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The ecology of lateral aquatic habitats along river corridors

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THE ECOLOGY OF LATERAL AQUATIC HABITATS ALONG RIVER CORRIDORS

A dissertation submitted to the
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presented by

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CONTENTS

SUMMARY

The “training” of most European rivers has led to a major decline of natural river corridors. Recent flood damage is only one consequence that shows the unbalanced use (e.g., navigation, energy source, agriculture) of our natural resources. Therefore, the restoration of impacted rivers is becoming increasingly recognized as a crucial political topic. However, a fundamental and holistic knowledge of natural river ecosystems is essential to develop and manage restoration projects.

The ETH project “*The role of island dynamics in the maintenance of biodiversity in an Alpine River system*” aimed at providing baseline knowledge about a near-natural river ecosystem (Tagliamento River, Italy). The present study is part of this project and contributes to the knowledge of the ecology of lateral aquatic habitats along riparian corridors. Aquatic habitats (main and side channels, tributaries, backwaters, and parafluvial ponds) occur in natural and semi-natural riverine flood plains. However, simultaneous investigations of all aquatic habitats, i.e., investigations on tributaries, backwaters and parafluvial ponds are scarce in river ecology.

The distribution and density of parafluvial ponds was investigated along the semi-natural Tagliamento River (**chapter 2**). In addition, environmental variables of ponds in a 1-km^2 island-braided segment were intensively monitored over a 6-month period. Along the corridor, pond density peaked in bar- and island-braided flood plains, but ponds were absent from regulated and constrained segments. Number of ponds seemed to be dependent on sediment grain size, corridor width, slope of the corridor, and degree of regulation. Furthermore, ponds in the main 1-km^2 study segment were identified as very heterogeneous riverscape elements. Thermal properties and water level fluctuations were the most important variables determining pond characteristics and heterogeneity. Heterogeneity among ponds was mainly caused by local conditions.

Macroinvertebrate communities of ponds were investigated simultaneously with the investigation of environmental variables (**chapter 3**). The main questions were: (1) Do ponds provide habitats for a distinct and diverse fauna? and (2) Do faunal composition and taxa traits reflect environmental heterogeneity? Seventy-two percent of a total of 91 taxa were restricted in their occurrence to ponds, and 10% to the channel. Community similarity among ponds was very low. A high proportion of pond taxa were classified as rare, occurring in <10% of all ponds. The number of taxa in ponds was negatively related to the temporal variability of environmental variables. Spatiotemporal dynamics of biological traits were not clearly related to environmental conditions, indicating early successional stages of parafluvial ponds.

Hydrological connectivity between the river and its flood plain is considered to be essential for the ecological integrity of river floodplain systems. The major driving force controlling the degree of connectivity is the pulsing of flow. The effect of hydrological connectivity on environmental conditions and on benthic community dynamics in water bodies across a lateral connectivity gradient was investigated over a one-year period in the semi-natural Tagliamento River (NE-Italy) (**chapter 4**). Connectivity was significantly related to concentration of total dissolved phosphorus (out of 17 measured environmental variables), invertebrate density, and the composition of Oligochaeta and Chironomidae. Frequently connected water bodies exhibited very similar environmental conditions, densities and community composition. In contrast, water bodies with a low degree of connectivity showed highly distinct environmental conditions and community compositions. Density and persistence of invertebrate communities were markedly lower in less-connected water bodies, which is expected to be related to environmental conditions and biotic interactions among invertebrates within individual water bodies. Concordance in abundances was lower compared to investigations in other river systems, indicating either a strong influence of flood disturbance on abundance patterns or specific adaptations (i.e., *r*-selected traits) to

the harsh environmental conditions characteristic for braided river systems. In summary, the results demonstrate that hydrological connectivity between the river and its flood plain cannot be reduced to a simple gradient.

The contribution of lateral aquatic habitats (i.e., channels, tributaries, backwaters, and ponds) to overall diversity of macroinvertebrates was investigated along three differently impacted river corridors (Tagliamento<Thur<Rhône) (**chapter 5**). Tributaries, backwaters, and ponds contributed >50% to total species richness along the Tagliamento, Thur, and Rhône corridors. Similarity in community composition among individual habitat types was low. The longitudinal distribution of taxa diversity differed among river corridors indicating the uniqueness of each river. The partitioning of diversity into its components (i.e., alpha- and beta diversity) revealed that among-sample and among-corridor components contributed most EPT-taxa richness, while <15% was due to within-sample and among-habitat diversity components. The study clearly emphasises the importance of lateral aquatic habitats for maintaining high aquatic biodiversity along river corridors. Consequently, these habitats need to be fully integrated in future conservation and restoration projects.

In conclusion, lateral aquatic habitats are dynamic and complex systems with respect to their environmental conditions and benthic communities. Lateral aquatic habitats of riverscapes can be regarded as a "shifting habitat mosaic". The interplay between local conditions and the degree of connectivity is responsible for the high environmental heterogeneity among ponds. The large contribution of lateral aquatic habitats to overall biodiversity is assumed to be promoted by: (1) high habitat heterogeneity, (2) irregular flood events which favor the coexistence of many species, and (3) the patchy nature of lateral aquatic habitats which promote high spatial turnover rates of benthic invertebrates. The significance of my results for river restoration is discussed and suggestions for future research are provided (**chapter 6**).

ZUSAMMENFASSUNG

Die Jahrhunderte lange Nutzung von Flüssen durch den Menschen hat zu einer starken Beeinträchtigung und Verminderung von natürlichen Auenlandschaften geführt. Die Schäden der jüngsten Hochwasserereignisse stellen nur eine Konsequenz der einseitigen Nutzung (Transportweg, Energiequelle, etc.) der natürlichen Ressourcen dar. Allgemein erklärtes Ziel ist daher die Renaturierung der Flüsse. Für die Entwicklung und Durchführung von Renaturierungen ist jedoch ein ganzheitliches Verständnis des natürlichen Ökosystems Flusslandschaft Voraussetzung. Das ETH-Projekt "The role of island dynamics in the maintenance of biodiversity in an Alpine River system" hat das Ziel, Grundlagenwissen über ein natürliches Flusssystem am Beispiel des Tagliamentos (Italien) zu vermitteln. Als Teil dieses Projektes liefert die vorliegende Arbeit einen wesentlichen Beitrag zur Ökologie aquatischer Lebensräume in Flusslandschaften. Aquatische Lebensräume, wie Haupt- und Nebengerinne, Zuflüsse, Hinterwasser und Tümpel der aktiven Aue, sind ein wesentlicher Teil natürlicher und naturnaher Flusslandschaften, wurden jedoch in wissenschaftlichen Untersuchungen meist vernachlässigt.

Entlang des naturnahen Tagliamento wurde das Vorkommen (Verteilung und Dichte) von Tümpeln der aktiven Aue untersucht (**Kapitel 2**). Zusätzlich wurden Tümpel der aktiven Aue über einen Zeitraum von 6 Monaten in einem 1-km^2 grossen Segment anhand verschiedener Umweltparameter charakterisiert. Die grösste Anzahl an Tümpeln wurde im Mittellauf in verzweigten Flussabschnitten nachgewiesen („island and bar braided"). In regulierten Abschnitten gab es keine Tümpel. Die Anzahl der Tümpel scheint stark von der Sedimentart, der Breite des Flusskorridors, dem Flussgefälle und dem Regulierungsgrad abhängig zu sein. Des Weiteren erwiesen sich die Tümpel bezüglich der gemessenen Umweltparameter sowohl räumlich als auch zeitlich sehr heterogen, was hauptsächlich durch Wasserstandsschwankungen und Temperatur bestimmt wurde. Diese

Heterogenität wurde durch die lokalen Bedingungen eines jeden Tümpels verursacht.

Parallel zur Aufnahme der Umweltvariablen wurde die Makroinvertebraten Gemeinschaft der Tümpel untersucht (**Kapitel 3**). Zentrale Fragen hierbei waren (1) gibt es eine eigene Tümpelfauna, die sich von der Fauna des Gerinnes unterscheidet und (2) spiegelt die abiotische Heterogenität der Tümpel die Zusammensetzung und die Eigenschaften der Makroinvertebraten („taxa traits“) wieder? Es konnte eine eigene Tümpelfauna nachgewiesen werden mit einem hohen Anteil an Taxa, die auf die Tümpel beschränkt waren (72% von 91 Taxa) und einem geringen Anteil (18%), der sowohl im Gerinne als auch in den Tümpel vorkam. Die Ähnlichkeit der Lebensgemeinschaften zwischen den Tümpeln war gering. Ein hoher Anteil der Taxa in den Tümpeln kam in weniger als 10% der Tümpel vor. Die Anzahl der Arten in den Tümpeln wurde stark von der zeitlichen Variabilität der abiotischen Faktoren (z.B. Temperaturschwankungen) eines jeden Tümpels bestimmt. Stark variable Tümpel zeigten die geringste Anzahl an Taxa. Die Eigenschaften der Makroinvertebraten reflektierten in begrenztem Umfang die abiotische Umwelt der Tümpel, was eine frühe Sukzessionsphase der Tümpel vermuten lässt.

