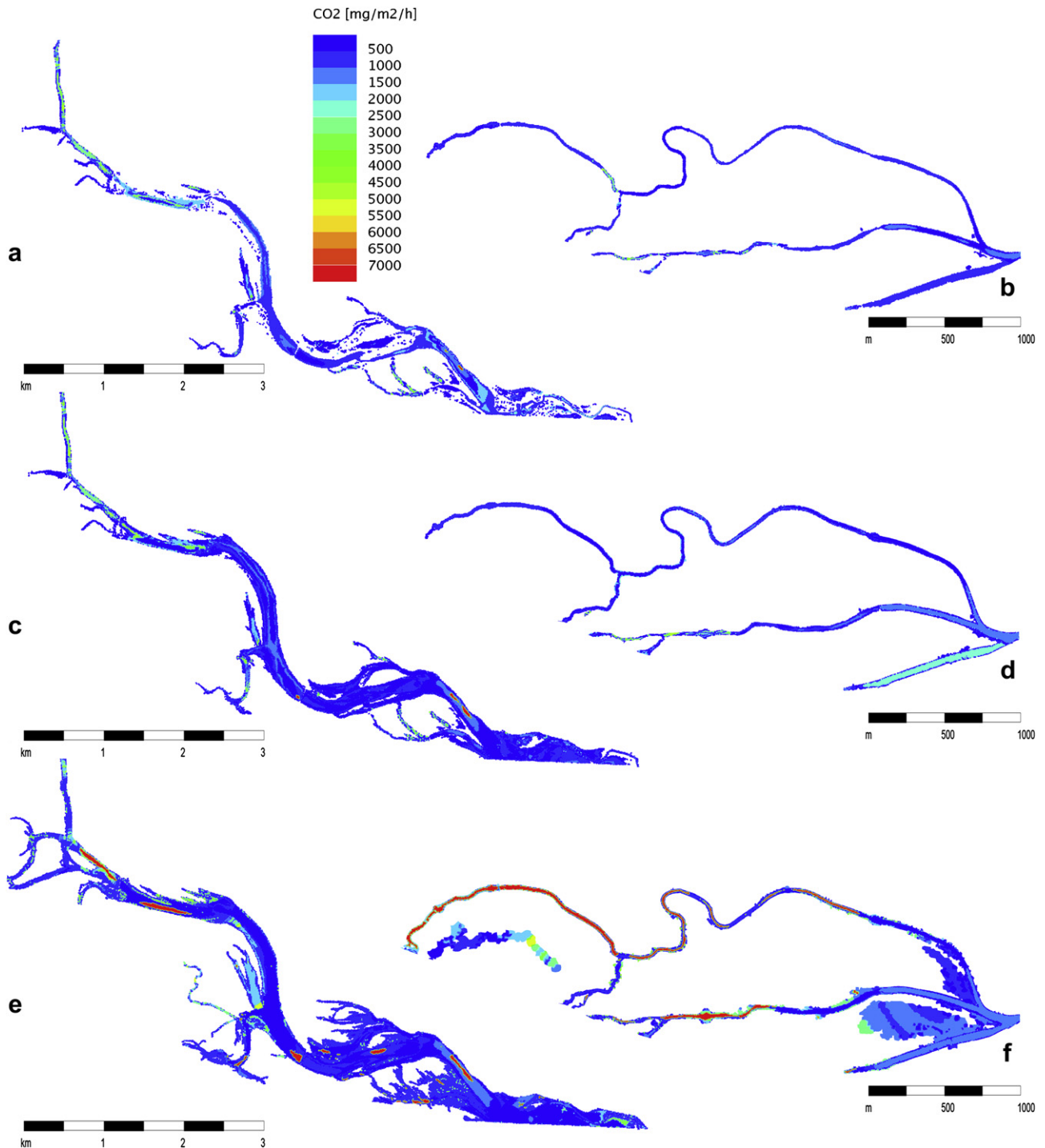

Fig. 9. Histograms of connectivity properties for both study sites, given as fraction of the total area: (a) connectivity in percent; (b) average duration of connection in days; (c) average duration of disconnection in days.
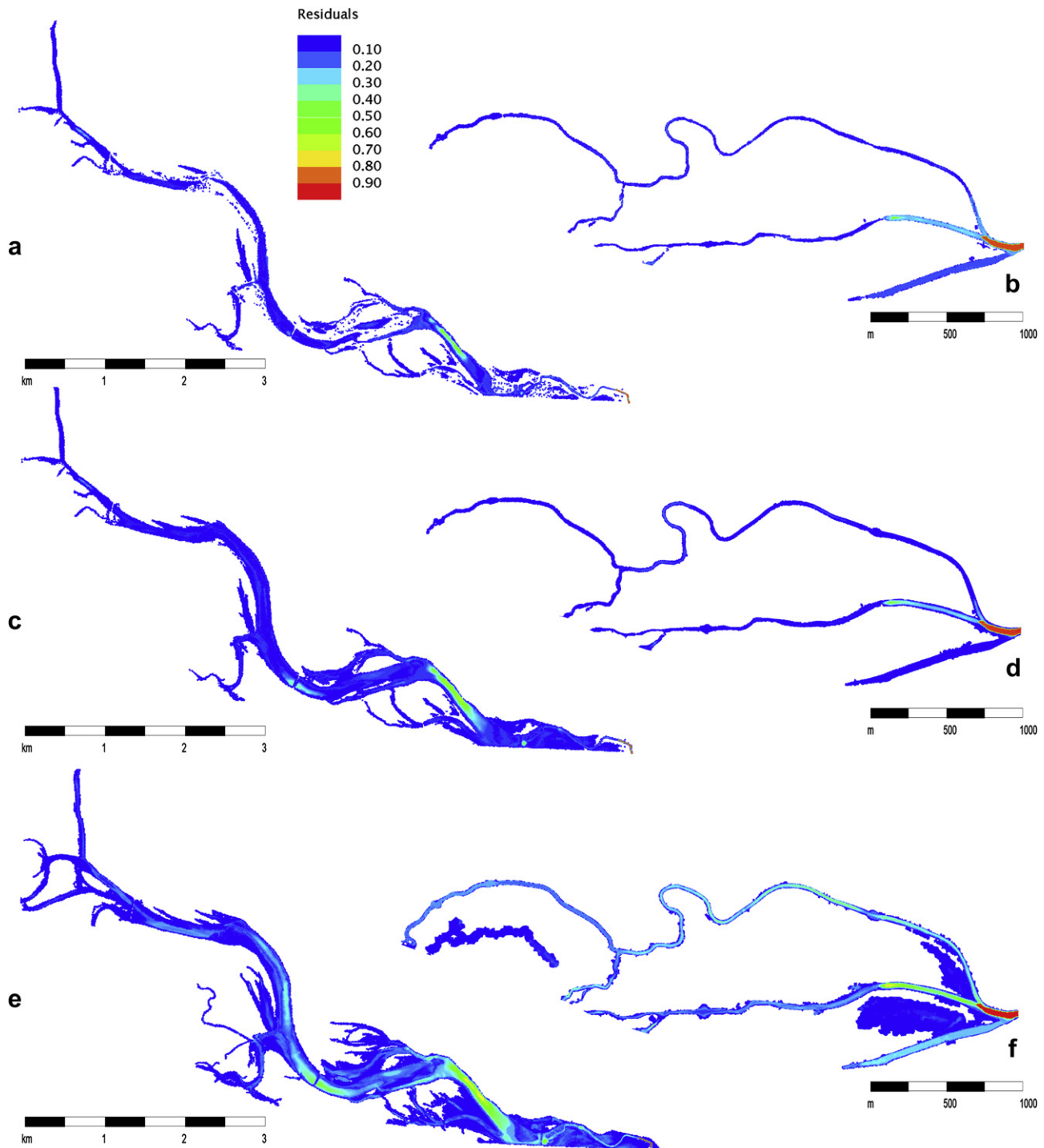
Fig. 10. Potential CO_2 emission modelling results of the output simulation module in wetted regions: (a) Lobau at 1930 $m^3 s^{-1}$ (mean flow, MQ); (b) Orth at 1930 $m^3 s^{-1}$ (mean flow, MQ); (c) Lobau at 3500 $m^3 s^{-1}$; (d) Orth at 3500 $m^3 s^{-1}$; (e) Lobau at 5300 $m^3 s^{-1}$ (annual flood, HQ_1); (f) Orth at 5300 $m^3 s^{-1}$ (annual flood, HQ_1).

of spatial parameter variability by morphological and retention structures – was visible for the Lobau. In contrast, hydrology was the prevailing factor in the Orth side arm system, as indicated by smooth patterns in the parameter distributions without major spatial discontinuities. This finding demonstrated the potential effects of restoration. A side-arm system restored through reconnection by lowering inlet elevations could be expected to exhibit generally higher connectivity values, while patterns of durations of connection or disconnection will be following the natural hydrographs of the main river rather than the discontinuities

induced by anthropogenic structures. In general, this will be accompanied by an increase in the average connection duration and a decrease in disconnection duration, particularly for areas distant from the main river.

6.2. Potential microbial sediment respiration

Following the approach outlined before, the output simulation module was run using the potential microbial respiration data and median sediment grain sizes determined from field samples as well

Fig. 11. Normalised residual maps of modelling in wetted regions: (a) Lobau at 1930 m^3 s^{-1} (mean flow, MQ); (b) Orth at 1930 m^3 s^{-1} (mean flow, MQ); (c) Lobau at 3500 m^3 s^{-1}; (d) Orth at 3500 m^3 s^{-1}; (e) Lobau at 5300 m^3 s^{-1} (annual flood, HQ$_1$); (f) Orth at 5300 m^3 s^{-1} (annual flood, HQ$_1$).

as the modelled connectivity characteristics of the study regions. The modelled potential CO$_2$ emissions for the wetted regions of both floodplain systems are depicted in Fig. 10. The potential output took values of up to 7000 mg CO$_2$ m^{-2} h^{-1}. While this is within the same range of observed data due to the underlying concept of the modelling framework, these values are far higher than actual respiration rates in the floodplain area previously found for a neighbouring side arm system by total respiration estimates (Preiner et al., 2008). However, the aim of the model was to identify

areas of increased potential microbial respiration during different hydrological conditions, not to calculate exact rates. It was found that lower discharges in the main river generally resulted in a comparably lower potential CO$_2$ output irrespective of floodplain morphology (e.g. mean flow; Fig. 10a and b). However, areas with a lower connectivity such as the upper stages of the Lobau floodplain system at the same time presented higher potential CO$_2$ emission values (up to 3000 mg CO$_2$ m^{-2} h^{-1}) than regions more frequently connected (overall less than 1000 mg CO$_2$ m^{-2} h^{-1} with

a few exceptions). While this pattern remained consistent with rising main river discharge, the potential CO_2 output increased in absolute value (Fig. 10c and d). In the Lobau floodplain, regions characterised by comparably larger water depths of 4–8 metres exhibited a few hot spots with potential output values of up to 7000 mg CO_2 m^{-2} h^{-1} for main river discharges between mean flow and annual flood level; these hot spots were not present in the Orth sidearm system as water depths were generally lower. The existence of hot spots in areas characterised by larger water depths could be due to the increased carbon accumulation rate in sediments of deeper water bodies compared to shallow water areas (<0.5 m depth) (Reckendorfer et al., unpublished).

For annual flood stage however, hot spots were identified in both floodplains investigated (Fig. 10e and f), as overall water depths showed a significant increase. These hot spots with a potential CO_2 output of over 7000 mg CO_2 m^{-2} h^{-1} were mostly found in areas characterised by lower connectivity, such as the upper stages of the Lobau floodplain, but also in sections of the Orth floodplain system connected only a couple of days per year during higher main river discharges. As widespread inundation of the floodplain side arms started during annual flood, some normally dry areas exhibited lower water depths of less than 0.5–1.0 m and also presented higher potential CO_2 output, with rates in the middle range (2000 to 5000 mg CO_2 m^{-2} h^{-1}). Environmental disturbances (i.e. flooding) have been shown to have a major impact on biogeochemical cycling in wetlands by increasing the substrate availability and stimulating bacterial activity (Song et al., 2010; Burns and Ryder, 2001). In general, the change between dry and wet phases was expected to impact the microbial activity and the oxygen availability and thus the processing of matter (Baldwin and Mitchell, 2000). These findings of the temporal and spatial distribution of potential rates underline the importance of connectivity patterns for the microbial processing and the sediment microbial activity. Yet, it should be remembered that in situ rates can deviate significantly from the measured potential rates. Changes in water temperature due to flooding and seasonality were not considered in this study; rather the relative changes occurring within the floodplain were compared. Therefore, the model output can only predict areas of potential hot spot activity in wetted areas under different flooding conditions.

Since the prediction of potential CO_2 emissions was performed using a modelling approach based on least squares residuals, the method allowed for a calculation and interpretation of the uncertainty inherent to the results presented. The square root of the residuals corresponding to the results is plotted in Fig. 11, normalised to fit the range of 0.0 (zero residuals, exact match with conditions encountered during field sampling) to 1.0 (maximum residuals, basically unobserved natural state). At mean discharge in the main river (Fig. 11a and b), the residuals were generally low for both floodplain systems, with two notable exceptions near the inlet of the Lobau and the outlet of the Orth side arm system. These states of frequent (Lobau) or permanent connection (Orth) have not been covered by field sampling due to technical difficulty. Therefore, the predictions in these regions were characterised by a higher uncertainty than those in other regions of the floodplain systems. Higher residuals were also present in areas of comparable large water depths. Again, these situations were rarely sampled due to technical difficulties; however, some data comparable to the conditions encountered were available. This is why the residuals were not as high as for the inlet/outlet sections. With rising discharge (Fig. 11c and d), the issue of unobserved situations of frequent connection was still visible, while the increasing areas of large water depths led to larger regions of higher uncertainties. A significant increase in overall uncertainty was finally encountered during the annual flood stage (Fig. 11e and f), as the combination of water depth and connectivity present under these conditions in many regions, oxbows and side arms within both floodplain systems was never observed during the field sampling campaign. However, a large number of areas and particularly those identified as hot spots by the model were still characterised by comparably low residuals and therefore low modelling uncertainty, even under annual flood conditions.

7. Conclusions

In this study a modelling framework capable of predicting patterns of potential microbial respiration in the aquatic compartment of complex floodplain landscapes has been derived. Hydrodynamics, hydrological connectivity and potential microbial respiration patterns were computed in a procedure performed in three modules. Based on the modelled water depths for characteristic discharges combined with a long-term hydrograph, flow events within the floodplain could be characterised regarding their frequency and duration at every point, eventually leading to the integrative parameters connectivity, average connection duration and average disconnection duration. These parameters were calculated for the corresponding locations of a statistically relevant number of field samples for which the potential biogeochemical output in terms of carbon had been measured. Subsequently a best-fit approach based on the method of least square errors was applied to every point within the floodplain in order to determine the sampling site that most closely resembles the environmental parameters encountered. The corresponding potential biogeochemical output was then assigned to the respective point, finally allowing for upscaling a limited number of samples to the entire floodplain and predicting potential microbial respiration patterns.

The modelling approach was used to evaluate the potential microbial respiration of the floodplain sediment under different river water discharges in two study sites at the Austrian Danube East of Vienna. Potential microbial respiration provided an assessment of the total heterotrophic respiration of the floodplain sediments and was tightly controlled by sediment aeration status, and in turn by water residence time. The spatial variability of the patterns obtained from connectivity calculations showed that a floodplain system strongly dominated by anthropogenic influences through the presence of retention structures (Lobau) was governed by geomorphology rather than hydrology, as opposed to a restored side arm system without human interference (Orth) which was mainly influenced by hydrology. The comparison of modelled and measured stage hydrographs for validation purposes exhibited good agreement, justifying the assumptions made in the design and implementation of the connectivity module.

By application of the output simulation module, patterns of potential microbial sediment respiration in the floodplains could be predicted. It was found that potential microbial respiration increases in aquatic regions of lower connectivity once they become connected during higher main river discharges. In addition, hot spots of potential CO_2 emissions were also found in areas characterised by larger water depths, which is credited to an increased carbon accumulation rate in sediments of deeper water bodies compared to shallow water areas. By plotting and analysing the residuals associated with the model output, the uncertainties corresponding to the results could be quantified. Regions of high connectivity and large water depths were found to exhibit larger uncertainties than those of low connectivity or water depth. This finding underlined that the transferability of these modelling results was given only to other floodplain systems of similar size, connectivity range and sediment properties, while the residuals and the associated uncertainty were assumed to increase if any of these parameters deviate significantly. While the modelling framework itself is invariant to the underlying hydrologic, geomorphic and sediment properties, a field sampling campaign would have to be conducted if the model was applied for floodplains differing significantly in size, connectivity or sediment quality.

The modelling framework presented here has shown to be a suitable tool to evaluate the consequences of river restoration and management on potential sediment microbial activities estimated by potential respiration. Furthermore, this modelling tool could be used to assess the effects of changing hydrology on microbial processing and to elucidate potential effects due to changed flow regimes at regional scales. Considerations for the future application of the approach include the availability of data in general, in particular regarding hydrologic and morphologic data sets, such as the length of time series observed at gauging stations or terrain elevations in reasonable accuracy. Moreover, a precondition for the applicability of the modelling framework is that hydrological connectivity between a river channel and its floodplain must be a primary driver for ecosystem processes. Future improvements of the modelling framework could be aimed towards the inclusion of actual instead of potential rates and the consideration of water temperature as additional variable; the model output could then be further enhanced by the conduction of a sampling campaign in non-saturated soils within the dry areas of the floodplain, thus eventually allowing for the calculation of actual respiration rates in the entire riverine landscape.

Acknowledgements

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Nitrogen dynamics in complex Danube River floodplain systems: effects of restoration

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with 4 figures and 3 tables

Abstract: We used a hydromorphological model to assess areas of potential high denitrification rates and nitrous oxide release in a frequently and an infrequently connected floodplain system of the Danube River under different river discharge conditions. Based on the model's projections, the decoupled floodplain was predicted to have more areas of high potential denitrification during mean and elevated discharge, but with more sites dominated by incomplete denitrification, resulting in higher N_2O emission. In the restored floodplain, frequently inundated, the model predicted that lower rates of denitrification would occur at lower river discharge levels, dominated by complete denitrification, resulting in N_2 rather than N_2O production. During an annual flood (5300 m^3s^{-1}), flooding both floodplains, the restored floodplain was predicted to have more areas of high potential denitrification activity than the decoupled floodplain. The model outputs suggest that floodplains subject to frequent inundations can effectively and efficiently use nitrate input from the main river channel, resulting in complete denitrification. Restoration measures should attempt to promote frequent inundation periods in order to fully realize the high denitrification potential of floodplain systems.

Keywords: floodplains, nitrous oxide, denitrification, restoration

Introduction

River systems are important for the biogeochemical budgets of their catchments (Behrendt & Opitz 2000), even though the depth related retention in large river channels decreases along the river continuum (Allan 1995; Alexander et al. 2000; Burt et al. 2010). Large rivers process high amounts of organic carbon (Hedges et al. 2000; Fischer et al. 2002; Fischer et al. 2005) and bio-reactive nitrogen (Gruber & Galloway 2008) playing a crucial role in the carbon and nitrogen cycling of estuarine and coastal regions (Raymond & Bauer 2001). Analysis of biogeochemical budgets indicates that river networks can remove 37–76 % of the total N-input, mainly via denitrification, with a sizeable contribution by high-order river sections (Seitzinger et al. 2002a and 2002b). Matter cycling within landscape elements is mostly related to the mode of water exchange between these riverine landscape

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elements and their water retention capacity (Carling 1992; McGinness & Arthur 2011) and in turn they impact river water quality at the larger scale (Brinson 1993; Pinay et al. 2002; Hefting et al. 2006; Lewis et al. 2006).

Large rivers and their – often extensive – floodplains are among the most productive and diverse ecosystems on our planet (Tockner & Stanford 2002). Floodplains incorporate a range of active zones, both spatially from in-channel to terrestrial and temporally from constantly to rarely connected areas (Schiemer et al. 2001; Weilhoefer et al. 2008). The distance to the main channel and the regularity of surface connectivity, i.e. flooding, determine the duration and frequency of nutrient pulses to these retention areas throughout the year (Scott et al. 2008; Fellows et al. 2011). The local morphology, i.e. width and location within the floodplain, of these areas together with the main channel's flow regime, govern the overall retention capacity of individual water bodies within the floodplain, especially during flooding (Heiler et al. 1995; Hein et al. 2004). Additionally, the intensity of exchange between surface and subsurface waters contributes significantly to the nutrient retention capacity (Hill et al. 2000).

Despite the obvious hazards, human populations have settled along river environments, with the first large settlements along the Danube River occurring 8500 years ago (Sommerwerk et al. 2009). As a consequence, rivers and their floodplains have been engineered to match society's need for development, agriculture and navigation, severely altering these ecosystems and rendering braided rivers among the most endangered ecosystems globally (Sadler et al. 2004). Numerous anthropogenic activities (e.g. dams and levees) have led to river ecosystem fragmentation, changes in matter cycling and habitat destruction, disrupting the structures and functions of lotic ecosystems (Friedl & Wüest 2002; Gergel et al. 2005):

Within the Danube River Basin, estimates suggest that about 95 % of the former floodplain areas have been lost in the Upper Danube section (Sommerwerk et al. 2009). Reduced retention areas combined with increased nutrient inputs have significantly decreased the nutrient and organic matter retention capacity along the river ecosystem; the outputs have even altered coastal ecosystems (Schmidt 2001). The remaining floodplain areas show a distinct decline of ecosystem function due to restricted hydrologic exchange (Hein et al. 2004; Reckendorfer et al. 2005); such an example can be found in the Danube River stretch downstream of Vienna.

Based on the assessment of ecological integrity, several large-scale rehabilitation and restoration projects to improve ecosystem functioning of riverine floodplains have been undertaken within the last 20 years (e.g. Jungwirth et al. 2002). Most measures have aimed at increasing the spatial heterogeneity of these ecosystems (Henry

et al. 2002). Yet, a more integrated approach including restoration of landscape dynamics and key ecosystem processes such as carbon and nutrient retention is necessary (Pedroli et al. 2002; Hohensinner et al. 2004; Canavan et al. 2007; Beechie et al. 2010). Large-scale projects should therefore also consider altered nutrient dynamics (Buijse et al. 2002) and aim at reducing nutrient transport in river corridors by increasing nutrient retention (Dahm et al. 1995; Mitsch & Day 2004).

Based on the importance of floodplain ecosystems and a better understanding on how floodplain restoration might affect nutrient cycles, the present research focused on the consequences of increasing hydrological connectivity on the potential denitrification in floodplains of the Danube River during different discharge situations. The local conditions within the floodplain provide the specific "spot" characteristics necessary for denitrification (i.e. fine sediment, low oxygen conditions, sediment pH 6–8) while the Danube River is the main source of nitrate and dissolved organic matter. During inundation, the combination of Danube River water at a site with optimal conditions can create a hot spot or hot moment where denitrification occurs (sensu McClain et al. 2003). These spots and moments can be highly variable in space and time, making them difficult to be identified and measured. Therefore, the objective of the study was to compare the temporal variability and spatial heterogeneity of a decoupled and restored floodplain system. Based on an integrated model we identified denitrification hot spots and hot moments in both floodplains.

Methods

Study site description

Two floodplain segments of the Danube River were studied: the Lower Lobau and Orth (Fig. 1). Both floodplains are located within the boundaries of the AlluvialZoneNational Park, downstream of the city of Vienna, Austria. In this area, the Danube River is a 9th order river with a drainage basin of 104 000 km^2. The flow regime has an alpine character with variable and stochastic patterns (regulated low discharge: 915 m^{3}s^{-1}, mean discharge: 1930 m^{3}s^{-1}, annual flood discharge: 5300 m^{3}s^{-1}, 30 year flood discharge: 9340 m^{3}s^{-1}). Following the major regulation scheme in 1875, the Danube River was confined between flood protection dams, effectively disconnecting the main channel from the adjacent floodplains (Chovanec et al. 2000). Restoration projects began in 1997 with the goal of reconnecting several floodplains to the main channel of the Danube (Schiemer et al. 1999; Hein et al. 2004).
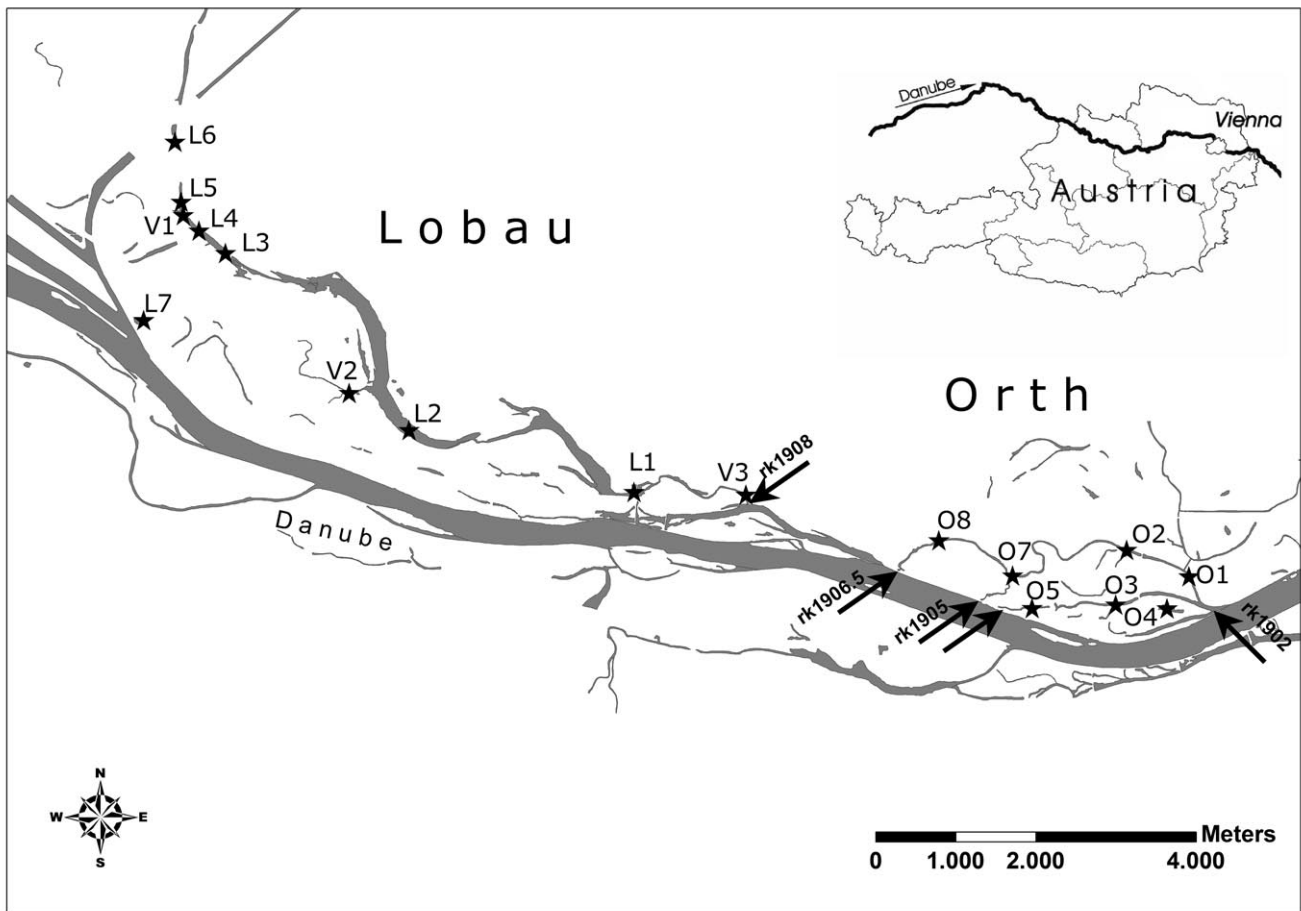
Fig. 1. Sites sampled for denitrification from 2006–2009 in the Lobau and Orth floodplain systems. Sites V1, V2, and V3 were sampled in 2010. Arrows mark the openings to the Danube River. Dashed arrows show the flow direction of the Danube River.

The Lobau covers an area of approximately 23 km². Except for ground-surface water exchange and a controlled small water intake, the primary water exchange with the main channel takes place through an artificial breach in the flood levee in the Lobau's south-eastern end (Fig. 1). Due to its regular surface water disconnection from the Danube River, for the purpose of this research, the Lobau is considered as a decoupled floodplain. Positioned at river km 1908, the opening in the flood protection dam allows surface water connection between the main river and the Lobau at discharge above 1500 m³s⁻¹ (approx. 235 days yr⁻¹). As the floodplain is connected at a downstream opening, floodwaters flow in an upstream direction into the side arms. As flood waters recede, the water discharges from the Lobau through the same opening back into the main channel of the Danube River. Three major retention structures with culverts prevent the side arms from becoming completely dry during low flow periods, resulting in shallow lake-like conditions. Phragmites sp. is present throughout the floodplain along the terrestrial aquatic boundary.

The restored sidearm system of Orth is located immediately downstream of the Lobau floodplain. It covers approximately 5.5 km² (Fig. 1), and is characterized by very diverse flow conditions. Some side arms have through-flow conditions just above summer mean flow (2230 m³s⁻¹), while others are connected only at much higher flow conditions. As part of the Danube River Restoration Project (Schiemer et al. 1999), most of the historical retention structures present in the Orth side arm system were removed, increasing the side arm discharge significantly, as well as the duration of surface water connection to the main channel, i.e. connection duration (Tritthart et al. 2009). The three openings (one at river km 1906.5 and two at river km 1905) and one outlet (river km 1902) connect parts of this side arm system to the main river at discharge of 4400 m³s⁻¹ (approx. 7 days year⁻¹), 1500 m³s⁻¹ (approx. 235 days year⁻¹), and less than 900 m³s⁻¹ (approx. 365 days year⁻¹), respectively. As a result of hydrological reconnection, the Orth floodplain is structured by the hydrology of the Danube River. The primary source of carbon, nutrients, and

sediments into the floodplain is the Danube itself. Woody debris and gravel are transported into and within the floodplains, thus constantly changing the local morphology. This is in stark contrast to the Lobau, where sediment traps throughout the floodplain change deposition patterns, and gravel and woody debris cannot be transported except during large inundation.

Modelling and statistical analysis

A numerical modelling framework (Tritthart et al. 2011) was applied for calculating connectivity properties and up scaling denitrification measurements for both study sites. Five data sets were required for this purpose: (i) a high-quality digital elevation model of the study area, derived from LiDAR and additional bathymetric measurements; (ii) a computation mesh representing the topography reasonably well, i.e. by applying local mesh refinement; (iii) water surface elevations for several characteristic discharges derived from hydrodynamic modelling; (iv) a long-term discharge hydrograph for the gauge that was used as boundary condition for the hydrodynamic model; (v) a statistically relevant number of field sediment samples and their biogeochemical properties measured in the lab. Based on these data sets, data processing was performed in three steps: (a) hydrodynamic modelling; (b) connectivity calculations; (c) output simulation, connecting biogeochemical properties to computation nodes according to a best fit of hydrological and morphological properties at sampling sites.

a) Hydrodynamic modelling and hydrological parameters

In the Danube side arm system near Orth, the 2-D hydrodynamic code Current2D (Milbradt 2002) was used to obtain water surfaces and flow velocities for a total of ten steady-state discharges in the spectrum between low flow and a one-year flood. The model solves the shallow water equations using stabilized finite elements on a triangular mesh. Turbulence is modelled by means of the Smagorinsky eddy-viscosity approach. Time discretisation is conducted by an explicit Euler technique. Previously, the numerical model was successfully applied in an analysis of the large flood of 2002 in the Danube River Basin (Tritthart & Milbradt 2003).

A different procedure was applied in the Lobau side arm system: from a modelling perspective, this system is characterized by a single boundary condition where inflow and outflow take place. In a retention system like this, the application of a hydrodynamic model is not required in order to obtain final steady-state water levels corresponding to specific discharges of the main river channel. Hence, a node-propagation technique (Tritthart et al. 2009), simplifying the governing equations of water

flow by dropping the dynamic components, was applied instead. The sediment area to water volume ratio was calculated using the RSim river simulation framework (Tritthart & Gutknecht 2007) based on the volume of water that covered a given area of sediment.

b) Connectivity calculations

Using the water surface elevations determined by the steady-state hydrodynamic simulations obtained in the previous step, characteristic discharge at a gauge were related to corresponding water levels at each mesh node. In a further step, each (hourly mean) value of a 30-year discharge hydrograph at the gauge was translated into water surface elevations at every mesh node by performing a linear interpolation within the water level range encompassed by the characteristic discharge higher and lower than the discharge for the current time step within the discharge hydrograph. Flood water levels were extrapolated based on the water surface gradient of the maximum simulated discharge. This procedure is referred to as gauge transformation. As result of these gauge transformations a local, virtual stage hydrograph for every computation node was obtained. This stage hydrograph was then converted into a time series of binary information between connected and disconnected states. Subsequently, by analysis of binary state changes, these time series were broken down into events. After a statistical evaluation, the resulting parameters for every computation node were obtained: (i) probability of connection (connectivity); (ii) average connection duration; (iii) average disconnection duration.

c) Output simulation

Besides the three connectivity properties given in the previous section, sampling sites and mesh nodes were further characterized by their respective water depths and the median diameter (D_{50}) of the sediment, resulting in a total of five model parameters. In the output simulation step, the properties of every computation node were compared with those contained in a table of all measurements (N = 116). The comparison was conducted by calculating weighted least-square differences (Tritthart et al. 2011) and applying weights for the five parameters derived statistically by Mantel tests, yielding the corresponding influence of the input on the output parameters (Table 1). Using data from a field survey completed in both the Lobau and Orth floodplains in 2006–2009, the physical conditions, nutrient, and carbon availability were used as explanatory links between hydrology and ecosystem processes (i.e., potential denitrification). Mantel and partial Mantel (controlling for effects of hydrology) statistics tested for associations between the metavariables. Mantel statistics do not have to be large, i.e. close to 1 or –1, to be

Table 1. Measured average and standard deviation (in parenthesis) of hydrological characteristics; sediment grain size, organic matter content and C:N; and rank of macrophyte coverage at each measured site.