Die hydrologische Vernetzung zwischen Gerinnen und deren Auen ist wesentlich für die Intaktheit von Flusslandschaften und wird im Wesentlichen durch ein natürliches Abflussregime gewährleistet. Letzteres unterliegt natürlichen Schwankungen und verursacht dadurch einen Gradienten der Verbindung und Fragmentierung zwischen den einzelnen aquatischen Habitaten. Über einen Zeitraum von 1 Jahr wurde der Effekt der hydrologischen Konnektivität auf die Dynamik benthischer Makroinvertebraten und auf die Umweltbedingungen in aquatischen Habitaten untersucht, die entlang eines Verbindungs-/Fragmentierungsgradienten angeordnet waren (**Kapitel 4**). Nur die Umweltvariable „gelöster Phosphor“ (DP) (von insgesamt 17 gemessenen Parametern), die Dichte der Makroinvertebraten und die Verteilung von

Chironomidae und Oligochaeta Taxa standen in engem Bezug zum Verbindungs-/Fragmentierungsgradienten. Verbundene Habitate ähnelten sich in Umweltbedingungen, Lebensgemeinschaften und der Dichte der Makroinvertebraten, wohingegen sich fragmentierte Habitate wesentlich voneinander unterschieden. Weiterhin war die Beständigkeit der Lebensgemeinschaft deutlich niedriger in fragmentierten Habitaten, was auf individuelle Umweltbedingungen und biotische Interaktionen schliessen lässt. Die zeitliche Veränderung der Abundanzen war höher verglichen mit anderen Studien. Dies könnte entweder die Folge eines starken Einflusses der Hochwasserereignisse auf Abundanz-Muster sein, oder spezifische Anpassungen (*r*-Strategen!) auf die harschen Umweltbedingungen von verzweigten Flusssystemen anzeigen. Es wurde deutlich, dass die hydrologische Vernetzung zwischen den einzelnen Habitaten nicht auf einen einfachen Gradienten reduziert werden kann.

Der Beitrag der einzelnen aquatischen Habitate (Gerinne, Zuflüsse, Hinterwasser und Tümpel) zur Gesamtdiversität der Makroinvertebraten wurde entlang von 3 Flusskorridoren untersucht (Tagliamento, Thur and Rhône) (**Kapitel 5**). Die 3 Flüsse wurden im Hinblick auf die Stärke ihres Verbauungsgrades ausgewählt (Tagliamento<Thur<Rhône). Hinterwasser, Tümpel und Zuflüsse trugen über 50% zur gesamten aquatischen Artenvielfalt der Flusskorridore bei. Die Artenzusammensetzungen der einzelnen Habitattypen unterschieden sich stark voneinander. Weiterhin zeigten die Flusskorridore eine unterschiedliche längszonale Verteilung der Taxa-Diversität, was die Einzigartigkeit eines jeden Flusses hervorhebt. Bei der Aufteilung der Gesamt-Diversität in ihre einzelnen Komponenten (alpha- und beta-Diversität) stellte sich heraus, dass die Diversität der Korridore und die Diversität zwischen den einzelnen Proben den höchsten Beitrag zur Gesamt-Diversität lieferten. Die Untersuchung hebt die Bedeutung von lateralen aquatischen Habitaten bei der Erhöhung der Biodiversität hervor. Dieses Ergebnis sollte bei zukünftigen Renaturierungsmassnahmen Berücksichtigung finden.

Zusammenfassend lässt sich feststellen, dass laterale aquatische Habitate überaus dynamische Ökosysteme darstellen, sowohl hinsichtlich ihrer Umweltbedingungen als auch ihrer benthischen Lebensgemeinschaften. Die aquatischen Habitate der Flusslandschaft sind sehr dynamisch und können daher einem sich permanent verändernden Habitatmosaik („shifting habitat mosaic“) gleichgesetzt werden. Die hohe Heterogenität zwischen den einzelnen Habitaten wird durch ein Wechselspiel aus lokalen Faktoren und durch Gradienten der Verbindung und Fragmentierung zwischen den einzelnen aquatischen Habitaten bestimmt. Der hohe Beitrag der lateralen aquatischen Habitate zur Gesamtdiversität wird begünstigt (1) durch die hohe Habitat Heterogenität, (2) durch unregelmässige Hochwässer, die die Koexistenz vieler Arten ermöglichen, und (3) durch die mosaikartige Anordnung der Habitate in der Flusslandschaft, die einen hohen „turnover“ der Tiere bewirken. Die Bedeutung der Ergebnisse für Renaturierungsmassnahmen wird diskutiert und Vorschläge für weiterführende Forschung werden unterbreitet (**Kapitel 6**).

CHAPTER 1

GENERAL INTRODUCTION

Endangered landscapes

Rivers and their adjacent flood plains have been severely altered during the past centuries (Petts *et al.* 1989; Dynesius & Nilsson 1994). Seventy-seven per cent of the total water discharge of the 139 largest river systems in the northern third of the world are affected by humans (Dynesius & Nilsson 1994). Alterations include dam constructing for domestic and industrial water supply, to generate electricity and reduce flood-risk; channelization and dredging for navigation and flood control; water withdrawal for irrigation and drinking water. Consequently, rivers and their adjacent flood plains are among the most endangered landscapes worldwide (Olson & Dinerstein 1998; Tockner & Stanford 2002). The effects of human modifications on river flood plains are extensive: suppression of the natural dynamics, simplification of formerly complex channel morphology, isolation of the flood plain from the channel; and the impairment of the water quality (Petts & Amoros 1996). In particular the reduction of functional flood plains has resulted in a decline of biodiversity (e.g., Allan & Flecker 1993; Jungwirth *et al.* 2002; Negishi *et al.* 2002). Therefore, the conservation and restoration of biodiversity in riverine landscapes is an important policy goal.

Natural rivers

Natural rivers form one of the most heterogeneous landscapes (Ward *et al.* 1999b). They consist of a dynamic mosaic of spatial elements and ecological processes arrayed hierarchically. Rivers are not simply uni-dimensional (upstream-downstream), but interact in four dimensions: they are dependant on longitudinal (upstream-downstream), lateral (main channel-flood plain) and vertical (surface water-groundwater) transfers of energy, matter and biota over a range of time scales (Ward 1989). This dynamic nature of rivers is mainly driven by hydrology (Tockner & Stanford 2002). Flow regimes are primarily responsible for the high level of habitat heterogeneity along natural river corridors. High flow, which alters floodplain morphology at various spatial scales, as well as low water level fluctuations (flow pulses, *sensu* Tockner *et al.* 2000) are important for creating and maintaining habitat heterogeneity. Moreover, water flow plays a key role in connecting various landscapes elements (Junk *et al.* 1989; Ward 1998).

Habitat diversity & heterogeneity in natural rivers

Beside the well-known diversity of in-stream habitats such as pools and riffles (Frissell *et al.* 1986), natural river corridors are characterized by a divers array of lateral aquatic habitats, grouped in lotic (main & side channels, tributaries), semi-lotic (backwaters), and lentic elements (parafluvial ponds, oxbow lakes). Investigations on environmental properties of lateral aquatic habitats are rather scarce and often of limited duration (Homes *et al.* 1999). Recent investigations showed that lateral aquatic habitats increased overall river corridor habitat diversity and environmental heterogeneity (Arscott *et al.* 2000). In particular, a high thermal heterogeneity was observed among aquatic habitats in the same flood plain (Mosley 1983; Arscott 2001). The distinctness of aquatic habitats was closely related to hydrological connectivity, i.e., the spatial or temporal association with the main channel. Aquatic habitats with least exchange with the main channel showed most divergent physical and chemical properties (Marchese & de Drago 1992; Ward *et al.* 2002a).

Aquatic invertebrates

Natural river corridors support one of the most species-rich landscapes (Ward *et al.* 1999b). The fauna is dominated by aquatic invertebrates of which insects comprise often more than 95% (Ward 1992). Environmental heterogeneity and disturbance regimes are primarily responsible for the diversity and organization of invertebrate communities (Poff & Ward 1990; Palmer & Poff 1997). Southwood (1977; 1988) proposed that environmental heterogeneity provides the templet on which evolution forges characteristic life history strategies. Many concepts have been developed to predict and explain diversity patterns of aquatic invertebrates along river corridors (e.g., Vannote *et al.* 1980; Ward & Stanford 1983; Statzner & Higler 1986; Ward & Stanford 1995; Stanford *et al.* 1996; Benda *et al.* 2004). Each of these concepts predicts a strong positive relationship between species richness and spatial and/or temporal heterogeneity. However, corridor habitat diversity, which also implies lateral elements of the river corridor (e.g., backwater, parafluvial ponds) have been seldom included in investigations of invertebrate diversity. Studies on standing aquatic habitats in alluvial flood plains were carried out in the Rhône and Ain flood plains (France) and in the Isar flood plain (Germany) (e.g., Bravard *et al.* 1986; Castella 1987; Castella & Amoros 1988; Castella *et al.* 1991; Homes *et al.* 1999). There, the mainly focus was on abandoned river beds, on cut off meanders or on floodplain ponds. In summary, most studies highlighted the importance of individual lateral aquatic habitats for overall river invertebrate diversity, although quantitative data are limited.