Site	Floodplain	Duration Connection	Duration Disconnection	Water Age	Sediment D_{50}	Organic Matter	C:N	Rank: Macrophytes
		Days	Days	Days	mm	% LOI		
L1	Lobau	31.14	13.48	4.50	0.09 (0.04)	18.98 (10.34)	10.38 (3.09)	2
L2	Lobau	11.54	22.33	2.00	0.09 (0.07)	11.88 (5.16)	10.19 (1.38)	2
L3	Lobau	5.38	41.40	21.50	0.51 (0.61)	8.47 (7.41)	10.06 (1.74)	4
L4	Lobau	3.81	79.60	15.00	0.14 (0.23)	9.72 (6.25)	11.09 (2.23)	3
L5	Lobau	3.81	79.60	23.00	0.06 (0.00)	11.21 (10.79)	9.56 (1.29)	3
L6	Lobau	3.81	79.60	12.80	0.14 (0.17)	6.39 (2.77)	11.04 (2.34)	4
L7	Lobau	2.50	830.40	13.00	1.96 (2.17)	10.22 (3.58)	10.02 (1.23)	3
O1	Orth	16.07	19.44	26.50	0.08 (0.03)	1.89 (0.73)	15.69 (5.58)	1
O2	Orth	16.07	19.44	26.50	0.07 (0.04)	2.21 (0.84)	18.29 (6.99)	1
O3	Orth	3.10	288.25	44.00	0.06 (0.02)	3.35 (1.19)	15.98 (4.65)	0
O4	Orth	4.93	60.97	32.00	0.06 (0.01)	3.05 (0.35)	17.75 (1.63)	0
O5	Orth	4.93	60.97	32.00	4.16 (0.66)	0.38 (0.07)	28.67 (3.62)	0
O7	Orth	7.76	30.58	22.67	0.23 (0.14)	0.90 (0.79)	18.37 (9.07)	0
O8	Orth	5.76	39.16	43.50	0.04 (0.03)	3.45 (1.61)	14.84 (4.59)	3

statistically significant. All Mantel calculations were done with R 2.9 statistical software (R-Development-Core-Team 2005), using the packages vegan (Oksanen et al. 2010) and sem (Fox et al. 2010). These links demonstrated to which extent the relationship between the floodplain hydrology and the potential denitrification was mediated by the geomorphological context of the area. The potential denitrification rates at the measurement point yielding the minimum difference were taken as representative for the computation node. Hence, simulated potential denitrification properties were determined for the entire computation mesh, allowing for plotting them in maps.

Field sampling

Fourteen sites were selected in the side arms of the Lobau and Orth floodplains, using the connectivity model to encompass varying hydrological and morphological characteristics and sampled between 2006 and 2009 (Fig. 1). Three additional sites were selected and used as a validation set for the integrated model (Fig. 1). All sampling occurred during the growing seasons under periods of stable hydrological conditions, when the Danube River was not experiencing a flood event. Triplicate sediment samples of 5–10 cm depth were taken randomly using a PVC corer (internal diameter 5 cm) in deep and shallow macrophytes-free areas within the floodplain side arm channel of each sampling site. Each triplicate sample was a homogenized mixture of 3–5 sediment cores from one loca-

tion which were mixed to provide a representative sample of the sampling location. To estimate the amount of macrophytes and terrestrial leaf litter, sites were ranked on a 0–5 scale following Udy et al. (2006), with 0 when neither macrophytes nor leaf litter were present and 5 with 100 % coverage.

Three sites were selected outside of the original dataset to check the validity of the model, as they were predicted to be areas of increased denitrification during elevated discharge. Triplicate sediment cores were taken from the validation sites (V1-3) during elevated discharge (3,500 m^3s^{-1}) and measured for both DEA and $N_2O:N_2 + N_2O$. Sites were chosen in the Lobau floodplain since the Orth floodplain was inundated during elevated discharge and sampling was not possible.

Sediment and water characteristics

Dry weight of the sediment samples was determined by oven-drying sediments at 70 ˚C to constant mass. Organic N and C concentration were measured with an elemental analyser (EA 1110, CE Instruments, Milan, Italy) connected to an isotope ratio mass spectrometry IRMS (DeltaPLUS, Finnigan MAT, Bremen, Germany). Dried sediments were size fractioned using a sieve tower. Sediment D_{50} was calculated from the sediment grain size. Organic matter content of the sediment fractions was determined as weight loss on ignition (LOI %) of dry sediment at 450 ˚C for 4 hours.

Nitrogen and phosphorus analysis

Nitrogen concentrations in the sediment were analysed for $N-NH_4^+$, $N-NO_3^-$, and $N-NO_2^-$ using standard colorimetric methods (APHA, 1998) for a continuous flow analyser (CFA, Systea Analytical Technology). Phosphorus fractions of inorganic P (HCl extraction), organic P (HNO_3), and soluble reactive P (water extraction) were determined following the protocol of Ruban et al. (2001) and using a continuous flow analyser (CFA, Systea Analytical Technology). From each site, a 50ml water sample was taken and filtered through a GF/F (Whatman) filter to analyse $P-PO_4$ $N-NH_4$, $N-NO_3$, and $N-NO_2$ using a continuous flow analyser (CFA, Systea Analytical Technology).

Potential denitrification enzyme activity (DEA)

Potential denitrification enzyme activity (DEA) was measured according to Smith & Tiedje (1979). Ten grams (fresh weight) subsets of sediment samples were weighed into 100 ml serum flasks, which were made anoxic by flushing the flask atmosphere with N_2. After adding 1 mg

C g^{-1} sediment (added as glucose) and 0.2 mg N g^{-1} sediment (added as KNO_3),the flask contents were shaken and incubated with 10 % (v/v) acetylene to block the last step of denitrification (N_2O reduction to N_2). DEA rates were calculated as the rate of N accumulated as N_2O in the headspace after 4 h in dark at 25 °C and analysed by gas chromatography with [63]Ni electron capture detector (HP 5890II GC). DEA was measured under the same conditions but without acetylene to determine the proportion of N denitrified as N_2O during the assay (DEA_{N2O}).

Statistics

All measured site characteristics (chemical, physical, and hydrological) were compared between floodplains using Mann Whitney U tests with the SPSS software package.

Results

Hydrology and nutrient characteristics and DEA

Clear hydrological differences (i.e. duration of disconnection and water age) exist between the sites in the Lobau and in the Orth floodplain (Table 1). While a small difference in the average duration of connection was estimated between the floodplains (average Orth = 10.1 days; average Lobau = 10.3) (U = 1674 p<0.05), the restored floodplain, Orth, had shorter periods of disconnection (average = 58 days) than the decoupled Lobau (average = 108) (U = 1653 p<0.05) and higher mean water ages (Orth = 32 days, Lobau = 11 days) (U = 504 p<0.001). Mean sediment grain size was slightly larger in the Lobau (average = 0.32 mm) than in Orth (average = 0.30) (U = 1550 p<0.05).The macrophyte development was more pronounced in the Lobau sites compared to the Orth sites (U = 637.5 p<0.001).

The organic content of the sediments tended to be higher at sites in Lobau (Lobau average = 10.1; Orth average = 2.3) (U = 498 p<0.001). The C: N ratio of the sediments showed clear differences between Orth and Lobau: in Orth, more nitrogen-depleted sediments were found. Overall, more NO_3-N was measured in the overlying water column in Orth than in Lobau (Table 2). Sediments in the Lobau contained higher concentrations of NH_4-N than in Orth.

DEA rates in sediments were much higherand more variable throughout the Lobau floodplain(average 63.9 mg N $m^{-2}h^{-1}$ ±73.6) than in the Orth floodplain (average = 5.9 mg N $m^{-2}h^{-1}$ ± 6.3) (Table 3). By comparing DEA measured with and without acetylene, a ratio between incomplete and complete denitrification ($N_2O:N_2 + N_2O$) can be calculated. This ratio was generally lower throughout the

Table 2. Measured average and standard deviation (in brackets) hydrological characteristics, leaf litter coverage, and the sediment and water nitrogen and soluble reactive phosphorus (SRP) pools at each site.

Site	Floodplain	Area: Volume	Water Depth	Dissolved Oxygen	Rank: Leaf Litter	N-NO₃	N-NO₃	N-NO₂	N-NO₂	N-NH₄	N-NH₄	SRP	SRP
			m	mg L⁻¹		mg kg dry sediment⁻¹	µg L⁻¹	mg kg dry sediment⁻¹	µg L⁻¹	mg kg dry sediment⁻¹	µg L⁻¹	µg L⁻¹	mg kg dry sediment⁻¹
L1	Lobau	0.99	2.2	9.50 (0.0)	1	2.70 (0.24)	675 (0.01)	0.24 (0.28)	10 (0.01)	132.06 (147.15)	9 (0.01)	0 (0)	0.30 (0.31)
L2	Lobau	1.06	1.6	9.36 (1.8)	1	11.90 (13.11)	230 (30.93)	0.21 (0.22)	4 (1.59)	71.68 (86.18)	32 (17.85)	3.60 (5.33)	0.39 (0.39)
L3	Lobau	1.11	0.7	7.85 (1.3)	3	5.07 (4.31)	173 (118.67)	0.21 (0.31)	3 (1.09)	83.86 (125.61)	16 (4.31)	0 (0.01)	1.78 (2.77)
L4	Lobau	0.92	1.4	5.20 (0.0)	4	3.02 (5.77)	88 (0.01)	0.71 (1.02)	2 (0.01)	427.68 (588.15)	30 (0.01)	3 (0.01)	2.63 (2.47)
L5	Lobau	1.10	1.4	5.20 (0.0)	4	0.63 (0.04)	82 (0.01)	0.07 (0.04)	2 (0.01)	12.63 (5.19)	40 (0.01)	3 (0.01)	2.35 (1.57)
L6	Lobau	1.14	1.4	3.00 (0.0)	5	3.27 (6.48)	80 (0.01)	0.45 (0.58)	1 (0.01)	132.88 (185.87)	36 (0.01)	0.6 (0.01)	0.78 (0.96)
L7	Lobau	1.33	2.6	10.59 (0.0)	4	3.95 (0.01)	200 (0.01)	1.34 (1.12)	2 (0.01)	795.38 (814.27)	10 (0.01)	4 (7.54)	3.61 (3.66)
O1	Orth	1.27	1.2	10.46 (0.2)	3	5.53 (5.10)	814 (685.05)	0.22 (0.20)	6 (1.99)	31.43 (39.74)	28 (22.08)	0 (0)	0.47 (0.30)
O2	Orth	1.27	1.5	10.70 (0.0)	3	8.84 (4.91)	758 (733.45)	0.18 (0.13)	6 (1.79)	22.51 (20.85)	22 (6.86)	0 (0)	0.95 (0.37)
O3	Orth	1.80	0.8	4.76 (0.0)	2	*	15	0.39 (0.06)	1	89.65 (52.99)	393 0	13	0.49 (0.36)
O4	Orth	1.80	0.3	13.26 (0.0)	2	*	441	0.11 (0.05)	9	25.83 (6.19)	95	3	0.35 (0.04)
O5	Orth	1.80	0.3	10.63 (0.0)	3	*	1703	0.03 (0.02)	28	8.65 (2.45)	70	9	0.15 (0.10)
O7	Orth	1.09	0.7	7.87 (3.0)	2	5.34 (2.30)	1000 (685.89)	0.09 (0.09)	5 (3.50)	5.35 (2.45)	18 (4.22)	8 (0.01)	0.44 (0.09)
O8	Orth	1.27	1.1	12.35 (1.7)	4	6.43 (5.00)	784 (0.01)	0.30 (0.26)	11 (9.69)	81.83 (87.13)	18 (3.48)	2 (0.01)	1.11 (0.73)

Table 3. Measured average and standard deviation (in brackets) denitrification enzyme activity rates with (DEA) and without acetylene (DEA$_{N2O}$) and the ratio DEA: DEA$_{N2O}$ (N$_2$O: N$_2$ + N$_2$O).

Site	Flood-plain	n	DEA	DEA$_{N2O}$	N$_2$O : N$_2$ +N$_2$O
			mg N m^{-2} h^{-1}	mg N m^{-2} h^{-1}	
L1	Lobau	12	100.45 (67.84)	105.47 (115.16)	0.66 (0.69)
L2	Lobau	3	197.93 (31.32)	198.18 (39.05)	1.00 (0.04)
L3	Lobau	5	27.58 (9.20)	4.76 (3.33)	0.18 (0.11)
L4	Lobau	12	20.52 (12.94)	8.57 (6.35)	0.46 (0.30)
L5	Lobau	6	21.62 (20.74)	15.66 (11.17)	0.94 (0.34)
L6	Lobau	11	24.36 (18.25)	2.67 (4.22)	0.07 (0.08)
L7	Lobau	15	55.00 (53.23)	49.17 (65.76)	0.47 (0.59)
O1	Orth	8	8.84 (9.00)	2.46 (2.95)	0.27 (0.25)
O2	Orth	6	8.00 (5.36)	1.92 (1.96)	0.28 (0.42)
O3	Orth	6	0.25 (0.25)	0.06 (0.01)	0.50 (0.32)
O4	Orth	3	0.45 (0.25)	0.05 (0.01)	0.16 (0.10)
O5	Orth	3	0.45 (0.28)	0.04 (0.01)	0.10 (0.05)
O7	Orth	4	2.08 (0.85)	0.18 (0.11)	0.08 (0.04)
O8	Orth	6	15.48 (7.75)	3.96 (3.60)	0.22 (0.15)

restored Orth floodplain (average = 0.24 ± 0.15) than in the Lobau (average 0.54 ± 0.34), with the lowest ratios calculated in the middle section of the Orth floodplain.

Model results of potential denitrification and nitrous oxide production

Using the model-integrated framework, maps of potential denitrification for riverine water levels in the two floodplains (Figs 2 & 3) were created. At mean (1930 m^{3}s^{-1}) and elevated discharge (3,500 m^{3}s^{-1}) few isolated areas (3.5 % and 3 % of the total wetted area, respectively) in the Lobau displayed high potential denitrification rates (defined as predicted rates above 75 mg N m^{-2}h^{-1}) (Fig. 2).

Areas in the decoupled floodplain were dominated by N$_2$O production (defined as N$_2$O:N$_2$ + N$_2$Oratios above 1) during mean and elevated discharge levels (15 % and 22 % total wetted area, respectively), yet the few spots of predicted higher denitrification potential had a lower N$_2$O:N$_2$ + N$_2$Oratio (Fig. 3). At HQ1 (5300 m^{3}s^{-1}) the total wetted area was predicted to increase from 11 % during mean discharge to 25 % although this area with predicted high potential denitrification drops to 4 %. Overall, the N$_2$O:N$_2$ + N$_2$Oratio decreases with an annual flood (8 %).

In the restored floodplain, Orth, fewer denitrification hot spots during both mean (1930 m^{3}s^{-1}) (0.4 %) and elevated (3,500 m^{3}s^{-1}) discharge levels (0.6 %) were predicted (Fig. 3). However, the Orth system has fewer predicted areas dominated by N$_2$Oproduction as 7 % and 10 % of the total wetted area indicated ratios above one during mean and elevated discharge, respectively (Fig. 3). During a HQ1 event, the newly inundated areas in the restored floodplain were predicted to be hotspots for potential denitrification (ca. 20 % of the total wetted area predicted above 75 mg N m^{-2}h^{-1}). These new areas were dominated by N$_2$ production, although the ratio of N$_2$O:N$_2$ + N$_2$O increased slightly for the overall area (ca. 18 % of the total wetted area above 1).

Using the three sites selected outside of the 14 original sampling sites, the model was validated during elevated discharge (3,500 m^{3}s^{-1}) for both DEA and N$_2$O:N$_2$ + N$_2$O. The model slightly over-estimated DEA and the N$_2$O:N$_2$ + N$_2$O in the most upstream site (V1), but for the other sites, the predicted values lie within the range of the measured values (Fig. 4).