The understanding of taxa richness patterns (measure of biodiversity) at various spatial scales is critical, because strong empirical foundation are lacking (Vinson & Hawkins 1998). Especially studies that examine the relationship between landscape and species diversity in alluvial river corridors are needed (Ward *et al.* 2002b). Therefore, investigations of lateral aquatic habitats and their invertebrate communities contribute to a better understanding of biodiversity patterns, also in regard to developing adequate management policies for river restoration.

THESIS OUTLINE

The present thesis intends to contribute to the ecology of lateral aquatic habitats along riparian corridors. We are mainly interested in individual aquatic habitat characteristics and associated benthic macroinvertebrates. Important in community ecology is to understand patterns in species diversity and their underlying determining processes (Townsend 1989). In this context, it is also important to consider the hierarchical organization of biodiversity at different scales, up to entire corridors (e.g., Noss 1990; Ward & Tockner 2001). Thus, the thesis focuses on: (1) the environmental characterization of habitats (chapter 2); (2) the relationship between environmental properties and invertebrate communities (chapters 3 & 4); and (3) the hierarchical structure of species diversity along entire riparian corridors (chapter 5).

In this thesis, aquatic habitats include main and side channels, tributaries, backwaters, and parafluvial ponds (Figure 1). A tributary is the smaller of two intersecting channels. Parafluvial (*sensu* Fisher *et al.* 1998) ponds are isolated lentic aquatic habitats within the active zone of the corridor (Frissell *et al.* 1986). Backwaters are habitats with a downstream connection to a lotic environment but with local conditions being lentic-like.

The predominant part (chapters 2-5) of the thesis was conducted along the Tagliamento River in NE-Italy. The Tagliamento represents one of the last morphologically intact river corridors in the Alps (Müller 1995; Ward *et al.* 1999a) and therefore, provides an adequate river system to study large-scale ecological processes under near-natural conditions. An additive part of the thesis (chapter 5) has been carried out along the Thur and Rhône Rivers. Both rivers are located in Switzerland. The Tagliamento, Thur and Rhône Rivers differ in their degree of anthropogenic impact (Tagliamento<Thur<Rhône).

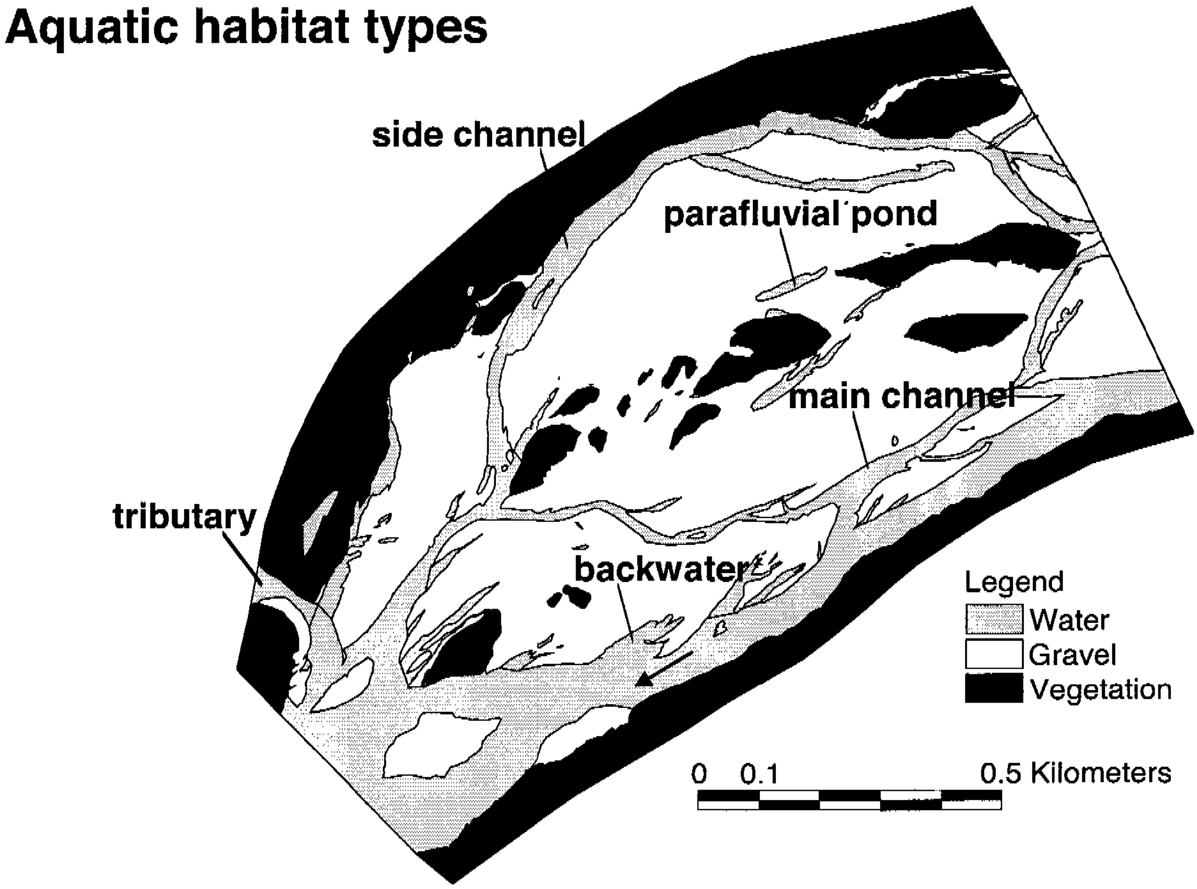

Figure 1. Tagliamento River (NE-Italy): Aquatic habitat types across a river-floodplain gradient (river-km 79.8 – 80.8).

In **chapter 2** the distribution, density, and diversity of parafluvial ponds in an island-braided section of the Tagliamento was investigated. The main objectives were to characterize the environmental conditions of parafluvial ponds and to quantify their physicochemical heterogeneity. The results of this work form the base for the subsequent research on biodiversity (chapter 3).

Chapter 3 focused on the influence of environmental conditions on composition, diversity, and dynamics of benthic macroinvertebrates in parafluvial ponds. Special attend was given to biological traits of benthic macroinvertebrates. The primary questions are: (i) Are individual ponds colonized by distinct benthic communities, which differ from those of the channel? (ii) Are individual biological traits of benthic invertebrates related to individual environmental pond conditions?

The major driving force that controls river-floodplain systems is the pulsing of the flow that determines the degree of connectivity and the exchange of matter, energy, and organisms across multiple gradients (Junk *et al.* 1989; Ward *et al.* 1999b). However, quantitative studies about the lateral organization of aquatic macroinvertebrates are scarce and do not consider seasonal dynamics (Castella *et al.* 1991; Foeckler *et al.* 1991; Obrdlik & Fuchs 1991; Van den Brink *et al.* 1996; Tockner *et al.* 1999). Therefore, the main aim of **chapter 4** was to examine seasonal dynamics of environmental variables and benthic invertebrates in water bodies across a lateral connectivity gradient.

A diversity of models has been developed to predict patterns in species diversity along river corridors (e.g., Vannote *et al.* 1980; Ward & Stanford 1983; Statzner & Higler 1986; Ward & Stanford 1995; Stanford *et al.* 1996; Benda *et al.* 2004). However, the lack of empirical data including the lateral dimension was the motivation of **chapter 5**. Main goals are to (i) to quantify the relative contribution of lateral aquatic habitats to river corridor diversity and (ii) to study the hierarchical structure of biodiversity along river corridors.

The dissertation was funded by two interdisciplinary projects: (1) The ETH project "The role of island dynamics in the maintenance of biodiversity in an Alpine River system" (ETH Forschungskommission grant 0-20572-98) aimed providing baseline knowledge about a natural river ecosystem (Edwards *et al.* 1999). It was conducted at the Tagliamento River in NE-Italy. The Tagliamento is, due to its low degree of regulation (Petts *et al.* 2000) and a near-natural flood regime (Müller 1995; Gurnell *et al.* 2000) considered as the last semi-natural river corridor in the Alps. It is proposed to serve as a model river of European importance (Müller 1995; Gurnell *et al.* 1999; Ward *et al.* 1999a; Tockner *et al.* 2003). The interdisciplinary research project included several complementary studies: Habitat and macroinvertebrate heterogeneity along the floodplain corridor (Arscott 2001), the ecology of woody pioneer species (Karrenberg van der Nat 2001), floodplain morphology and ecosystem processes (Van der Nat 2002), dissolved organic matter dynamics (Kaiser 2002), the ecology of river shores (Achim Paetzold), and the ecology of lateral aquatic habitats along river corridors (present thesis). (2) The "Rhône-Thur project" is a cooperation of different research institutes (see http://www.rhone-thur.eawag.ch/ for detailed information) with the main goal to develop the scientific background to restore ecological conditions of the two rivers.