## Discussion

Qualification of model output

In this study, we have shown how the developed modelling tool can be applied for DEA and denitrification efficiency at different riverine discharge levels in order to identify hot spots and hot moments of N cycling within two floodplain systems of different hydrological exchange conditions. This model is based on laboratory assays at optimal temperature and nutrient levels; therefore the values produced by the model cannot be directly related to the in situ conditions. Potential denitrification assays are known to have high variability due to the blocking of both denitrification and nitrification (Groffman et al. 2006), but in this case, we selected this method in order to remove the influence of in situ conditions and compare the relative rates between sites and years. This modelling tool can be used to consider the relative changes of activity within the system, which can be very useful in identifying theoretically optimal areas and conditions for denitrification.
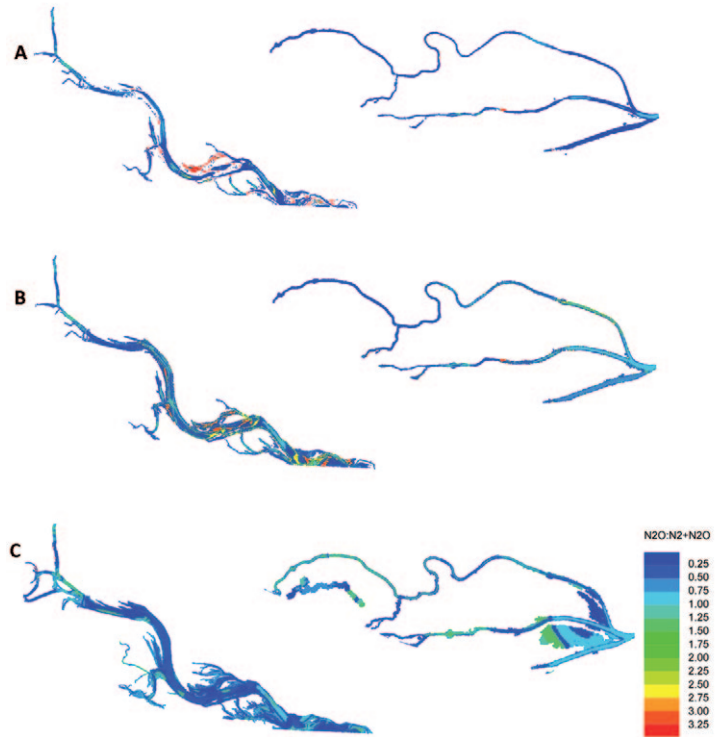
Fig. 2. $N_2O:N_2 + N_2O$ ratios as predicted by the integrated modeling tool for the Lobau (left panel) and Orth floodplains (right panel) during A) average discharge of 1900 m³s⁻¹, B) elevated discharge of 3500 m³s⁻¹, and C) annual flood discharge of 5300 m³s⁻¹.
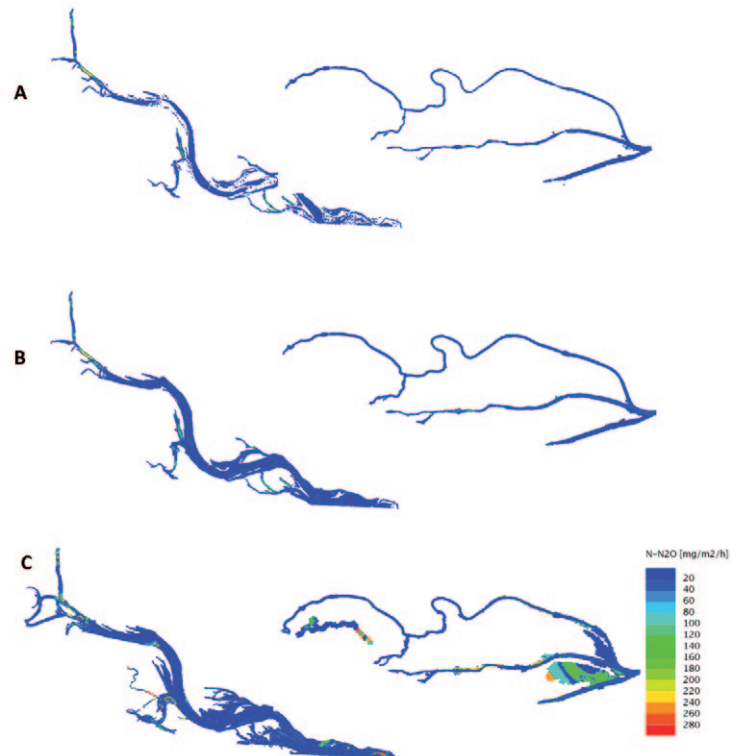
Fig. 3. Denitrification enzyme activity (DEA) rates as predicted by the integrated modeling tool for the Lobau (left panel) and Orth (right panel) floodplains during A) average discharge of 1900 m³s⁻¹, B) elevated discharge of 3500 m³s⁻¹, and C) annual flood discharge of 5300 m³s⁻¹.
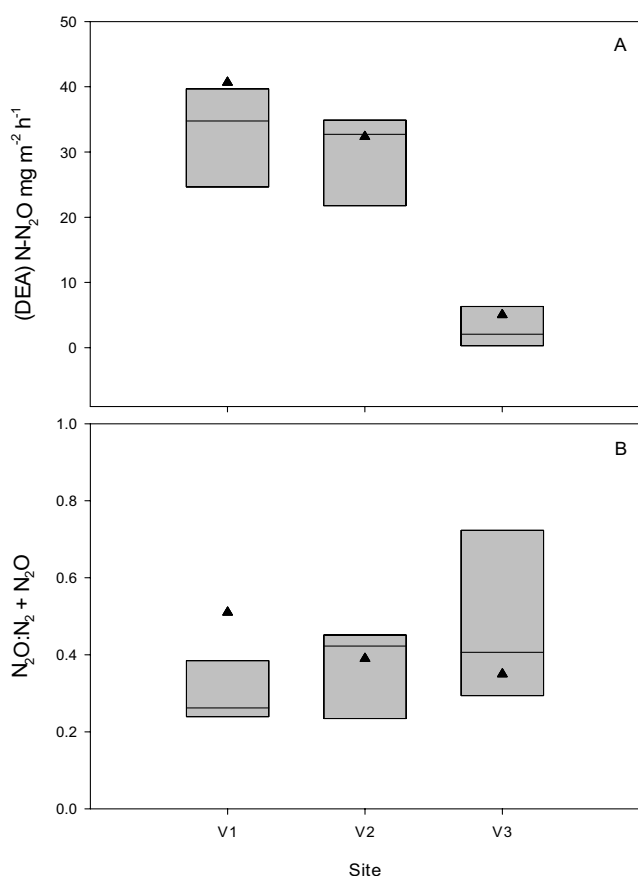
Fig. 4. Validation set for integrated model as measured and predicted during elevated discharge of 3500 m³s⁻¹. Boxplots are the measured values (n = 3) and the triangles the predicted modeled value for DEA (A) and N_2O:N_2+N_2O (B) at the respective sites.

Discharge above HQ1 were not observed during the study period, so at higher discharge model uncertainty increases. Although this is a limited sample size (N = 116) over a few years, the validation set demonstrates that it provides an accurate prediction even in conditions that were not previously measured. This tool combines both the spatial and temporal variability within floodplains to show where potential areas of activity occur.

Denitrification potential in restored floodplains

As denitrification potential is not simply controlled by surface water connection (Pinay et al. 2000; Pinay et al. 2007), it is important to consider the local morphology. The restored floodplain (Orth) has shorter periods of disconnection to the Danube River along with longer retention times (i.e. water age) than the degraded floodplain (Lobau; Tab. 1). Due to the differences in hydrology, the

local morphology and structure are different between the two floodplains with more established macrophyte communities and higher organic content in the sediment of the Lobau than in the Orth floodplain. Fine sediments were measured throughout both floodplains, providing the necessary sediment characteristics for denitrification to occur. Although the measured rates are high, especially in the Lobau floodplain, they are within the range of previously measured potential denitrification measurements in other floodplains (Fellows et al. 2011; Forshay & Stanley 2005). The large variability demonstrates the heterogeneous nature of these measurements. These changes in hydrology and site morphology caused by restoration and regulation change the biogeochemical cycling within the floodplain. In the decoupled system, Lobau, while overall higher potential denitrification was measured, the model predicted few specific sites of high denitrification. Additionally, more spots with higher N_2O:N_2 + N_2O ratios at average discharge were predicted (Fig. 2). When the Lobau is inundated at annual flood levels, these ratios are predicted to decrease. On the contrary, in the restored site, lower ratios are predicted during mean water conditions. At annual flood discharge, hot spots of lower N_2O production become noticeable (Fig. 3). This suggests that restoration by increasing the area and frequency of inundation from the Danube increases denitrification rates and stimulates complete denitrification, resulting in lower N_2O production.

Inundation into the floodplain fosters overall anoxic conditions, increasing the physical area available for denitrification (i.e. anoxic sediments). Higher amounts of nitrate are exported into the backwaters, where it is either denitrified or assimilated by biota. Sites within the Upper Mississippi have shown that backwaters are capable of high rates of nitrate removal (James et al. 2010; Kreiling et al. 2011). Inundation not only provides more surface area for denitrification, but also delivers river-derived carbon, which can be of a higher bioavailability for denitrification processes (Hadwen et al. 2010; McGinness & Arthur 2011). As demonstrated along the South River Platte, where potential denitrification were shown to be carbon-limited, the carbon originating from the surface water provided the necessary carbon source (Pfenning & McMahon1996). Along with carbon, the main source for nitrate is the river water (Hein et al. 2004) and thus, flood pulses increase nitrate concentrations in the floodplain water bodies. Low sediment nitrate concentrations were measured in both floodplains, but higher nitrate concentrations were measured in the overlying water column of the restored floodplain, which would provide the necessary substrate for denitrification (Tab. 2). Despite large variability within different habitats, as demonstrated in Mississippi coastal floodplains, an increase of nitrate can

correspond to an increase of potential denitrification (Scaroni et al. 2011). Similarly, as in the restored Baraboo River floodplains (Orr et al. 2007), increasing inundation frequency would create more areas with favourable conditions for denitrification, restoring the ability of a floodplain to respond to the variability of the riverine discharge conditions and nutrient inputs associated to it (Forshay & Stanley 2005). A long-term study of a restored wetland system has shown that frequent flood pulses results in higher nitrogen retention and denitrification than during steady flow conditions (Mitsch et al. 2008). During such inundation, denitrification can be stimulated, despite oxic conditions or dry periods (Olde-Venterink et al. 2002, Song et al. 2010, Fromin et al. 2010).

Based on the model outputs presented here, increased flooding not only increases potential denitrification, but results in N_2 rather than N_2O production (Fig. 2). The decoupled floodplain Lobau is predicted to have more areas dominated by incomplete denitrification (resulting in N_2O production) than the restored floodplain which is more frequently inundated by the Danube River. In other wetlands, $N_2O: N_2 + N_2O$ ratios have been shown to be higher in the intermittently flooded areas than in the permanently flooded areas (Hernandez & Mitsch 2007). The Lobau floodplain is dominated by permanently wet areas, which could lead to the higher ratios predicted. Nitrous oxide reductase, the enzyme responsible for the reduction of N_2O to N_2, is known to be highly sensitive to oxic conditions. In a comparison between different sediments and terrestrial soils, N_2O yields were lower in conditions with low oxygen availability (Terry et al. 1981; Beaulieu et al. 2011). As restoration increased the surface water connection and duration of inundation, and hence the overall inundated area, the area of oxic sediments decreases, which could potentially reduce N_2O production from denitrification. The fate of denitrification is of critical importance as the ratio of $N_2O:N_2$ production in riverine wetlands has far reaching implications for the global greenhouse gas balance (Verhoeven et al. 2006). As previously mentioned, the presence of acetylene can block N_2O production from nitrification. This can result in measured $N_2O:N_2 + N_2O$ ratios higher than 1. The model predicts ratios of higher than 1, which must be treated with caution. The high amount of ammonia present in some of the sites in the Lobau floodplain could provide the necessary substrate for N_2O production from nitrification. But, as sites within the Orth floodplain have lower ammonia concentrations; nitrification may be of lower importance. In soil and riparian buffer areas, N_2O production can dominate over N_2 production (Hefting et al. 2003; Ciarlo et al. 2007). Although oxygen concentration, pH, and organic matter availability are known to control N_2O production, predicting N_2O portioning is difficult, due to the spatial variability and range of variables which can control N_2O production (Garcia-Ruiz et al. 1998).The location of the predicted hot spots change along with discharge conditions, demonstrating the spatial and temporal heterogeneity of floodplain systems, and highlights one of the main challenges in understanding the specific cycling patterns of floodplains.

In accordance with the restoration changes in the floodplain (e.g. plant communities and hydrological changes), the indicators of denitrification (i.e. sediment oxygen conditions and substrate availability) are variable. In the Lobau, where inundation conditions are less stochastic, more are a sexhibit incomplete denitrification; increasing inundation frequency in such disconnected systems could result in more areas of complete denitrification, as predicted in the Orth floodplain. By limiting the frequency of inundation, the microbial communities in the Lobau floodplain may be less prone to use pulses of nitrate and different carbon substrates when they become available (i.e. during flooding). The concentration of denitrification enzymes is defined by past water regimes so that even dry sites can have active heterotrophic communities which have been primed by the previous water regime (Dendooven et al. 1996; Fromin et al. 2010). Sites which receive frequent inputs of nitrate and dissolved organic carbon from the Danube River may be likewise primed for denitrification and therefore demonstrate a tendency towards more complete denitrification. Intermittently connected sites, which experiences frequent changes in substrate variability, may be more sensitive to hydrological changes than deep water sites (Song et al. 2010). Accordingly, our model predicts that in these areas, most changes in the $N_2O:N_2 + N_2O$ ratio occur.

Implication for river systems and global cycles

Floodplains are considered to be the kidneys of the river system with high rates of nutrients and carbon cycling. During a flood, high amounts of nitrate and organic carbon substrates are transported into the floodplain and used quickly and efficiently (Gallardo 2003; Ahearn et al. 2006; Sheibley 2006). River systems have been estimated to denitrify 35 Tg N yr^{-1} (Seitzingeret al. 2006), with the majority taking place in riparian zones (Sebilo et al. 2003). Based on our model outputs, increasing variability (i.e. inundation) in the floodplain would increase the efficiency of N biogeochemical cycling and especially denitrification. Floodplains, with distinct local morphology and hydrological exchange regimes, demonstrate how variation in the hydrological exchange can alter local biogeochemical cycling. In our study, the restored floodplain would be capable of higher potential denitrification rates during an annual flood than the decoupled floodplain, al-

though lower rates are predicted at mean and elevated discharge ($3,500$ m^{3}s^{-1}). This suggests that the restored area is able to react to the changing redox and nutrient conditions more rapidly than the decoupled area. The increased variability of inputs (i.e. nitrate and carbon sources) brought into the floodplain by the main river discharge result in frequently inundated areas adapting to disturbances. These areas have the ability to react quickly to the changes in environmental conditions, i.e. oxygen, temperature, and chemistry. Areas rarely connected are not adapted to react quickly to changing conditions. These discrepancies within a floodplain create a complex temporal and spatial biogeochemical pattern based on the overall hydromorphological situation of the floodplain.

In regulated braided river stretches, restoration measures should be aimed at increasing the hydrologic exchange patterns between different landscape elements (i.e. frequent inundation) in order to exploit the cycling capacity of a floodplain (Opperman et al. 2010). The intensified cycling capacity at local scales stimulated by restoration measures can affect nutrient transport at larger scales (Stadmark et al. 2009).

Yet, as demonstrated here, when floodplains are decoupled for long periods of time from the main channel, denitrification potential rates decrease. This model gave insights as to where and when denitrification can occur within two floodplain systems. Further research efforts are needed to understand the effects of hydrological exchange at the landscape scale and the underlying mechanisms which cause more efficient biogeochemical cycling in floodplains. Addressing this gap will improve the understanding of restoration effects in complex riverine landscapes.

Acknowledgments

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Mimicking floodplain reconnection and disconnection using ^{15}N mesocosm incubations

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Abstract

Restoration of floodplains changes the nitrate delivery pattern and dissolved organic matter pool in backwaters. However, the effects of these changes in floodplains are not well known. Thus, two experiments were performed to elucidate the effect of nitrate delivery and dissolved organic matter (DOM) quality on nitrate metabolism in two types of floodplains. Rates of denitrification, dissimilatory nitrate reduction to ammonium (DNRA) and anammox were measured using ^{15}N tracer approaches in mesocosms incubations from undisturbed floodplain sediments originating from a restored and isolated site in the Alluvial Zone National Park on the Danube River downstream of Vienna, Austria. DNRA rates were an order of magnitude lower than denitrification, with higher rates measured in the isolated site, while neither rate was affected by changes in nitrate delivery pattern or organic matter quality. Anammox was not detectable in any of the sites. Denitrification was competing with assimilation which was estimated to use up to 70% of the available nitrate. Overall, denitrification was higher in the restored sites, with mean rates of 5.7 ± 2.8 mmol N m^{-2} h^{-1} compared to the isolated site (0.6 ± 0.5 mmol N m^{-2} h^{-1}). Denitrification rates were higher in the restored site, but also more complete, (i.e. with lower calculated $N_2O:N_2$ ratios). Nitrate addition did not have any effect on denitrification, nor on the $N_2O:N_2$ ratio. However, DOM quality significantly changed the $N_2O:N_2$ ratio in both sites. Addition of riverine derived organic matter lowered the $N_2O:N_2$ ratio in the isolated site, whereas addition of floodplain derived organic matter increased the $N_2O:N_2$ ratio in the restored site. These results demonstrate that increasing floodplains hydrological connection to the main river channel increases nitrogen retention and decreases nitrous oxide emissions.

1. Introduction

Floodplains are biogeochemical hot spots for carbon and nitrogen cycling and storage (McClain et al., 2003). Depending on the local morphology and hydrology (i.e. vegetation, mean water depth, redox conditions, sediment type, and discharge pattern), floodplains can act either as a carbon and nitrogen sink via microbial respiration and denitrification or as a source via organic matter production or nutrient export (Pinay et al., 2007). Flood pulses control organic carbon transformations and processes in floodplains and can trigger an increase of bacterial enzyme activity (Burns and Ryder, 2001; Wantzen et al., 2008). Surface water derived carbon and benthic organic carbon are adequate sources of energy for denitrification when these areas are receiving high nitrate inputs during floods (Arango et al., 2007; Pfenning and McMahon, 1996). Yet, several results suggest that none of these factors alone controls denitrification (Dodla et al., 2008; Sutton-Grier et al., 2009; Wall et al., 2005).

Denitrification, a particular form of microbial respiration, is a process controlled by O_2, NO_3, and C availability (Knowles, 1982) which reduces nitrate (NO_3^-) to nitrite (NO_2^-), nitric oxide (NO), nitrous oxide (N_2O), and ultimately to dinitrogen (N_2) (Zumft, 1997). Incomplete denitrification results in the production of N_2O, a greenhouse gas with 300-times the warming potential of CO_2 and a precursor molecule for ozone-depleting NO radicals in the stratosphere (Bates et al., 2008; Dickinson and Cicerone, 1986). With rates ranging from 0 to 345 µmol N m^{-2} h^{-1}, rivers systems are estimated to contribute approx. 1Tg N y^{-1} to the global N_2O emissions (Seitzinger, 1988). Up to 80% of denitrification is estimated to occur in soils and freshwater systems (Galloway et al., 2008).

For instance, the Lotic Intersite Nitrogen Experiment (LINX II) found that denitrification increases with increasing nitrate concentrations, while the efficiency of denitrification declined with rising concentrations, despite a small peak of improved efficiency with elevated nitrate concentrations, particularly in larger streams (Mulholland et al., 2008). In the Upper Mississippi, denitrification in the floodplains was nitrate limited throughout the growing season, but the backwaters were capable of reacting quickly to a pulse of nitrate as shown by Richardson et al. (2004). Increasing nitrate loads has also been shown to increase the N_2O emissions in both field and laboratory experiments (Barnard et al., 2005; Verhoeven et al., 2006).

Dissimilatory nitrate reduction to ammonium (DNRA) and anammox, two other anoxic nitrate removal processes, are also of interest in floodplains (Burgin and Hamilton, 2007). DNRA has the same environmental requirements as denitrification (anoxia, high nitrate and carbon substrate availability), but rather than a removal pathway, bioreactive nitrogen is conserved and nitrate transformed into a more bio-available form (ammonium). Although DNRA has been reported as a significant pathway in marine and terrestrial systems accounting for 15-75% of nitrate removal (An and Gardner, 2002; Morley and Baggs, 2010), it may be a minor route of nitrate removal in wetland systems (Matheson et al., 2002; Scott et al., 2008). While there are few studies that explicitly measured DNRA rates in floodplains, DNRA bacteria have been shown to survive in frequently flooded areas (Sgouridis et al., 2011). With restoration, the ratio of denitrification: DNRA may change along with the changing morphology and substrate availability, thus altering the nitrogen balance (Fazzolari et al., 1998). Anammox, the anaerobic oxidation of ammonium coupled to nitrite reduction with N_2 as the end product, is present throughout the marine system, but its presence in floodplains is not well known (Jetten, 2001). Few studies have measured this pathway of nitrate removal in freshwater systems, let alone in riverine floodplains (Zhu et al., 2010). However, autotrophic NO_3 assimilation can be a dominating pathway in freshwater ecosystems and perhaps even out-compete denitrification, DNRA and anammox for substrates (Hall et al., 2009; James, 2010).

Historically in Europe, river floodplains have been decoupled from their rivers, resulting in an alteration of the natural nutrient spiraling. As a result, nutrients are transported downstream without being incorporated in floodplain biogeochemical processes (Hein et al., 2004; Tockner et al., 1999). Recent floodplain restoration efforts involve reconnecting the floodplain to the river, reestablishing the flow regime and altering the nutrient load in the floodplain (Buijse et al., 2002). Restoration of large floodplains via surface water reconnection provides an opportunity to observe the effects of changing nitrogen and carbon pools on denitrification, DNRA and anammox activity. Indeed, it is necessary to understand how these restoration efforts affect floodplain nitrogen removal and N_2O emissions in riverine landscapes (Welti et al., 2012).

We hypothesized that the restoration of the hydrological exchange conditions between a river and its floodplain (i.e. hydraulic reconnection) would mainly enhance denitrification rates by

increasing nitrate and easily mineralizable organic carbon availability. We established two experiments in order to separate the effects of the riverine nitrate input and changes in DOM composition on the rate of anammox, DNRA, denitrification and the proportion of N_2O produced as an end product relative to the produced N_2 pool (N_2O: N_2). We undertook these experiments on two types of sediment originating from disconnected (isolated) and reconnected (restored) floodplains of the Danube River, downstream Vienna, Austria, incubated in large mesocosm chambers.

We hypothesized that isolated sites, being naturally nitrate depleted, would present lower denitrification rates than connected sites under high nitrate input, and would present higher N_2O to N_2 ratio. We tested this hypothesis by measuring the response of the denitrifying community of both isolated and restored sites to pulsed or constant (over a 5 days period) input of ^{15}N labeled nitrate. We also hypothesized that adding Danube River water would increase the denitrification rate in the isolated site due to labile DOM components and a more heterogeneous carbon pool present in the Danube River. The resulting $N_2O:N_2$ ratio would decrease due to an increase of carbon substrate available. Therefore, we incubated isolated sediment with high nitrate levels and riverine dissolved organic carbon to determine whether this treatment would enhance its denitrification rate and decrease the $N_2O:N_2$ ratio.

2. Methods

2.1. Study Site Description

Two sites were chosen within the boundaries of the Alluvial Zone National Park, located downstream of the city of Vienna, Austria. In this area, the Danube River is a 9th order river with a drainage basin of 104 000 km^2. The flow regime has an alpine character with variable and stochastic patterns (regulated low discharge = 915 m^3s^{-1}, mean discharge = 1930 m^3s^{-1}, annual flood discharge = 5300m^3s^{-1}, 30 year max. flood discharge = 9340 m^3s^{-1}).

The two chosen sites represent (1) a typical disconnected, backwater pool (isolated), located in the Lower Lobau floodplain, and (2) a reconnected channel site (restored) located in the restored floodplain Orth. The restored site is connected via surface water exchange to the Danube main channel more often and for longer periods than the isolated site (Table 1). The difference in hydrological conditions of the two sites also impacts their average water

chemistry, with the restored site receiving frequent inputs of NO_3^- from the Danube (Table 1). These sites were chosen because they represent two distinct floodplain morphologies (channel vs. pool) and were predicted by a model to react differently with increasing hydrological connection in terms of sediment respiration (Tritthart et al., 2011) and potential denitrification (Welti et al., 2011).

The Lower Lobau floodplain, downstream of Vienna, covers approximately 23 km². Except for groundwater-surface water exchange and a controlled small water intake, the primary water exchange is through an artificial small breach in the flood levee located at the downstream end at 1908 river km.This artificial opening in the flood protection dam allows limited connection to the main river at discharges above 1500 m³s^{-1} (approx. 235 days year^{-1}). Three major retention structures with culverts prevent the side arms to fall completely dry during low flow periods, resulting in shallow lake-like conditions throughout the floodplain. The selected sampling site (Isolated) is typical of this floodplain as it is a shallow pool, dominated by groundwater flow and rarely connected to the Danube River via surface water. High macrophyte coverage and stands of *Phragmites sp.* are present at this site.

The floodplain Orth is directly downstream of the Lower Lobau, covering approximately 5.5 km² (Figure 1), and featuring very diverse flow characteristics. Generally characterized as a through-flow system above a river discharge of 2230 m³s^{-1}, some sites are only connected during higher discharges. Most of the historical retention structures present in the Orth floodplain have been removed in recent years, increasing the side-arm discharge significantly as well as the connection duration (Tritthart et al., 2009). The three openings (at river km 1906.5 and two at river km 1905) and one outlet (river km 1902) connect parts of this side-arm system to the main river at discharges of 4400 m³s^{-1} (approx. 7 days year^{-1}), 1500m³s^{-1} (approx. 235 days year^{-1}), and less than 900m³s^{-1} (approx. 365 days year^{-1}), respectively. The selected sampling site (Restored) is a flow-through channel site, bounded on one side by a gravel bend and the other by fine silt and sand. No macrophytes or other floating vegetation are present at this site.

2.2. Mesocosm Sampling

The Plexiglas mesocosms used for sampling and incubation were 50cm tall with a diameter of 24cm (total volume: 22.6L). An open bottom is closed by screwing on the bottom plate

which seals the mesocosm tightly (Figure 2). Three sets of sediment cores (depth = 10cm) and the overlying water column (15-17L) (n = 9) were taken from each site. In the field, the mesocosms were emptied except for the last 2L of water in order to maintain sediment saturation and anoxic conditions during transport. Black plastic sheeting was wrapped around the sediment column in order to prevent light penetration into the sediment column. Upon return to the lab, the mesocosms were re-filled with *in situ* water, which had been collected and filtered on site (10µm) to remove large phytoplankton assemblages, macrophytes, and coarse sediments. Triplicate cores were connected to a reservoir containing 40L of filtered site water. Water was pumped via a peristaltic pump from the reservoir to the individual cores at a rate of $5L\,hr^{-1}$, creating a residence time of approximately 2 hours in each mesocosm. Mixing tests prior to the start of the experiments showed complete mixing within the mesocosms. The mesocosms were completely closed to the atmosphere, but the reservoirs were open. Between the mesocosm triplets and the reservoir, a filter (10µm) prevented large phytoplankton assemblages from occurring and removed coarse suspended sediments. In order to prevent 29/30 N_2 accumulation in the mesocosm cores, water in the reservoirs was bubbled with air before returning to the mesocosms. All corers were kept at constant *in situ* water temperature at the time of sampling (range 19-22°C) for the entirety of the incubation with 12h dark/light cycles.

2.3. Tracer Addition

In order to mimic the chemistry of a flood, two incubation setups were used - one to follow the effect of nitrate input (Experiment 1), the other to follow the effect of changing DOM composition (Experiment 2). Mesocosms were stabilized for 48h until N-NO_3 and N-NH_4 reached constant concentrations. Following the 48h stabilization period, labeled nitrate ($K^{15}NO_3$) was added to each of the treatments to quantify nitrate transformations throughout the experiments.

2.4. Experiment 1 & 2

The purpose of Experiment 1 was to simulate the nitrate input of either flooding or long-term surface water reconnection. Following the stabilization phase, the mesocosm either received 1) a spike addition (PEAK) of ^{15}N-NO_3 (target concentration: 130 µmol ± 10%) or 2) a constant addition of ^{15}N-NO_3 to maintain a concentration of 75 µmol ± 10%

(PLATEAU).The control treatment (CONTROL N) received no increase in absolute nitrate concentration, but labeled ^{15}N-NO$_3$ was added to increase ^{15}N to circa 20 AT%.

In Experiment 2, *in situ* water was replaced with water from 1) an open backwater pool in the Lobau (POOL) or 2) the Danube main channel (RIVER) in order to assess the role of the available organic matter source on denitrification rate and the N$_2$O:N$_2$ ratio. For control treatment (CONTROL C), no water was exchanged and water originating from the sampling site was used. Once the chambers were re-filled, ^{15}N-NO$_3$ was added to a concentration of 130 µmol ± 10% to all treatments and kept constant for the five day incubation in order to prevent N limitation for denitrification.

2.5. N measurements

Water column sampling occurred through a tube extending into the water column, ending 1cm above the sediment surface, separated from the atmosphere with a three-way stopcock. Water samples for nutrients, dissolved gases, and isotope analysis were collected using the protocols established in the NICE handbook (Dalsgaard et al., 2000). Water samples were taken at times 0, 2, 4, 8, 10, 24, 36, 48, 72, 96, and 108 h through the tube with a 60ml syringe. Water samples (50ml) for N-NH$_4$, N-NO$_3$, and N-NO$_2$ were filtered through a Whatman GF/F filter (pore size 0.7µm) and analyzed using a continuous flow analyzer (CFA, Systea Analytical Technology).

Before the incubations, 50g sediment subsamples were taken from the field site and again upon completion of the incubation from the incubated sediments. Nitrogen concentrations in the sediment were analyzed for N-NH$_4^+$ (KCl extraction), N-NO$_3^-$, and N-NO$_2^-$ (H$_2$O extraction) using standard colorimetric methods for a continuous flow analyzer (APHA, 1998; CFA, Systea Analytical Technology). Organic matter content of the sediment fractions was determined as weight loss by ignition (LOI %) of dry sediment at 450˚C for 4 hours. Dry weight of the sediment samples was determined by oven-drying sediments at 70˚C to constant mass.

2.6. N species isotope composition

To measure the isotopic composition of N$_2$ and N$_2$O, water samples (50ml) were collected by 60ml plastic syringes equipped with a 10cm long Nalgene® tube at sampling times 0, 2, 4, 8,

10, 24, 36, 48, 72, 96, and 108 h. The syringe was flushed with sample water prior to the transfer of the actual sample and no bubbles were present during sampling. The water was transferred to a gas tight vial (12ml Exetainer, Labco, High Wycombe, UK) which was filled without air bubbles and preserved with 250µl $ZnCl_2$ (50% m/v).

N_2 and N_2O were extracted from the water in the Exetainers by introducing a helium headspace to remove 6 ml of water which was simultaneously replaced with an equivalent volume of He. Vials were shaken vigorously for 5min so that more than 98% of the N_2 and N_2O would be in the headspace (Weiss, 1970). All vials were frozen and shipped to LMGEM (CNRS Marseilles, France) for analysis. Corrected against air, samples were measured for $^{28}N_2$, $^{29}N_2$, $^{30}N_2$, $^{44}N_2O$, $^{45}N_2O$, $^{46}N_2O$, Ar, and O_2, with a mass spectrometer (Quadruple mass spectrometer Anagaz 100, MKS, England) in the headspace.

Signals at different m/z values were collected every 0.5 s intervals and were stored by a desktop computer for later analysis. N_2 was measured at m/z = 28, 29 and 30 corresponding to $^{28}N_2$, $^{29}N_2$ and $^{30}N_2$, respectively, and O_2 and Ar were measured at m/z = 32 and m/z = 40, respectively. Ar was used as an internal standard. The raw value collected at m/z = 30 was corrected according to Minjeaud et al. (2008) in order to take into account interference due to NO_x ions formation from N_2 and O^+ inside the MS. As m/z= 44, 45, and 46 can either originate from N_2O or CO_2, these were summed and corrected using the calculated ratio of $N_2O:CO_2$ from potential denitrification assays prior to the mesocosm incubation.

The isotopic composition of $N-NO_3^-$, $N-NO_2^-$ and $N-NH_4^+$ in the overlying water column and in the sediments was determined according to Lachouani et al (2010) and measured on a 96-slot autosampler with a double-hole needle (GC-PAL, CTC Analytics, Zwingen, Switzerland) connected via a Gasbench II headspace analyzer (Thermo Fisher, Bremen, Germany) to an IRMS (Delta V Advantage, SILVER lab, University of Vienna). Organic N and C concentration and isotope abundances from sediment samples were measured with an elemental analyzer (EA 1110, CE Instruments, Milan, Italy) connected to an isotope ratio mass spectrometry IRMS (DeltaPLUS, Finnigan MAT, Bremen, Germany) in Vienna (SILVER Lab, University of Vienna).

2.7. Denitrification, Anammox, and Dissimilatory nitrate reduction to ammonium (DNRA)

At each time step, denitrification and anammox rates were calculated using the comprehensive method as outlined by Spott & Stange (2007). This approach allows for a precise calculation of the contribution of denitrification and anammox to an N_2 mixture, while taking into consideration the contamination by atmospheric N_2. The following calculations (Eq. 1-3) were used to determine the portion of atmosphere (A), denitrification (B), and anammox (C) contributing to the N_2 mixture.

$$A = \frac{2b(\alpha_{30}-cd)+(c+d)(b^2-\alpha_{30})-(b^2-cd)(\alpha_{29}+2\alpha_{30})}{(a-b)[2(ab+cd)-(a+b)(c+d)]}$$

Eq. 1

$$B = \frac{2a(cd-\alpha_{30})+(c+d)(\alpha_{30}-a^2)+(a^2-cd)(\alpha_{29}+2\alpha_{30})}{(a-b)[2(ab+cd)-(a+b)(c+d)]}$$

Eq. 2

$$C = \frac{2ab-\alpha_{29}(a+b)+2\alpha_{30}(1-b-a)}{2(ab+cd)-(a+b)(c+d)}$$

Eq. 3

Where α_{28}, α_{29}, and α_{30} are the mole fractions of masses 28, 29, and 30 within the N_2 mixture and a, b, c, d, are the ^{15}N atom fraction of N_2 (a), NO_3^- (b), NO_2^- (c), and NH_4^+ (d).

The rate of dissimilatory nitrate reduction to ammonia (DNRA) was determined in the sediment after completion of the five day incubation. Rates were calculated using Gilbert et al.(1997) (Eq. 4).

$$DNRA = \frac{(AT\% \ NH_4^+)([NH_4^+])}{(AT\% \ enrichment \ NO_3^-)(incubation \ duration)}$$

Eq. 4

Where AT% NH_4^+ is the mole fraction of ^{15}N-NH_4^+ determined at the end of incubation. All rates were calculated per square meter for the upper 10 cm of the sediment layer.

The sum of masses 28, 29, and 30 (m_{28}, m_{29}, and m_{30}), and the corrected sum of masses 44, 45, and 46 (m_{44}, m_{45}, and m_{46}), were used to calculate ratios of N_2 produced as an end product

versus the amount of N_2O produced (Eq. 5). The closer the ratio is to zero, the larger the percentage of N_2 is produced relative to N_2O.

$$\frac{N_2O}{N_2} = \frac{m_{44} + m_{45} + m_{46}}{m_{28} + m_{29} + m_{30}}$$

Eq. 5

The percentage of used nitrogen was estimated for denitrification and DNRA; pelagic and benthic bacterial secondary production (BSP); and biomass assimilation for each treatment. A C:N ratio of 5:1 was used to estimate the N-requirement for BSP (Gruber and Galloway, 2008, references therein). All unaccounted nitrogen loss was attributed to biomass assimilation.