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CHAPTER 2

“CONCAVE ISLANDS”: HABITAT HETEROGENEITY OF PARAFLUVIAL PONDS IN A GRAVEL-BED RIVER

Ute Karaus, Laurenz Alder, and Klement Tockner, Wetlands 25 (1): 26-37.

Parafluvial pond distribution, density, and diversity were investigated along the active river corridor of the Tagliamento River in northeastern Italy, the last major semi-natural river in Central Europe. Along the corridor, ponds peaked in bar- and island-braided flood plains but were absent in constrained sections. Within the main study area, a 1.0-km^2 large braided flood plain, the number of ponds containing water ranged between 18 and 39 depending on the water level in the main channel. Thermal properties and water-level fluctuations were the most important variables determining pond characteristics and heterogeneity. Results from a PCA on environmental variables distinguished four groups of ponds distributed along a hydrologic and thermal gradient. Parafluvial ponds are short-lived, discrete, aquatic “islands” within the floodplain matrix. They are expected to contribute disproportionately to aquatic biodiversity; however, they are very sensitive landscape elements that disappear as a consequence of river regulation, wood removal, and flow control.

INTRODUCTION

Riparian corridors are characterized by a large diversity of aquatic and terrestrial landscape elements (Ward *et al.* 2002). Surface waters include lotic, semi-lotic, and lentic water bodies distributed along an inundation continuum. Cut-and-fill alluviation, coupled with ground- and surface-water interactions, create a complex array of shallow lentic habitats, including parafluvial ponds. While lentic water bodies such as vernal ponds, forested wetland ponds, prairie ponds, man-constructed ponds, and small lakes have been extensively studied (Batzer *et al.* 1999; Schwartz & Jenkins 2000; Brönmark & Hannsson 2002; Brooks 2002; Oertli *et al.* 2002), alluvial ponds have been almost completely ignored (Drago 1989; Homes *et al.* 1999).

Ponds are important for biodiversity conservation, but they have been lost on a large scale during the twentieth century, reaching 40-90% for Western European countries and for the U.S.A. (Hull 1997; Mitsch & Gosselink 2000; Wood *et al.* 2003). Ponds in dynamic flood plains are among the most endangered landscape elements since they disappear rapidly as a consequence of river regulation (Homes *et al.* 1999; Gurnell & Petts 2002; Ward *et al.* 2002). Ecologically, parafluvial ponds can be viewed as "concave islands" that are embedded into the alluvial floodplain matrix (c.f. Holland & Jain 1981).

The main objectives of the present study were to characterize the environmental conditions of alluvial ponds and to quantify their physicochemical heterogeneity. Our focus was on parafluvial (*sensu* Fisher *et al.* 1998) ponds within the active zone of the river corridor and the riparian forest ponds. We recognized three main questions (1) Where do ponds peak in number along the corridor? (2) How are pond density and pond area related to river hydrology? (3) Which environmental variables explain pond diversity within the active flood plain? The semi-natural Tagliamento River in northeastern Italy offers the rare opportunity to study the density, diversity, and dynamics of parafluvial ponds under near-natural conditions (Tockner *et al.* 2003).

STUDY AREA

The Tagliamento is a large, gravel-bed river located in northeastern Italy (Friuli-Venezia Giulia; 46°N, 12°30´E; Figure 1). The river originates at 1195 m a.s.l. in the Carnian Alps and flows 170 km to the Adriatic Sea. The catchment covers 2580 km^2, with more than 70% of its catchment located in the Alps. The mountainous part of the catchment consists of limestone and Flysch deposits, and the Friulian plain is filled with Tertiary and Quaternary sediments (Petts *et al.* 2000; Tockner *et al.* 2003). The riparian corridor consists of five major landscape elements: surface water (12.4 km^2), bare gravel (38.7 km^2), vegetated islands (10.6 km^2), riparian forest (32.0 km^2), and topographical low areas that are not forested (~50-km^2) (Tockner *et al.* 2003). The Tagliamento has an average discharge of ~70 m^3s^{-1}, whereas floods with 2-, 5-, and 10-yr recurrence intervals are estimated to be 1100, 1600, and 2150 m^3s^{-1} (Petts *et al.* 2000). High flow is caused by snowmelt (spring) and by heavy rainfall (autumn), with discharge maxima of ~4000 m^3s^{-1} (Ward *et al.* 1999). The near-natural morphological character of the Tagliamento is reflected by a complex channel morphology structured by a dynamic hydrologic flood regime, an idealized longitudinal sequence of constrained, braided, and meandering sections, and low human impacts. In the braided section, the active plain is up to 1.5 km wide and characterized by a variable cover of vegetated islands (Petts *et al.* 2000; Arscott *et al.* 2001; Gurnell *et al.* 2001; Van der Nat *et al.* 2002).

The main study area is a 1-km^2 flood plain in the middle section of the river corridor (Figure 1; river kilometer 79.8 – 80.8; 135 m a.s.l.). It consists of lotic and lentic water bodies (ponds), gravel bars, wooded islands, and a fringing riparian forest. 17.6°C. Detailed information on the catchment and the main study area are given by Ward *et al.* (1999), Arscott *et al.* (2000), and Gurnell *et al.* (2000).

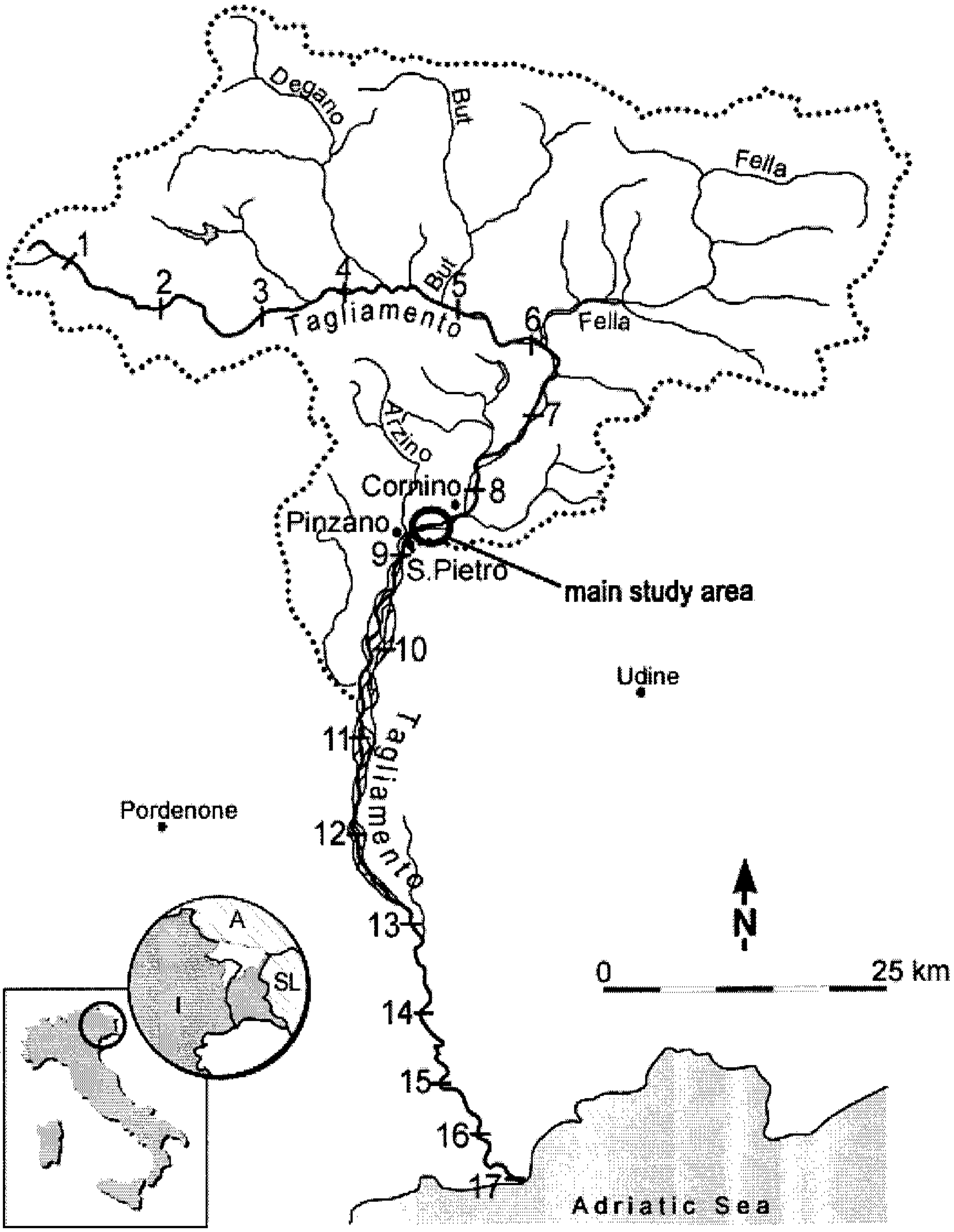


Figure 1. The catchment of the Tagliamento and the location of study sites. I = Italy, SL = Slovenia, A = Austria. Numbers (1-17) stand for the study segments of the longitudinal survey.