2.8. Pelagic and benthic bacterial secondary production (BSP)

Pelagic bacterial secondary production (BSP) was measured at times 0h, 72h, and 108h according to Kirchman et al. (1986), while benthic BSP was measured at time 0 and 108h with a modified method of the Leu incorporation technique according to Wieltsching et al. (1999) and Fischer and Pusch (1999). Three replicate sub-samples taken from the sediment and two blanks (0.2 g) were weighted into 1.7 ml screw-cap microcentrifuge tubes. The samples were then incubated at in situ temperatures for 1h. The incubation was terminated by the addition of formaldehyde (final concentration = 3.2%).

The fixed samples were vortexed, sonicated (10 min, 60% power) in a sonication bath (Elma T 710 DH) and vortexed again. After this step, trichloroacetic acid (TCA) was added to a final concentration of 5%. In order to dissolve the non-protein fraction of the cells, the samples were then incubated at 95°C for 30 min. After cooling on ice, the remaining precipitate was filtered onto 0.2-mm-pore-size membrane filters (polycarbonate filters [Nuclepore]). Filters were thoroughly rinsed with deionized water to eliminate unincorporated leucine. Filters were then put into 7-ml scintillation vials and completely dissolved in 5 ml scintillation cocktail (Ultima Gold; Canberra Packard). Radioactivity was measured in a Beckman 6500 scintillation counter. Controls were fixed with formaldehyde (final concentration, 3.2%) immediately at the start of the incubation and generally contributed less than 10% of the total leucine incorporation.

2.9. Dissolved organic matter (DOM) & dissolved organic carbon (DOC) measurements

Dissolved organic matter (DOM) and dissolved organic carbon (DOC) were measured from the water column at each time step for all mesocosms during the carbon exchange experiment. Fluorescence excitation–emission matrices (EEMs)—three-dimensional contour plots which display fluorescence intensities as a function of a range of both excitation and emission wavelengths—were used to characterize DOM (dissolved organic matter) composition (Baker and Spencer, 2004).

The water samples were filtered through a prepared Whatman GF/F filter (2.5 h at 490°C; diameter 0.7 µm) and stored in purged glass tubes (24h in 10% HCl, 4h combusted at 490°C) at 4°C and analyzed within 24 hours.

The fluorescence measurements were undertaken using a Hitachi Fluorescence Spectrophotometer F-7000 and all samples were scanned in the following wavelength regions: excitation 200–400 nm at 5 nm steps and emission 280–500 nm at 2 nm steps.

Blank water scans were run before and after every sample run using Milli-Q water to measure the Raman signal at excitation 350 nm (emitted at 397 nm) and all results are standardized to a mean Raman peak of 150 intensity units.

For characterization of DOM, three fluorescence peaks were used (the maximum intensity at an excitation-emission wavelength pair) according to Coble (1996). Peaks B and T occur at excitation wavelengths of 225–275 nm and emission at wavelengths of 300–325 nm and 340–385 nm, respectively, and have been related to protein-like substances (peak B = Tyrosine-like, peak T = Tryptophan-like) (Baker, 2001). Peak C is a fluorophore at 300–370 nm excitation and 400–500 nm emission and is attributed to humic-like substances.

To calculate the specific fluorescence intensity, the DOC concentration of the filtered water samples was measured using a TOC analyzer (Sievers 900), and ratios of peak X_{Fint}/DOC mg l^{-1} were calculated.

Ratios between the fluorescence peaks (C, T, and B) and DOC concentration were calculated to allow the partitioning of humic and protein-like DOM. The ratios T: DOC and B: DOC

were summed to create a total protein-like pool of DOM in the overlying water column. The following indices were calculated using the fluorescence peaks to further classify the DOM pools: fluorescence index (FI), $\beta:\alpha$ ratio, and the humification index (HIX). FI was calculated from excitation 370 nm as the ratio of intensities at 450 nm and 500 nm (McKnight et al., 2001). FI is inversely related to the lignin content of DOM, where values around 1.3 suggest a dominant terrestrial DOM and values around 1.8 suggest a dominant microbial DOM source. The $\beta:\alpha$ ratio was calculated at excitation 310 nm from the emission intensity at 380 nm divided by the emission intensity maximum observed between 420 and 435 nm (Wilson and Xenopoulos, 2008). The $\beta:\alpha$ values >1 indicate that DOM is primarily of autochthonous origin and values <0.6 indicate primarily allochthonous origin (Huguet et al., 2009). Finally, HIX was calculated from excitation 255nm as the ratio of the peak area under each curve at emissions 434-480 nm and 300-346 nm (Zsolnay et al., 1999). HIX values around 1-2 are associated with non-humified plant material and values >10 are commonly reported for fluvic acid extracts (Ohno, 2002).

2.10. Statistics

Mann-Whitney U tests were used to test differences between the sites and treatments. General linear models were used to assess the change of N species over time for the individual treatments. One-way independent ANOVA was used to test the change of N-species over time between the sites and treatments. Stepwise multiple linear regression models between water chemistry ($N-NO_3^-$, $N-NO_2^-$, $N-NH_4^+$), carbon quality (Peaks C, T, and B and DOC concentration) were used to elucidate their overall influence on the denitrification rate and ratio of $N_2O:N_2$. Significance for all tests was set at $p<0.05$. All tests were performed using the SPSS software package.

3. Results

3.1. Site differences

Measured denitrification rates and calculated $N_2O:N_2$ ratios did not change significantly over time at either site during any treatment (linear regression; $R^2 < 0.5$, $p > 0.05$,, both sites and treatments). Therefore, the five day average was used for all further comparisons between sites and treatments. No significant differences were observed between the two control

treatments (Control N and Control C) at either site for denitrification or the $N_2O:N_2$ ratio (Isolated; p = 0.98 and p = 1.0; Restored p = 0.86 and p = 0.88, respectively).

The restored site exhibited a larger range and a higher maximum in the measured rates of denitrification in the control treatments (Control N vs. Control C) than the isolated site (U = 2520, $p<0.001$) (Figure 3). More incomplete denitrification was measured at the isolated site than at the restored site, as revealed by the higher calculated $N_2O:N_2$ ratios in the control treatments (Control N vs. Control C; U=5610, $p<0.001$) (Figure 4).

No anammox was detected during the five day incubation at either site. Low DNRA rates were calculated after 5 days and were higher and more variable at the backwater site than in the restored site (U=31.0, $p<0.001$) (Table 2).

Pelagic and benthic bacterial secondary production were both higher in the isolated site ($2.45 \pm 1.26\,\mu g\,C\,L^{-1}h^{-1}$; $2063 \pm 1040\,\mu g\,C\,kg^{-1}h^{-1}$, respectively) than in the restored site ($1.94 \pm 1.2\,\mu g\,C\,L^{-1}h^{-1}$; $1294 \pm 331\,\mu g\,C\,kg^{-1}h^{-1}$, respectively) (U=873, $p<0.05$; U=370, $p<0.001$, respectively).

Based on estimated nitrate allocation, biomass assimilation was estimated to be the main biological mechanism of N retention in the isolated site (Figure 5). None of the experimental treatments significantly affected the portioning of N uptake between benthic algae, bacterial secondary production and denitrification. Due to the low sample number (n=3) and high standard deviation, no significant differences between the sites and their portions can be calculated (Mann-Whitney U) (Figure 5).

3.2. Experiment 1: Effect of NO3- addition on denitrification rates

3.2.1. Isolated site

The mean *in situ* $N\text{-}NO_3^-$ and $N\text{-}NH_4^+$ concentrations in the overlying water column measured prior to the incubation were 3.84 µM $N\text{-}NO_3$ and 16.4µ $MN\text{-}NH_4$. The $^{15}N\text{-}NO_3$ additions increased the $N\text{-}NO_3$ concentration and ^{15}N enrichment (at%) in all mesocosm treatments (34.7 µM, 22 at% Control N; 106µM, 88 at% Plateau; 189µM, 90 at% Peak). Within two hours, once mixing within the mesocosms and the reservoir was complete, the Plateau and Peak treatments reached the target concentrations of 75µM $N\text{-}NO_3$ and 130µM $N\text{-}NO_3$, respectively. The control treatment decreased to 25µM $N\text{-}NO_3^-$ after two hours.

No significant differences (one-way independent ANOVA) were observed for denitrification rates, which ranged from 0–2.1mmol N $m^{-2}h^{-1}$, between the three treatments (Control N, Peak and Plateau) (F = 4.6, p = 0.06) (Figure 3). One-way independent ANOVA did not show any significant differences in the $N_2O\text{:}N_2$ ratio between the nitrogen treatments ($p = 0.16$) (Figure 4). DNRA rates were an order of magnitude lower than denitrification rates (Table 2).

A significant increase of DOC was observed over the five days for all treatments ($r^2 = 0.80$, $p < 0.01$) during the experiment. No significant correlation between NO_3^- concentration and denitrification was observed for any treatment. Changing the nitrate delivery regime resulted in a significant (one-way independent ANOVA) decrease in the percentage of N consumed by BSP between the treatments from 66% (Control N) to 17% (Peak) and 26% (Plateau) (F = 35.5, $p < 0.01$) and increase in biomass assimilation from 27% (Control N) to 77% (Peak) and 71% (Plateau) (F =35.6, $p < 0.01$) (Figure 5). However, the estimated percentage of N uptake via denitrification did not change significantly and remained <10% (F = 1.8, $p = 0.2$).

3.2.2. Restored site

The mean *in situ* $N\text{-}NO_3^-$ and $N\text{-}NH_4^+$ concentrations in the overlying water column were 74 µM $N\text{-}NO_3^-$ and 24.7 µM $N\text{-}NH_4^+$. Because the *in situ* concentration of $N\text{-}NO_3^-$ was higher than the goal concentration for the plateau treatment, water from another adjacent restored site was used. This site was pre-selected because of its similar DOM characteristics and average hydrology. The i*n situ* $N\text{-}NO_3^-$ concentration at this site was 4.20 µM $N\text{-}NO_3^-$ at the sampling

time. Tracer additions increased the N-NO$_3$ concentrations in all mesocosm treatments (140.1 µM N-NO$_3^-$, 43 at% Control N; 111.0 µM N-NO$_3^-$, 93 at% PLATEAU; 171.9 µM N-NO$_3^{-1}$, 46 at% PEAK). Within two hours, once mixing within the mesocosms and the reservoir was complete, the Plateau and Peak treatments reached the target concentrations of 75 µM N-NO$_3^-$ and 130 µM N-NO$_3^-$, respectively. The control treatment decreased to 123 µM N-NO$_3^-$ after 2 hours.

Denitrification rates ranged from 0.6 -8.6mmol N m^{-2} h^{-1}(mean = 1.1 ± 1.9 mmol N m^{-2} h^{-1}) (Figure 3). One-way independent ANOVA did not show any significant differences in either the rates of denitrification or the N$_2$O:N$_2$ ratio between the nitrogen treatments (p=0.32, p=0.91, respectively) (Figures 4). DNRA rates were consistently low in all treatments (Table 2).

Changing the nitrate delivery regime significantly decreased (one-way independent ANOVA) the estimated nitrogen use by BSP from 40% (Control N) to 20% (Peak) and 30% (Plateau) (F = 9.4, $p < 0.05$) (Figure 5). Although assimilation was estimated to be <1% in the control treatment, due to the high standard deviation in the treatments, the estimated increase was not significant (F = 2.3, $p = 0.2$). No significant changes were estimated for denitrification (F = 1.5, $p = 0.3$).

3.3. Experiment 2: Effect of carbon quality on denitrification rate and on N2O:N2 ratio

3.3.1. Isolated site

Prior to the water exchange, the *in situ* concentrations were 6.0 µM N-NO$_3^-$ and 5.8 µM N-NH$_4^+$. Tracer additions increased the N-NO$_3^-$ concentrations in all treatments to 225.4 µM, 93 at% (Control C), 183.7 µM, 86 at% (POOL) and 189.9 µM, 45 at% (RIVER). Within two hours, all treatments reached the target concentrations of 130µM (140.7 µM CONTROL C; 131.2 µM POOL; 149 µM RIVER). Once the target concentration was reached, N-NO$_3^-$ was kept constant by an addition of N-NO$_3^-$ after each sampling time. N-NO$_2^-$ concentrations increased over the five day incubation for all treatments.

The lowest *in situ* DOC concentrations (2.6 mg l^{-1}) were measured in the Danube River and the highest (13.2 mg l^{-1}) in the open pool site. *In situ* DOC concentrations in the isolated site

were in between these two extremes (6.9 mg l^{-1}) (Table 3). In two of the three treatments the DOC concentration increased significantly over the five day incubation (Control r² = 0.35 p<0.05; RIVER r² = 0.82 p < 0.01; POOL r² = 0.01 p = 0.97). Although the measured DOC concentration was lowest in the Danube River water, the ratios of T: DOC and B: DOC were highest (Table 3) (one-way ANOVA p<0.01 and p<0.01) indicating a high content of protein-like DOC.

Denitrification rates ranged from 0.02 -10.7mmol N m^{-2} h^{-1}, with no significant differences in the denitrification rate between treatments (F = 2.9, p=0.06) (Figure 3). The $N_2O:N_2$ ratios are shown in in Figure 4. A significant difference was measured between the Control C and the two treatments (p<0.001) as well as a further decrease between RIVER and POOL (p<0.001).

DNRA rates increased to 15-22 µmol N m^{-2} h^{-1}(Table 2). No significant differences in DNRA rates were observed between any of the treatments (p=0.13). The percentage of N used did not change significantly between treatments, with denitrification accounting for <20%, BSP <20% and assimilation >50% in all treatments (one-way independent ANOVA) (F = 0.6, p = 0.6; F = 4.3, p = 0.07; F = 1.2, p = 0.4, respectively).

3.3.2. Restored site

Prior to the water exchange, the *in situ* concentrations in the restored site were 89.3 µM N-NO_3^- and 1.9 µM N-NH_4^+. Tracer additions increased the N-NO_3^- concentration in all treatments to 159.5 µM, 51 at% (CONTROL C), 188 µM, 96 at% (POOL) and 152 µM, 33 at% (RIVER). Within two hours, two treatments reached the target concentrations of 130 µM (137 µM POOL; 135 µM RIVER). The control treatment reached the target concentration (144 µM) within 4 hours.

At the restored site DOM was higher in overall protein-like carbon relative to the dissolved organic carbon pool (T+B: DOC) than the isolated site in the water column (U = 521, p < 0.001) (Table 3). Yet, the DOC content at the isolated site was significantly higher (U = 957, p < 0.01) than at the restored site. Using the calculated ratios for FI, HIX, and β:α to distinguish the DOM characteristics in the water column, small, but significant differences were only observed for HIX and β:α between the sites (U = 36, p < 0.01; U = 0.5 p < 0.01, respectively) with the isolated site having higher humic content in the DOM pool than the restored site (Table 3).

The *in situ* DOC concentration was very similar to the Danube River. The water from the Danube River was highest in protein-like DOC. DOC concentration increased slightly over the five day incubation in the POOL treatment (Control $r^2 = 0.14$ p = 0.23; RIVER $r^2 = 0.03$ p = 0.59; POOL $r^2 = 0.38$ p < 0.05). No significant differences in the measured denitrification rates were observed between the two control treatments (Control N & Control C) for either site (*p* = 1.0). No significant differences in DNRA were observed between the POOL and RIVER treatments (F = 1.29, p = 0.329).

A significant increase of the $N_2O:N_2$ ratio was observed between the CONTROL C and POOL treatments (*p* < 0.05), but not between the CONTROL C and RIVER treatments. DNRA rates remained low in all treatments (Table 2). No change was measured in the estimated percentage N uptake for denitrification (<10%), BSP (9 - 30%) and assimilation (66 – 90%) (One-way independent ANOVA) (F = 1.1, *p* = 0.4; F = 2.9, *p* = 0.1; F = 3.1, *p* = 0.1, respectively).

3.3.3. Factors influencing N2O:N2 ratio

All water chemistry and DOM quality data were combined for both sites and all three treatments in Experiment 2 to investigate their effect on denitrification rates and $N_2O:N_2$ ratios in the sites. A stepwise regression was created for the $N_2O: N_2$ ratio (R^2=0.67). All variables were originally included, but the $N-NO_2^-$ concentration in the water column, the positive relation of the proportion of humic-like carbon relative to the total DOC pool (C: DOC) and the negative relation of total protein-like carbon pool relative to the total DOC pool (T:DOC + B:DOC) were the only significant variables in the final regression (Table 4).