METHODS

In the present study, we defined ponds as isolated water bodies with a surface area >2 m^2 and a water depth >10 cm. Hydrologically, ponds were divided into three categories: permanent, ephemeral and episodic. Permanent ponds carried water during the entire investigation period, ephemeral ponds dried up for some periods, and episodic ponds had surface water only during short–term flow or flood pulses (*sensu* Tockner *et al.* 2000)

Pond dynamics in space and time

In spring 2002, around mean water level, pond density was systematically investigated within 17 segments of 1-km length; equally spaced (every 10 km) along the entire corridor (Figure 1, see also Karrenberg *et al.* 2003). Within each segment, all ponds were mapped.

Between April and October 2001, all ponds in the main study area were repeatedly mapped (total 46 dates). In addition to all ponds in the active zone, we included ponds in the adjacent riparian forest (right bank, in flow direction). The interval between individual sampling dates ranged from 3 to 12 days depending on the relative change of the water level (main channel). The exact position, area, and distance to vegetated islands, main channel, and side channel were measured for each pond using a Global Positioning System (GPS, TCS 1, Trimble Inc., USA). On each sampling date, shape, length, width, and maximum depth were determined for all ponds that actually contained water. The surface area of each pond was calculated during filling and drying periods by multiplying maximum length and maximum width. Furthermore, the degree of surface connectivity of individual pond with channels was recorded.

Pond hydrology

Water level was determined by installing simple graduated staff gauges vertically at the deepest point of each pond. Staff gauges were read manually at each sampling date (totaling 46 dates). A permanent gauging station at a knick point 1.5-km downstream of our investigation site (location name: S. Pietro) was used as a reference point in the main channel. Stage data were used rather than discharge because discharge data were not available for the investigation period. A problem using stage data from a morphologically dynamic river is that channel bed elevations change frequently; these changes could affect the stage discharge relationship. The gauging station from which the data were obtained is located at a stable bedrock constriction and therefore minimized instability in the stage discharge relationship. Daily changes and cumulative water-level fluctuations (sum of daily change) were calculated for each pond.

Thermal heterogeneity

From April to October 2001, surface-water temperature was recorded at hourly intervals. Temperature data-loggers (VEMCO Minilog, Nova Scotia, Canada) were installed at the deepest point of each pond (Arscott *et al.* 2001; Uehlinger & Malard 2003). The following variables were calculated to characterize thermal heterogeneity: (i) average daily temperature, (ii) average minimum daily temperature, (iii) diel temperature amplitude (maximum – minimum difference), (iv) seasonal variation expressed as the difference between minimum and maximum values during the investigation period; and (v) cumulative degree days (sum of daily mean temperature).

Physicochemical characterization

Oxygen (mg/l, % saturation) was measured with a portable oximeter (Oxi 320, WTW, Germany), pH with a portable pH meter (pH 340, WTW, Germany), turbidity (Nephelometric Turbidity Units: NTUs) with a portable turbidity meter (Cosmos, Züllig, Switzerland), and specific conductance (μS cm^{-1}, T_{ref} at 20°C) with a portable specific conductance meter (LF 325, WTW, Germany). All ponds were sampled between 8:00 and 11:00 a.m. at the central part of the pond to minimize diel influences (at the location of temperature loggers).

Statistical analyses

Synchrony was used to assess the seasonal patterns in pond dynamics. Synchrony or temporal coherence is a measure of the similarity between a pair of sampling sites (e.g., Soranno *et al.* 1999; Kling *et al.* 2000; Tockner *et al.* 2002). High synchrony is generated when sites respond similarly to a common driver. For each variable, synchrony was calculated as the Pearson product-moment correlation coefficient (r) between time series of all data ($n = 46$) for each pair of ponds. In order to classify individual pond types, a principal components analysis (PCA, CANOCO 4.02, Ter Braak & Smilauer 1998) was applied by integrating morphological, physicochemical, and hydrologic variables. To reflect the within- and between-pond heterogeneity, we used ranges (maximum – minimum differences) for turbidity, water-level fluctuation, specific conductance, oxygen, and pH.

RESULTS

Pond dynamics in space and time

Along the active river corridor, density ranged from 0 to 22 ponds per 1-km study segment, with greatest pond density in bar- and island-braided floodplain segments (Figure 2). In 8 out of 17 segments, ponds were absent during the sampling campaign, either because there was no surface flow or because the segment was constrained naturally (canyon sections) or artificially (canalization in the most downstream sections, Figure 2).

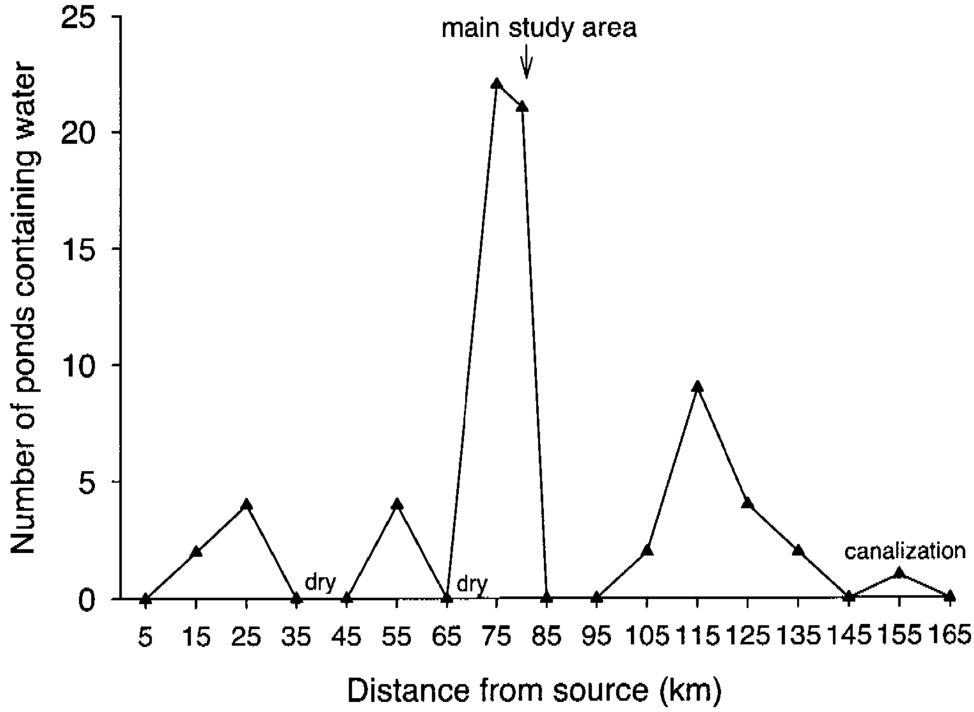


Figure 2. Number of ponds containing water per river-km along the Tagliamento corridor (April 2002).

Of the 39 ponds in the main study area, 18 were permanent, 18 ephemeral, and 3 episodic (Figure 3). Based on their location, 31% of all ponds were associated with vegetated islands, and 61% were bare-gravel ponds, the latter mostly associated with large wood accumulations. Three permanent ponds (8%) were located in the riparian forest. Pond shape was from near circular to extremely elongated, with length-to-width ratios ranging from 1.1 to 23.3.

Pond density increased exponentially from 18 ponds at a water level of 100 cm to 39 ponds at 230 cm (Figure 4). At a specific water level, the density of ponds varied considerably. For example, at a water level of 190 cm, pond density in the main study area ranged from 24 (1 May) to 32 (23 April).