4. Discussion

4.1. Comparison between sites

High denitrification rates were measured at both sites (Figure 3), demonstrating the microbial nitrate removal capacity within the floodplain. This is in accordance with the high rates measured in wetlands along the Po River where Racchetti et al. (2010) also measured the same trend of increased rates in connected wetlands compared to isolated areas. Higher denitrification rates (94 mg N $m^{-2}h^{-1}$, ca~ 279 µmol m^{-2} h^{-1}) were estimated by James (2010)

for a backwater system of the Mississippi River, which receives similar $N-NO_3^-$ inputs from the river, accounting for 57% of nitrate removal. This highlights the buffer capacity of floodplains and the potential for nitrate removal therein, which can be up to 100% of a river's nitrate load (Fennessy and Cronk, 1997). Accordingly, nitrate concentrations in the floodplain lakes of the Wisconsin River declined below detection level 6 days following isolation from the river channel (Forshay and Stanley, 2005). Similarly, in a nearby disconnected floodplain downstream of Vienna, Hein et al. (1999) demonstrated that following a flood, NO_3^- concentrations in unrestored, decoupled backwaters returned to pre-flood levels after one month. Based on our measured denitrification rates, the restored Orth floodplain connected at the average yearly discharge of approx. 2000 $m^3 h^{-1}$, would be capable of reducing 130 µmol L^{-1} $N-NO_3^-$ within 24 hours, compared to the estimated 6 days that would be required in the Lobau floodplain. Previous models have estimated that a large range of denitrification rates can occur in these floodplains (Welti et al., 2012; Welti et al., 2011). Sites within the Lobau floodplain that receive more frequent inputs from the Danube River may have denitrification rates similar to those measured in the Orth floodplain. Moreover, at the landscape scale, nitrate removal capacity is influenced by seasonality and discharge levels (Alexander et al., 2009; Hernandez and Mitsch, 2007), neither of which were taken into consideration in this study.

Higher, but variable, denitrification rates were consistently measured at the restored site compared to the isolated site, demonstrating higher denitrification capacity (Figure 3). The lower $N_2O:N_2$ ratios observed at the restored site suggest more complete denitrification, indicating more efficient nitrate removal. It is not clear if this efficiency is due to different microbial communities or a decoupling between the water column and the anoxic sediment layer. Yet, more $N-NO_3$ was removed in the system than could be accounted for by denitrification, DNRA and anammox, suggesting a competition with primary producers either in the water column or at the sediment surface, which is confirmed by the larger proportion estimated to be used by biomass assimilation. The increase in DOC at the isolated site suggests an autotrophic system dominated by benthic algae.

When water column nitrate was the main nitrate source, as is in this case, Christensen et al. (1990) reported that denitrification was inversely proportional to the thickness of the oxic surface layer, as nitrate has to diffuse through this layer, and proportional to the nitrate

concentration in the overlying water. Carbon supply stimulates denitrification activity directly by supplying the necessary substrate for growth and indirectly as the oxygen consumption is increased by the supply of carbon, thereby decreasing the thickness of the oxic zone (Chalamet, 1986; Seitzinger, 1988). Moreover, Kana et al. (1998) indicated that *in situ* denitrifying bacteria respond rapidly to increases in nitrate concentration in the overlying water. Gross primary production, rather than community respiration, has been shown to control NO_3^- uptake in streams (Hall and Tank, 2003). More primary producers (autotrophs) on the sediment surface would change the size of the oxic layer, which would not only drop the rate of denitrification but also disrupt the conversion of N_2O to N_2 because N_2O reductase is sensitive to changes in oxygen concentrations. In experiments conducted with soil-extracted bacteria, an oxic phase following anoxia decreased denitrification rates and resulted in more N_2O production (Morley et al., 2008).

The appearance of ^{15}N-NH_4^+ in the water column suggests algal assimilation of NO_3^-. The communities in the water column may out-compete denitrification for both nitrogen and organic carbon via nitrification (Sloth et al., 1995). Despite being short term, biomass assimilation can provide a rapid sink for nitrate (Hefting et al., 2005). Although autotrophs are generally assumed to prefer ammonium than nitrate, biological assimilation and BSP seem be of more importance than denitrification, accounting for the majority of DIN uptake in both systems (Figure 5).

In other created wetlands, up to 36% of nitrate loss can be accounted for via anammox (Scott et al., 2008), suggesting that this pathway could complement the nitrate removal process However, anammox was not a pathway of quantitative importance in this floodplain system, with rates below detection limit.. DNRA, while not a rate of high proportion in the floodplains, was measurable and detectable. Soil aeration, which can be altered by the presence of vegetation, has been thought to be a principle regulator of NO_3^- partitioning between denitrification and DNRA (Matheson et al., 2002). In terrestrial agricultural sites, DNRA can be favored over denitrification, if the C: NO_3 ratio in the soil is greater than 4 (Fazzolari et al., 1998). The isolated site was higher in overall C and terrestrially-rooted vegetation than the restored site, which might explain the observed differences between the DNRA rates in our two study sites (in the isolated site, DNRA was 3% of denitrification while it was 0.1% in the restored one). Despite these differences, DNRA does not appear to be a

quantitatively important pathway, as these rates were an order of magnitude lower than denitrification in both sites.

4.2. Effects of changing NO3- concentrations

Denitrification rates and denitrifier efficiency (as shown by $N_2O:N_2$) in stream sediments varies with nitrate concentration and discharge, as shown in Alexander et al. (2009). We assumed that, due to the high supply of carbon and anoxic conditions in the isolated sediments, the isolated site would be nitrate limited, as has been demonstrated in different riverine sediments (Forshay and Stanley, 2005; Hill et al., 2000; Silvennoinen et al., 2008), streams (Smith et al., 2006), constructed wetlands (Scott et al., 2008) and estuaries (Teixeira et al., 2010). Therefore, by increasing the nitrate concentration in the water column of the isolated site, which is high in organic carbon, we expected to measure a corresponding increase in denitrification. However, increased nitrate concentrations had no effect on the denitrification rates implying that denitrification at both sites was not simply nitrate limited (Table 2). After 5 days of constantly elevated NO_3^- concentrations, no adaptation effects were observed in the denitrification rate for either site or any treatment. While the percentage of N used by denitrification did not change with the treatments, the estimated amounts for assimilation and BSP did, suggesting that these processes can react quickly with changes in nitrate concentration (Figure 5). The opposite trends observed (increasing assimilation, decreasing BSP) in the isolated site suggest that assimilation can out-compete the heterotrophs for the available nitrogen.

Although we did not measure bacterial density or microbial community structure in this study, previous studies have shown that the bacterial community is conditioned to respond quickly and efficiently to flooding events (Sanchez-Perez, 2003). Nitrogen saturation can occur when bacterial communities are overloaded with constantly elevated nitrate concentrations. However, communities in pulsed systems with short-term increases (ex floodplains) the bacterial communities may not experience this overloading and can be stimulated by such pulses (Bernot and Dodds, 2005; Burns and Ryder, 2001). In this study, the restored floodplain typically receives frequent pulsing from the river which could be a reason for the described differences in denitrification rates.

4.3. Effects of DOM quality

Dynamic floodplains are affected by the complete exchange of their water mass with that of the river water. This changes the available organic carbon substrate pool, originating in the riverine water column, to the bacterial community, located in the sediment of the floodplain. By changing the overlying water column in the mesocosms, we altered the available organic carbon pool with the hypothesis that by adding water high in DOM along with increased nitrate concentrations, denitrification would be stimulated. Yet, there was no significant difference in denitrification rates in any of the treatments at either site (Figure 3).

However, the ratio of $N_2O:N_2$ differed significantly between the sites and treatments. Similar rates of denitrification with varying $N_2O:N_2$ have been previously reported (Hefting, 2003). Generally, the ratio of $N_2O:N_2$ was lower in the restored site (Figure 3), implying that denitrification was more efficient and reached completion in the connected site. N_2O production has been related to high organic sediment content and eutrophic environments (Kenny et al., 2004; Sloth et al., 1995; Teixeira et al., 2010), which are the conditions found at both sites. When riverine water was added to the isolated site (i.e. mimicking a reconnection event), the $N_2O:N_2$ ratio decreased, increasing the fraction of denitrification resulting in N_2. The reverse was true when water from a backwater site was added to the restored site (i.e. mimicking a disconnection event), increasing N_2O over N_2 production.

It was not the purpose of this study to investigate the different available substrates in each of the source waters, but rather the effect of the mixture of substrates on denitrification. In soils with changing oxygen conditions, it has been demonstrated that the carbon source becomes important for N_2O production (Morley and Baggs, 2010). Using the three DOM indices, we observed minor, but significant, differences in the carbon pools of the Danube River and the floodplains (mostly autochthonous, with a dominant terrestrial DOM source and non-humified plant material). The HIX and $\beta:\alpha$ ratios of both sites were in the range associated with humic material and suggest DOM of primarily allochthonous origin. Yet, as shown by the T+B: DOC ratios, the DOC pools between the source waters were significantly different: the Danube River had a lower concentration of DOC compared to waters originating from the backwaters, but this carbon pool was more protein dominated and therefore more bio-available (labile) to the sediment microbe community (Table 3). This difference could be the reason for the different responses in the $N_2O: N_2$ ratio we observed. In the isolated system, where the oxic layer may be changing diurnally due to a higher number of autotrophs, the

same co-regulation between oxygen and carbon source may be occurring (Christensen et al., 1990; Laursen, 2004).

The regression model produced for the ratio of $N_2O:N_2$ production lists the carbon characteristics of the DOC pool (C: DOC and T: DOC + B: DOC) as the second and third controlling variables. The negative relationship between the portion of protein-like carbon and the $N_2O: N_2$ suggests that the more protein-like DOC is, the lower the $N_2O:N_2$ ratio, resulting in more N_2 production. The appearance of NO_2^- in the multiple regressions can be interpreted as a proxy for nitrogen cycling. Nitrate was kept in constant abundance in the experiment, but NO_2^- increased throughout the incubation period, a result of NO_3^- reduction. The DOC pool originating from the Danube River, although a lower total amount, had a higher percentage of protein-like carbon, which stimulated decreased $N_2O:N_2$ ratios in the isolated site. DOC originating from the Danube River has been shown to be a mixture of terrestrial and microbial derived sources, depending on the discharge and season (Besemer et al., 2009; Peduzzi et al., 2008; Preiner et al., 2008). Previous studies have suggested that OC is primarily derived from terrestrial sources (dominated by protein-like signatures)) during average flow conditions (Hein et al., 2004), however during high discharge, more humic carbon may be transported into the floodplains.

4.4. Importance of restoration

In this study, the restored site experienced an increase in denitrification rates compared to the isolated site, suggesting that increasing the continuous and long lasting surface water connection periods will increase the overall denitrification rate as well as its efficiency (Kjellin et al., 2007; Klocker et al., 2009; Racchetti et al., 2010). Yet, as shown in Experiment 1, increasing nitrate concentration does not lead to higher denitrification rates in short time. Rather, changing water sources led to changes in the $N_2O:N_2$ ratio. Therefore, prolonged connection to the river may increase the denitrification efficiency; however, surface water connections solely during floods will not increase the overall, long term denitrification efficiency as these sites do not respond quickly to an increase of NO_3. Previous work modeled the response of the $N_2O:N_2$ ratio in the similar floodplains at the floodplain scale, which predicted similar responses of DEA to flooding (Welti et al., 2011).

In the case of the studied restored floodplain, opening the embankments and allowing the Danube water to pulse into the floodplain changed the flow pattern and physical characteristics of the site. The restored site was in a channel dominated by a gravel bed, whereas the isolated site was a shallow pool higher in organic material and fine sediments. In the restored floodplain (Orth), the depth of sediment as well as the sediment organic substrates decreased with the level of connection to the Danube (Reckendorfer, 2006). Compared to the disconnected floodplain (Lobau), which covers more surface area with finer and more organic rich sediments, the absolute area available for denitrification was lower. Reconnection of the Lobau floodplain would increase the rate of denitrification and lower overall N_2O production, resulting in a net gain of ecosystem services. Along with the changes in denitrification, increasing the surface water connection could prime the benthic and pelagic algal communities, thus increasing the nutrient retention capacity of the floodplain (Ahearn et al., 2006; Scott et al., 2009).

In this study, we demonstrated that while denitrification rates were not directly influenced by NO_3^- or DOC concentrations in the overlying water, the end product of denitrification was controlled by changes of carbon quality in the overlying water column. By increasing the frequency of flooding into the backwaters, N_2O production could be mitigated and the NO_3^- removal capacity of the floodplain could be increased. Creating regular surface water connection to the Danube River would reduce N_2O emissions by 50% in the isolated site. Hydrologic pulsing has been shown to decrease greenhouse gas emissions, organic matter accumulation and increase nutrient retention (Mitsch et al., 2008). In terms of ecosystem management and restoration, it is apparent that frequent, longer lasting, pulsing creates ideal conditions for efficient denitrification, resulting in lower N_2O production.

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6. References

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7. List of tables & figures:

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Figure 2. Schematic of one mesocosm chamber setup. Each reservoir was connected to three mesocosm chambers.

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Figure 5. Estimated percentage of total N pool used by denitrification and DNRA (dark gray), bacterial secondary production (middle gray) and biomass assimilation (light gray) using the 5 days averages. Solid bars are estimates from the isolated site, hashed bars from the restored site. N=3

Table 1. Site descriptions of hydrology, of the sediment carbon pools, and *in situ* water
chemistry prior to mesocosm incubations (N=6) (mean ± stdev). The two water ages
refer to the two separate sampling days.

	Restored		Isolated	
Days Connected (days year^{-1})	71.5		3.5	
Duration of Disconnection	30.6		426	
(30 year average)				
Duration of Connection	7.8		3.0	
(30 year average)				
C:N (Sediment)	8.99	*±1.3*	8.97	*±1.6*
δ^{13}C (Sediment)	-29.41	*±3.5*	-25.55	*±2.4*
N-NH$_4^+$ (μmol L^{-1})	8.2	*±2.1*	11.3	*±6.1*
N-NO$_2^-$ (μmol L^{-1})	0.4	*±0.1*	0.7	*±0.5*
N-NO$_3^-$ (μmol L^{-1})	80.6	*±7.7*	5.0	*±1.3*
DOC (μmol L^{-1})	4.1	*±2.5*	6.8	*±3.8*
Water Age (Days)	7 ; 8		294 ; 24	

Table 2: Mean DNRA rates (n=3) measured and standard deviation in the sediment after 5 day
incubation.

Site	Treatment	DNRA (μmol N m^{-2} h^{-1})	
Isolated	Control N	1.7	±0.1
	PEAK	1.5	±0.3
	PLATEAU	1.5	± 0.7
Restored	Control N	2.7	±3.1
	PEAK	2.8	± 3.5
	PLATEAU	0.9	±0.6
Isolated	Control C	15.1	±12.3
	POOL	15.7	±12.9
	RIVER	22.7	±19.8
Restored	Control C	0.1	±0.1
	POOL	0.0	±0.0
	RIVER	0.3	±0.3

Table 3. Dissolved organic matter quality and dissolved organic carbon (DOC) over five days and standard deviation in italics (N = 33). Peaks B and T occur at excitation wavelengths of 225–275 nm and emission at wavelengths of 300–325 nm and 340–385 nm, respectively, and have been related to protein-like substances (peak B = Tyrosine-like, peak T = Tryptophan-like). Peak C is a fluorophore at 300–370 nm excitation and 400–500 nm emission and is attributed to humic-like fluorescence. Fluorescence index (FI) β:α ratio, and the humification index (HIX) were calculated using the fluorescence peaks as described in the methods.

		DOC (mg C l^{-1})		B:C		T:C		B:DOC		T:DOC		(B+T):DOC		C:DOC		FI		HIX		β:α	
Isolated	Control C	6.9	*0.7*	0.8	*0.2*	0.9	*0.1*	99.2	*13.2*	119.2	*9.4*	218.4	*20.8*	127.3	*13.4*	1.2	*0.02*	5.0	*0.2*	0.6	*0.0*
	RIVER	2.6	*0.8*	1.7	*0.4*	1.8	*0.3*	196.6	*50.3*	212.8	*42.5*	409.4	*91.1*	115.4	*11.1*	1.1	*0.01*	3.5	*0.3*	0.6	*0.1*
	POOL	13.2	*0.6*	0.4	*0.06*	0.7	*0.02*	41.3	*5.8*	62.8	*3.9*	104.5	*8.5*	93.8	*4.9*	1.0	*0.01*	5.9	*0.2*	0.6	*0.0*
Restored	Control C	2.9	*0.2*	2.2	*0.2*	0.4	*0.02*	286.4	*24.5*	305.7	*27.7*	592.1	*47.4*	129.9	*14.4*	1.1	*0.02*	3.3	*0.2*	0.7	*0.01*
	RIVER	2.6	*0.2*	2.3	*0.1*	0.4	*0.02*	329.9	*37.3*	397.4	*54.2*	727.3	*90.3*	142.4	*13.3*	1.1	*0.03*	2.9	*0.3*	0.8	*0.07*
	POOL	10.7	*1.3*	0.7	*0.02*	0.9	*0.01*	104.3	*14.9*	161.6	*21.9*	265.9	*36.6*	138.8	*16.4*	1.1	*0.02*	3.8	*0.8*	0.7	*0.01*

Table 4. Predictor variables and coefficients (β) influencing the calculated 5-day $N_2O:N_2$ ratio.