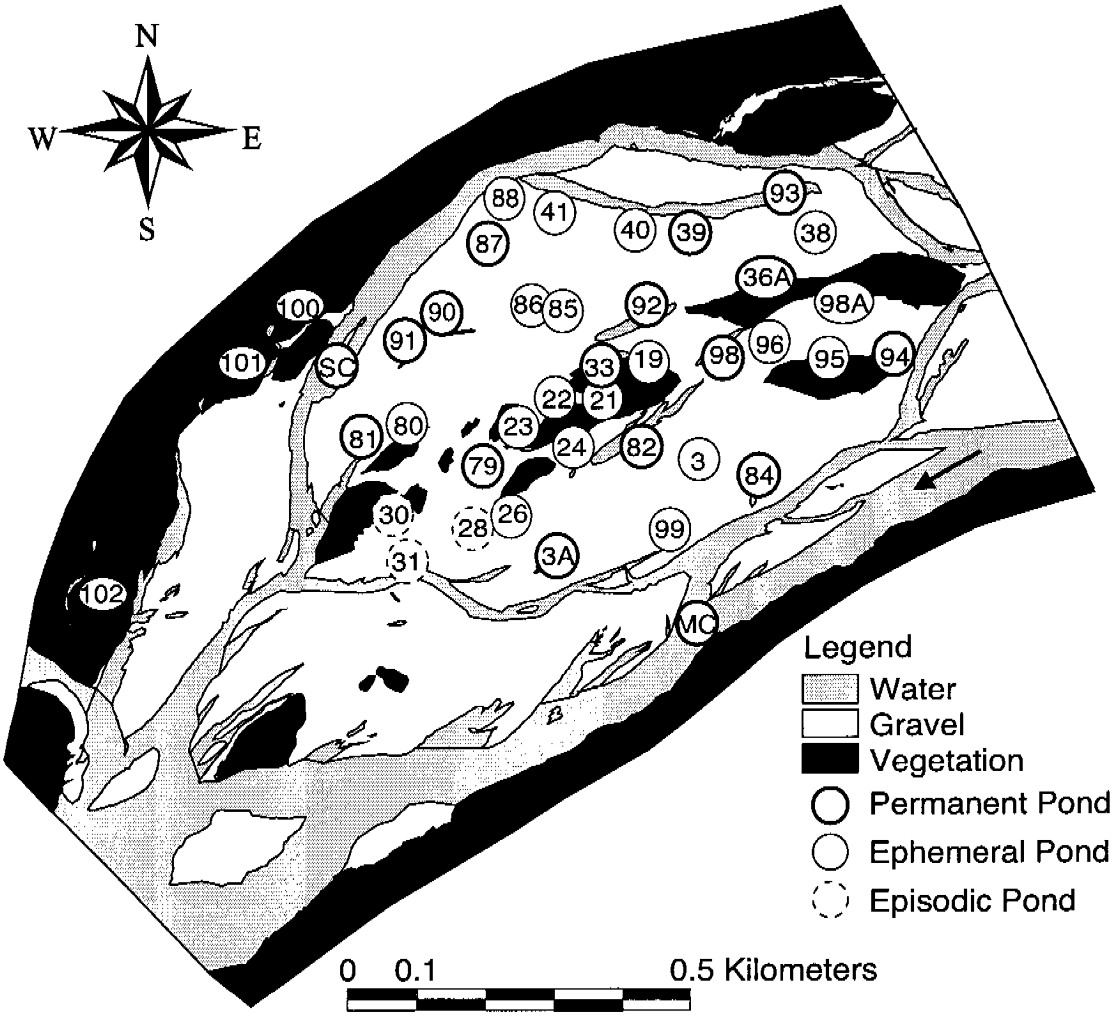


Figure 3. Map of the main study area and location of permanent, ephemeral, and episodic ponds. In the active corridor, only ponds within the large gravel bar / island complex were considered. Ponds 100 to 102 are in the riparian forest.

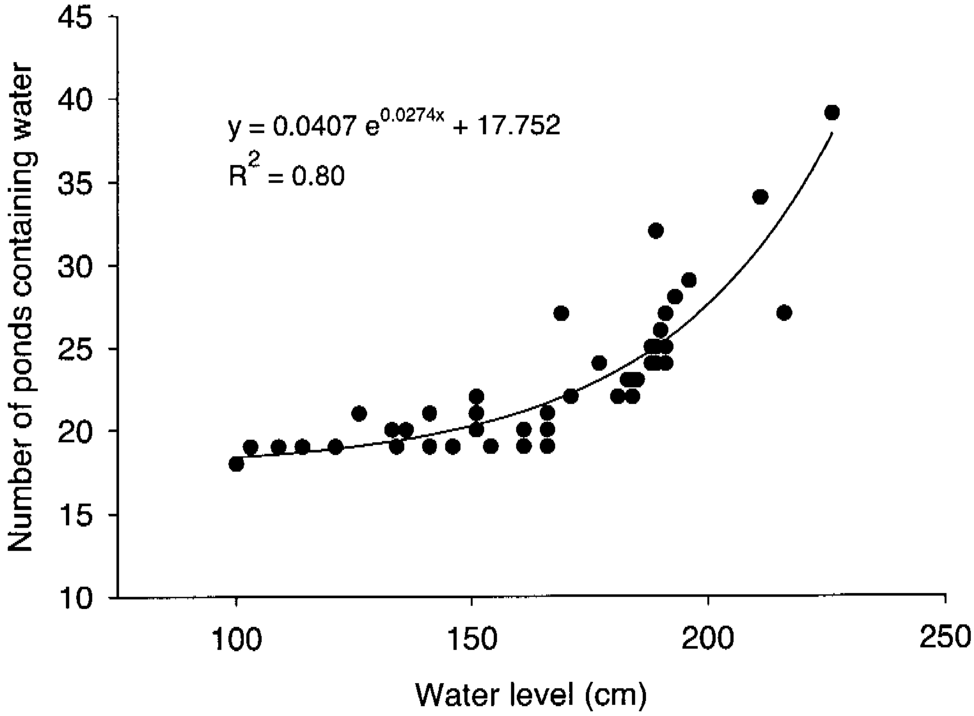


Figure 4. Relationship between water level of the main channel (S. Pietro) and the number of ponds containing water.

Based on the observed relationship between water level and pond density, an entire year of water-level data were converted into a time series of pond densities (Figure 5). As expected from this relationship, pond density strongly resembled the dynamic hydrograph, with an expected peak at ~250 cm, close to the maximum water level sampled during the present study. However, a sharp decrease in density was observed above a water level of ~250 cm (U. Karaus, personal observation). At this water level, around 50% of the flood plain is inundated (Van der Nat *et al.* 2002). Based on this prediction, about 50% of all ponds contained water only during short periods, often only for 1-2 days after flood events (Figure 5).

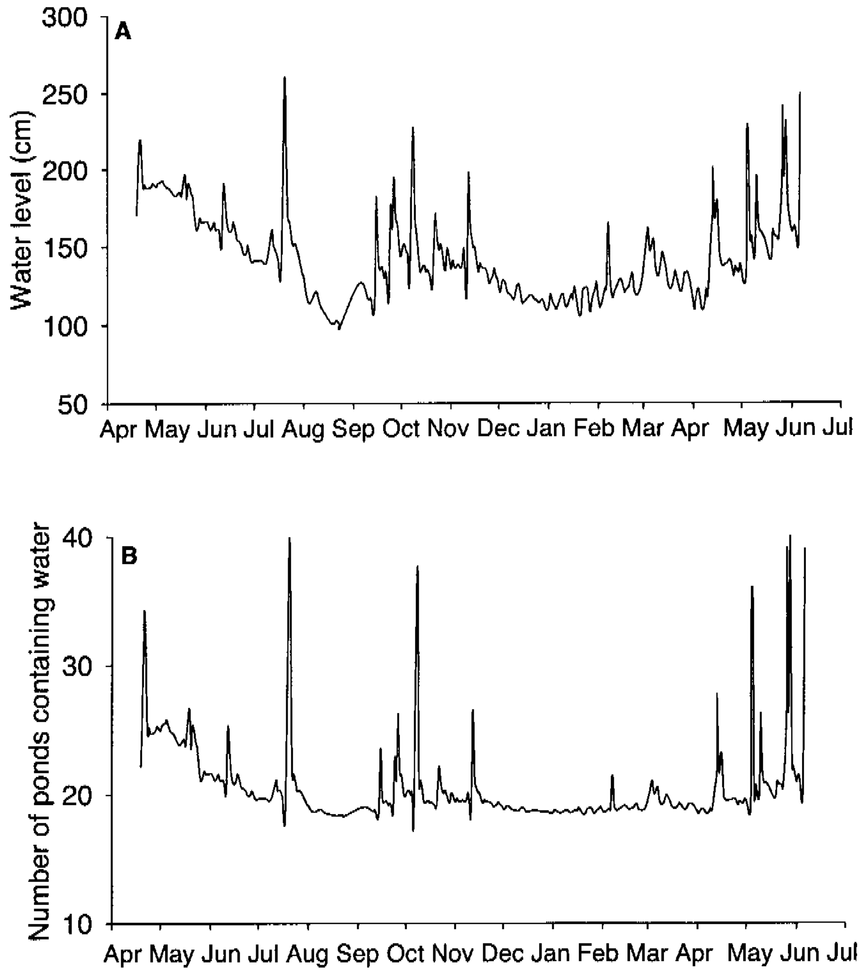


Figure 5. A: Water level (S. Pietro) from May 2001 to June 2002. B: Number of ponds predicted from the water level – pond number relationship (see Figure 4) for this time period.

The aquatic surface area of all ponds combined increased exponentially from 1503 m^2 at low water level to 18204 m^2 at 216 cm ($y = 113.3\ e^{0.022x}$, $r^2 = 0.92$). Area of the smallest permanent pond (39) was 3 m^2 at lowest measured water level and 48 m^2 at highest water level. Pond 92 was the largest pond at lowest water level (618 m^2). At highest measured water level, pond 82 was the largest pond (7965 m^2). The area ratio of high to low water level (A_{high}/A_{low}; Table 1) ranged from 2 (pond 33) to 470 (pond 82).

Table 1. Area (m^2) of selected floodplain ponds at low water level (A_{low}; 103 cm) and high water level (A_{high}; 216 cm), and area variation (ratio A_{high}/ A_{low}).