	β
Constant	
N-NO_2^- μmol	0.44 *
C:DOC	0.62 *
T:DOC + B:DOC	-0.83 *

Dependent variable: $N_2O:N_2$
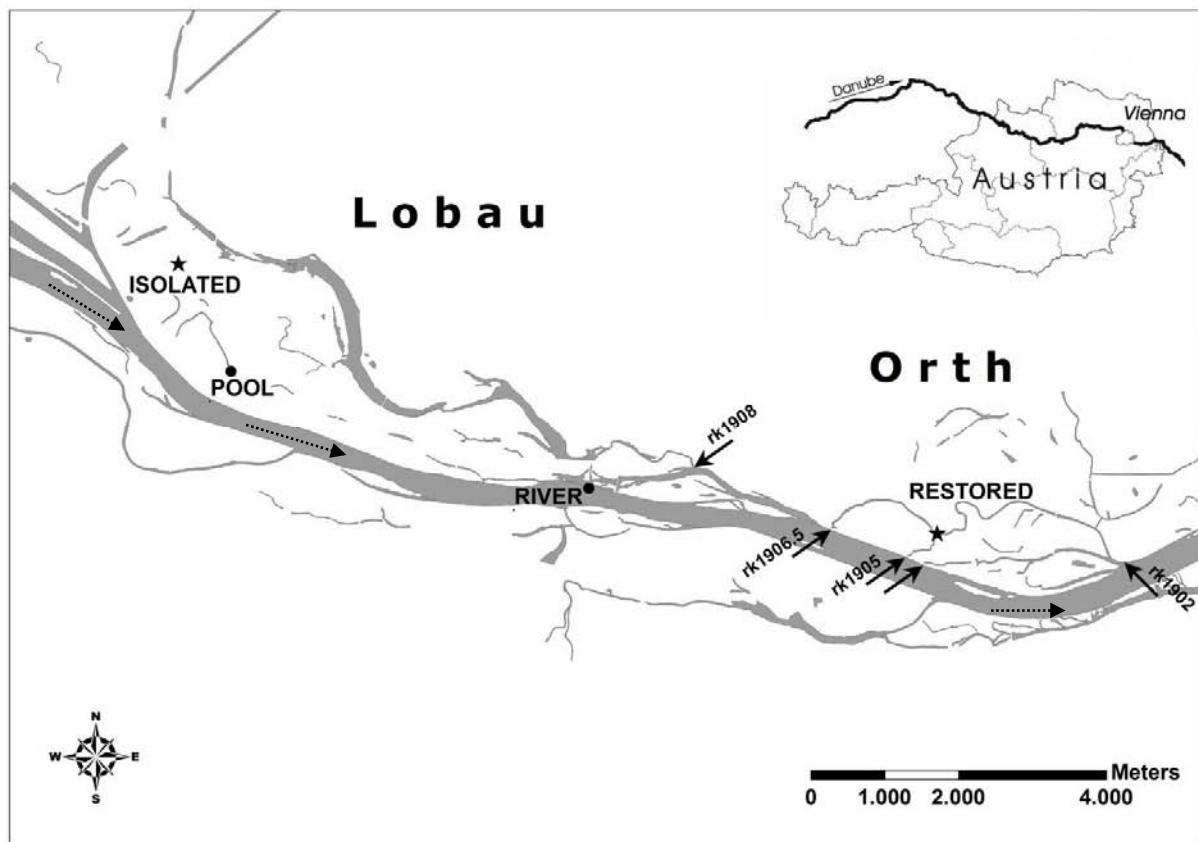$R^2 = 0.67$
*p < 0.001

Figure 1. Sampling sites are marked with stars; water exchange sites for Experiment 2 are marked with circles. Dashed arrows show the flow direction; solid arrows mark the openings to the Danube River.
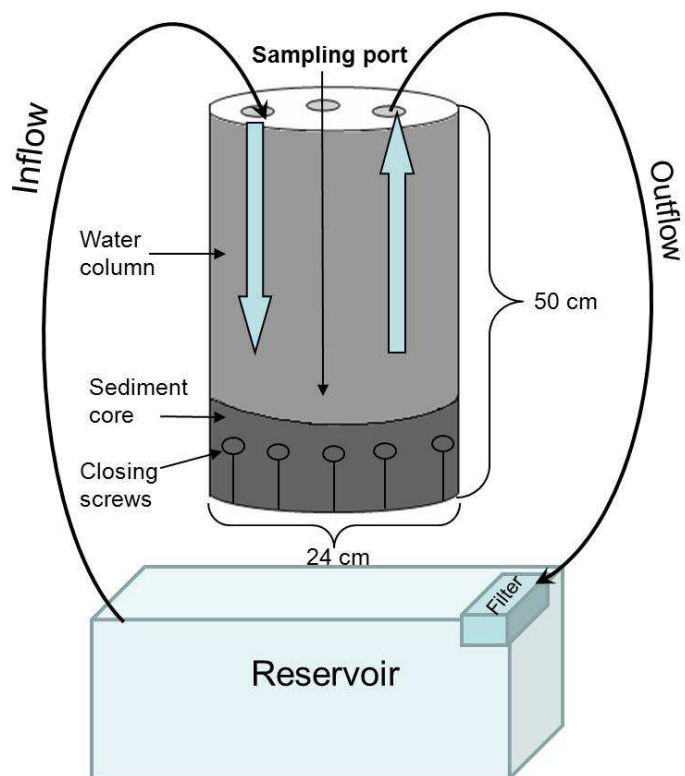
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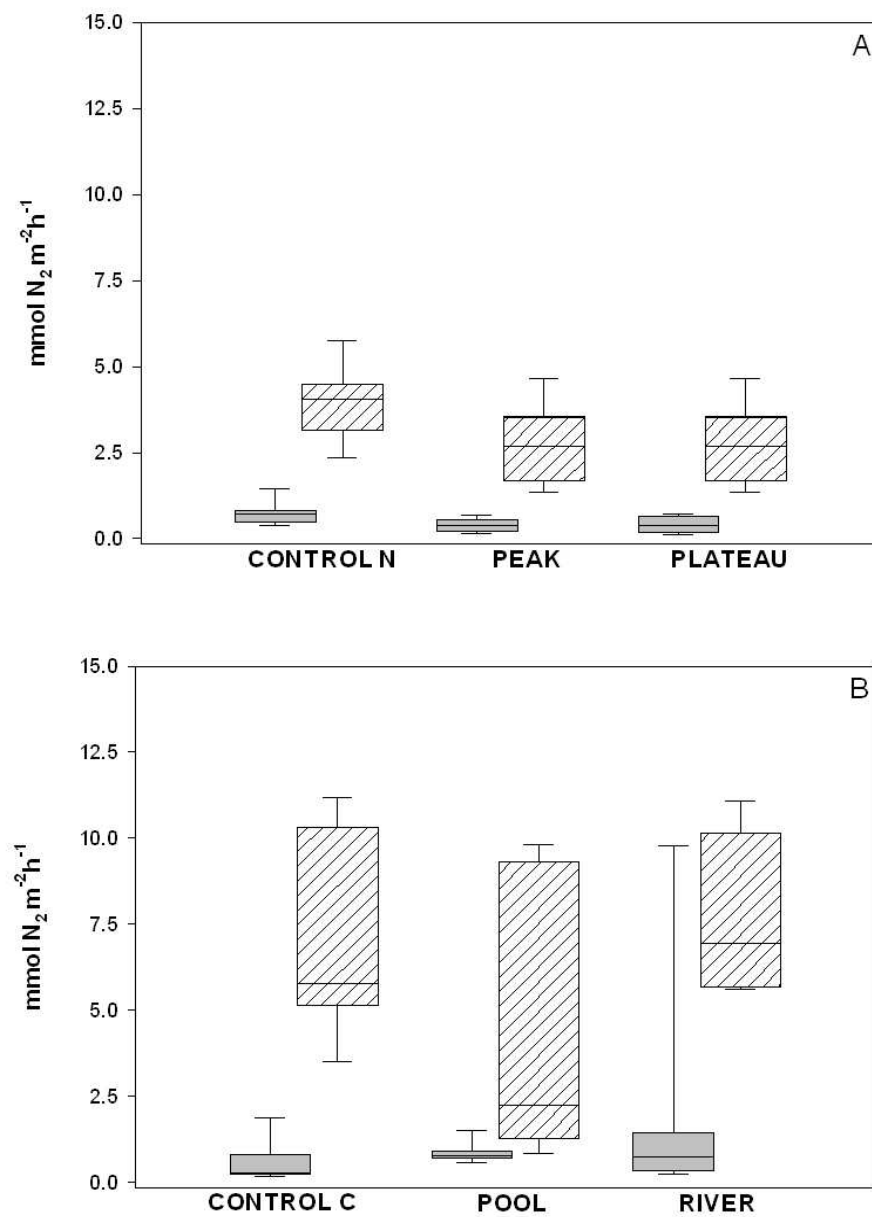mesocosm chambers.

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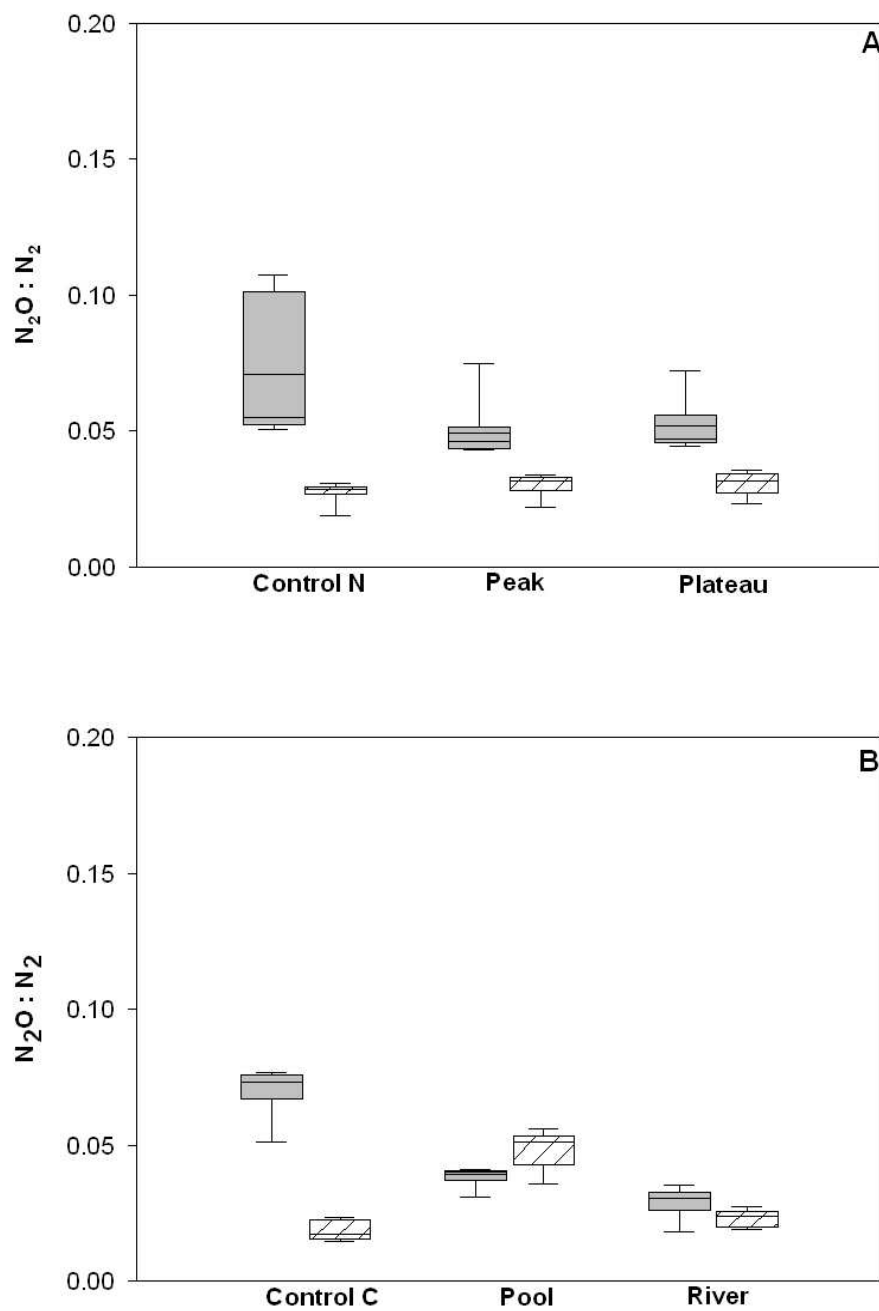
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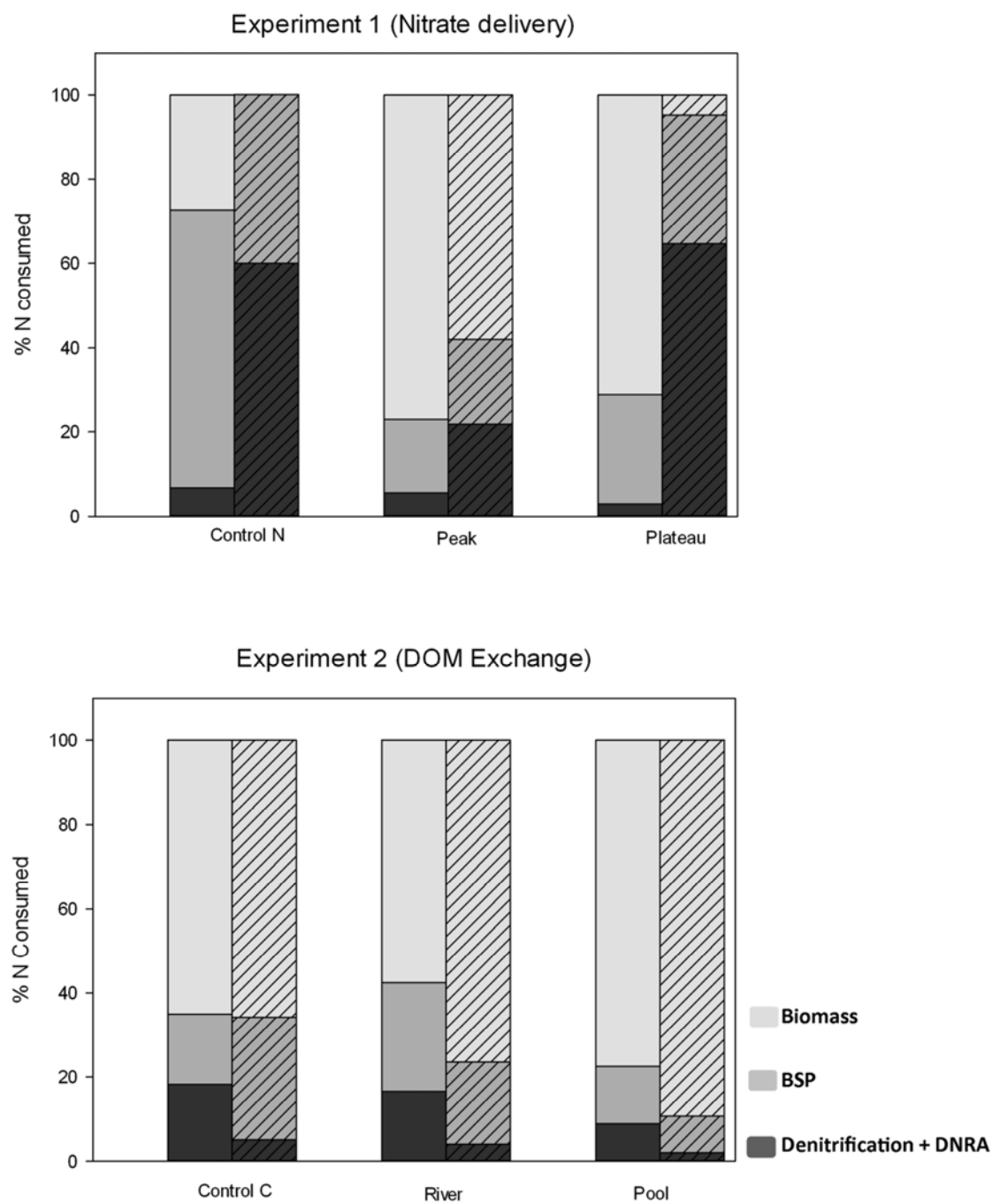
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PUBLICATIONS

Welti, N., E. Bondar-Kunze, G. Singer, M. Tritthart, S. Zechmeister-Boltstern, T. Hein, and G. Pinay. 2012. Large-Scale Controls on Potential Respiration and Denitrification in Riverine Floodplains. Ecological Engineering *In Press*

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> (2009, 2010) Teaching Assistant

Conservation and Restoration Ecology (2008-2011)
> International Post-Graduate Course in Limnology, Mondsee Austria. Teaching Assistant & Lecturer

Advisor to **Matthias Mair** (MSc graduate student) (2009):
> Nitrogen cycling in wetland sediments influenced by different surface water exchange conditions. Diplomarbeit am Department für Wasser, Atmosphäre und Umwelt der Universität für Bodenkultur Wien, 69; Universität für Bodenkultur Wien

SCHOLARSHIPS

ÖN-IAD (Österreichische Nationalkomitee der Internationalen Arbeitsgemeinschaft Donauforschung) *Nitrogen dynamics in restored side arms*

COLLABORATIONS

Coordinated research project (International Atomic Energy Agency): Isotopic Techniques for Assessment of Hydrological Processes in Wetlands
Fresh Blood for Fresh Waters: A meeting of young aquatic scientists.
Lunz am See, Austria July 2008 and 2010. Member Organizing Committee

PROFESSIONAL MEMBERSHIPS

Advancing the Science of Limnology and Oceanography (ASLO)
European Geoscience Union (EGU)
Society of Wetland Scientists (SWS)