Pond	A_{low}	A_{high}	A_{high}/A_{low}
3A	36	239	7
33	173	408	2
36A	6	85	15
39	3	48	16
79	289	2718	9
80	5	86	18
81	63	165	3
82	17	7965	469
84	70	321	5
87	39	150	4
92	618	4343	7
94	17	268	16
98	167	1345	8
98A	0 (dry)	64	>64

Pond hydrology

During the investigation period, the maximum change in water level ranged from 11 cm (pond 93) to 72 cm (pond 84), compared to 116 cm in the main channel (Figure 6). Cumulative water-level change (sum of daily changes during the investigation period) ranged from 56 cm (pond 93) to 311 cm (pond 94), compared to 348 cm in the main channel. A distinct hydrologic gradient occurred across the flood plain. Ponds close to the right bank (in flow direction) had small water-level fluctuations, ponds close to the main channel and ponds located in former channels (ponds 82, 79) showed large amplitudes (Figure 6). Water level fluctuations in all permanent ponds except pond 102 were strongly related to the hydrograph of the main channel ($r^2 > 0.5$). Pond 102 had a very constant water level.

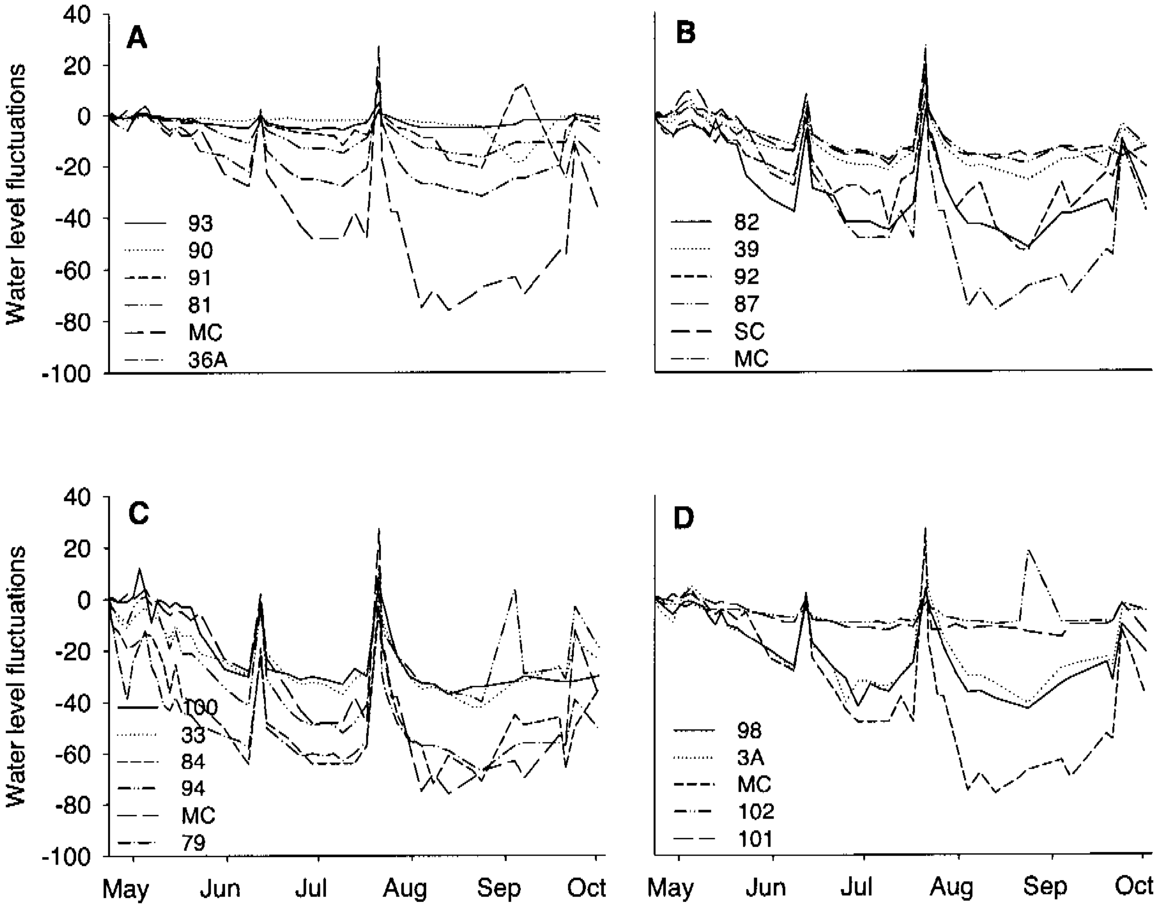
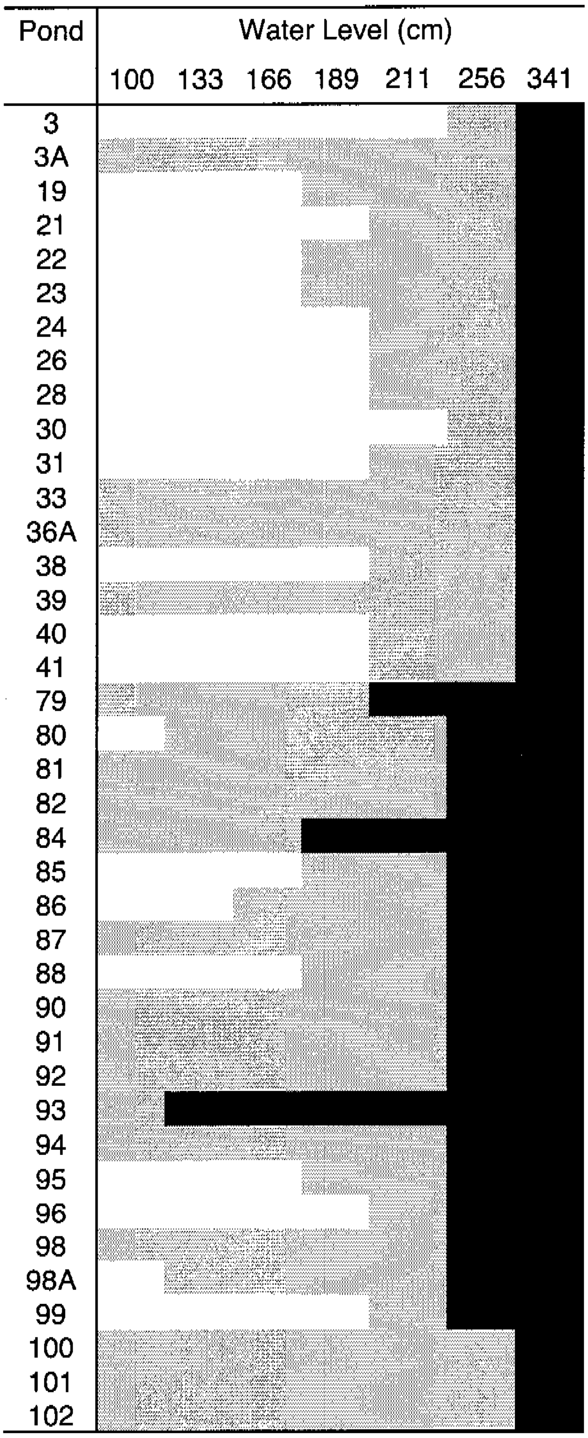


Figure 6. Relative daily water-level changes (cm) of all permanent ponds compared to the main channel (MC) during the investigation period. Ponds are grouped according to the outcome of the PCA (see Figure 10).

At low water level (100 cm), 54% of the ponds were dry and 46% remained disconnected. At mean water level (189 cm), 31% were dry, 64% remained disconnected, and 5% were already connected. At about 340 cm, all water bodies (ponds and channels) merged into a single channel (Figure 7).



Pond	Water Level (cm)						
	100	133	166	189	211	256	341
3	☐	☐	☐	☐	☐	▨	■
3A	▨	▨	▨	▨	▨	▨	■
19	☐	☐	☐	▨	▨	▨	■
21	☐	☐	☐	☐	▨	▨	■
22	☐	☐	☐	▨	▨	▨	■
23	☐	☐	☐	▨	▨	▨	■
24	☐	☐	☐	☐	▨	▨	■
26	☐	☐	☐	☐	▨	▨	■
28	☐	☐	☐	☐	▨	▨	■
30	☐	☐	☐	☐	☐	▨	■
31	☐	☐	☐	☐	▨	▨	■
33	▨	▨	▨	▨	▨	▨	■
36A	▨	▨	▨	▨	▨	▨	■
38	☐	☐	☐	☐	▨	▨	■
39	▨	▨	▨	▨	▨	▨	■
40	☐	☐	☐	☐	▨	▨	■
41	☐	☐	☐	☐	▨	▨	■
79	▨	▨	▨	▨	■	■	■
80	☐	▨	▨	▨	▨	■	■
81	▨	▨	▨	▨	▨	■	■
82	▨	▨	▨	▨	▨	■	■
84	▨	▨	▨	■	■	■	■
85	☐	☐	☐	▨	▨	■	■
86	☐	☐	▨	▨	▨	■	■
87	▨	▨	▨	▨	▨	■	■
88	☐	☐	☐	▨	▨	■	■
90	▨	▨	▨	▨	▨	■	■
91	▨	▨	▨	▨	▨	■	■
92	▨	▨	▨	▨	▨	■	■
93	▨	■	■	■	■	■	■
94	▨	▨	▨	▨	▨	■	■
95	☐	☐	☐	▨	▨	■	■
96	☐	☐	☐	☐	▨	■	■
98	▨	▨	▨	▨	▨	■	■
98A	☐	▨	▨	▨	▨	■	■
99	☐	☐	☐	☐	▨	■	■
100	▨	▨	▨	▨	▨	▨	■
101	▨	▨	▨	▨	▨	▨	■
102	▨	▨	▨	▨	▨	▨	■

Figure 7. The shift of ponds from a dry (white) to a disconnected lentic (gray) and finally to a connected (black) state with increasing water level in the main channel (S. Pietro). Data from the water level 256 cm are obtained from a preliminary sampling in March 2001.

Thermal heterogeneity

Over the 6-month period (May to October 2001), cumulative degree-days were from 1924°C (pond 102) to 3308°C (pond 87). Across the flood plain, average daily temperature difference between the coolest and the warmest pond ranged from 4.0°C to 16.1°C, with an average difference of 9.8°C. Within individual ponds, average daily temperature (May until October) ranged from 13.4°C (pond 102) to 22°C (pond 92), and average diel amplitude was from 0.9°C (pond 102) to 11.6°C (pond 92). Maximum diel amplitude was between 1.3°C (pond 102) and 26.2°C (pond 39). Individual ponds can be arranged across a gradient from small to large diel and seasonal amplitudes (Figure 8).

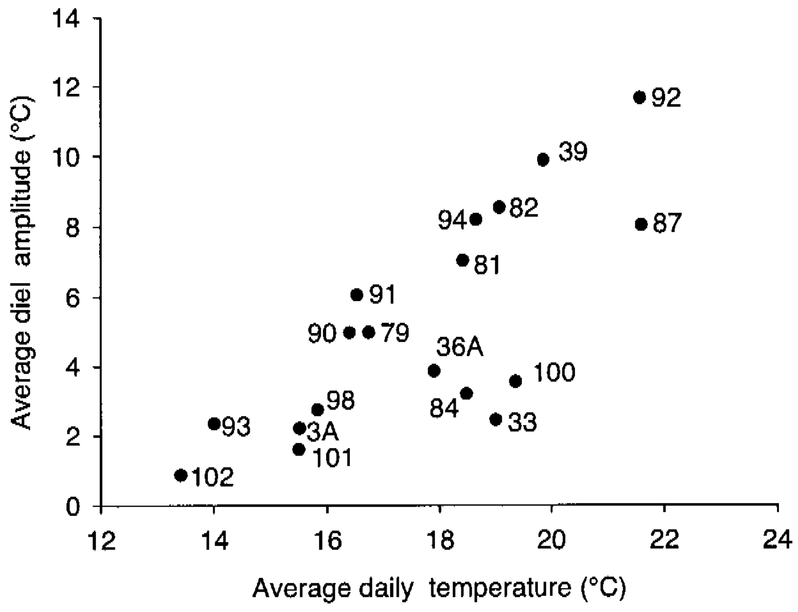


Figure 8. Average daily temperature (May until October 2001) vs. diel amplitude for all permanent ponds ($r^2 = 0.58$).

Diel and seasonal temperature patterns (based on hourly measurements) illustrate differences in thermal regimes across the flood plain (Figure 9). Pond 33, for example, had low diel variation but a distinct seasonal variation. A similar seasonal variation, but with larger daily fluctuations, was observed in pond 36A. Distinct diel temperature fluctuations were measured in ponds 88, 90, 92, and 94. Small temperature fluctuations at the beginning of the investigation period and a continuous increase during the investigation period were featured in pond 90. A weak seasonal temperature pattern was shown in ponds 98 and 102.

Classification of ponds

Average synchrony for all variables was 0.33. This average was taken across all pairs of ponds. Synchrony of individual ponds with all other ponds was low and ranged from 0.21 (pond 100) to 0.47 (pond 84). Synchrony between individual ponds and the lotic channel ranged from 0.15 (pond 15) to 0.53 (pond 53). Synchrony of variables was 0.18 for turbidity, 0.22 for specific conductance, 0.42 for pH, and 0.50 for dissolved oxygen.

The first two axes of the principal components analysis PCA explained 51% of the total variance within the data matrix (14 environmental variables, 18 permanent ponds). Average, maximum, and minimum daily temperature (73%, 64%, and 56%), water-level fluctuation (67%), turbidity (42%), and specific conductance (28%) accounted for the definition of the F1 axis (Figure 10). Average water depth (45%), average diel temperature amplitude (45%), and pH (31%) accounted for most of the definition of the F2 axis. Distance to channel and island (69 and 46%) and variability in surface area (40%) accounted for the definition of the F3 axis (not shown in Figure 10). Oxygen (77%) explained the F4 axis (not shown). Results from the PCA on these environmental variables distinguished four groups of ponds along the F1 and F2 axis (Figure 10). Group 1 (39, 82, 87, and 92; see Figure 3 for location) was characterized by a large thermal heterogeneity. In contrast, group 2 (3A, 98, 101, 102) had a very low thermal heterogeneity. Group 3 (33, 79, 84, 94, 100) was hydrologically very dynamic and had a wide range in specific conductance, turbidity, pH, and oxygen values. Group 4 (81, 90, 91, 93) had small water-level fluctuations and showed a narrow range in specific conductance, turbidity, pH, and oxygen values. Pond 36A did not fit into any of the groups.

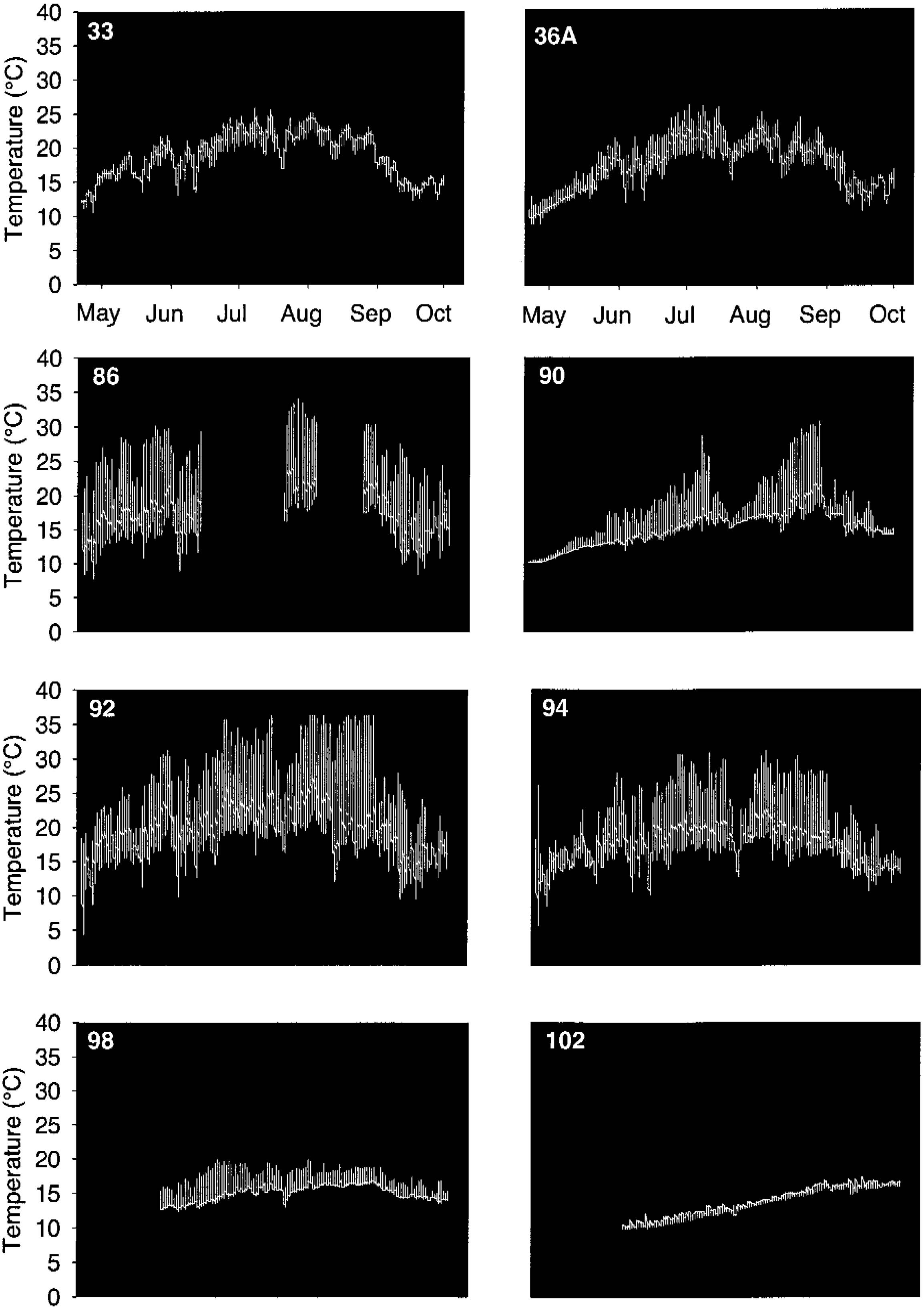


Figure 9. Hourly values of surface temperature in eight selected ponds (April to October 2001).

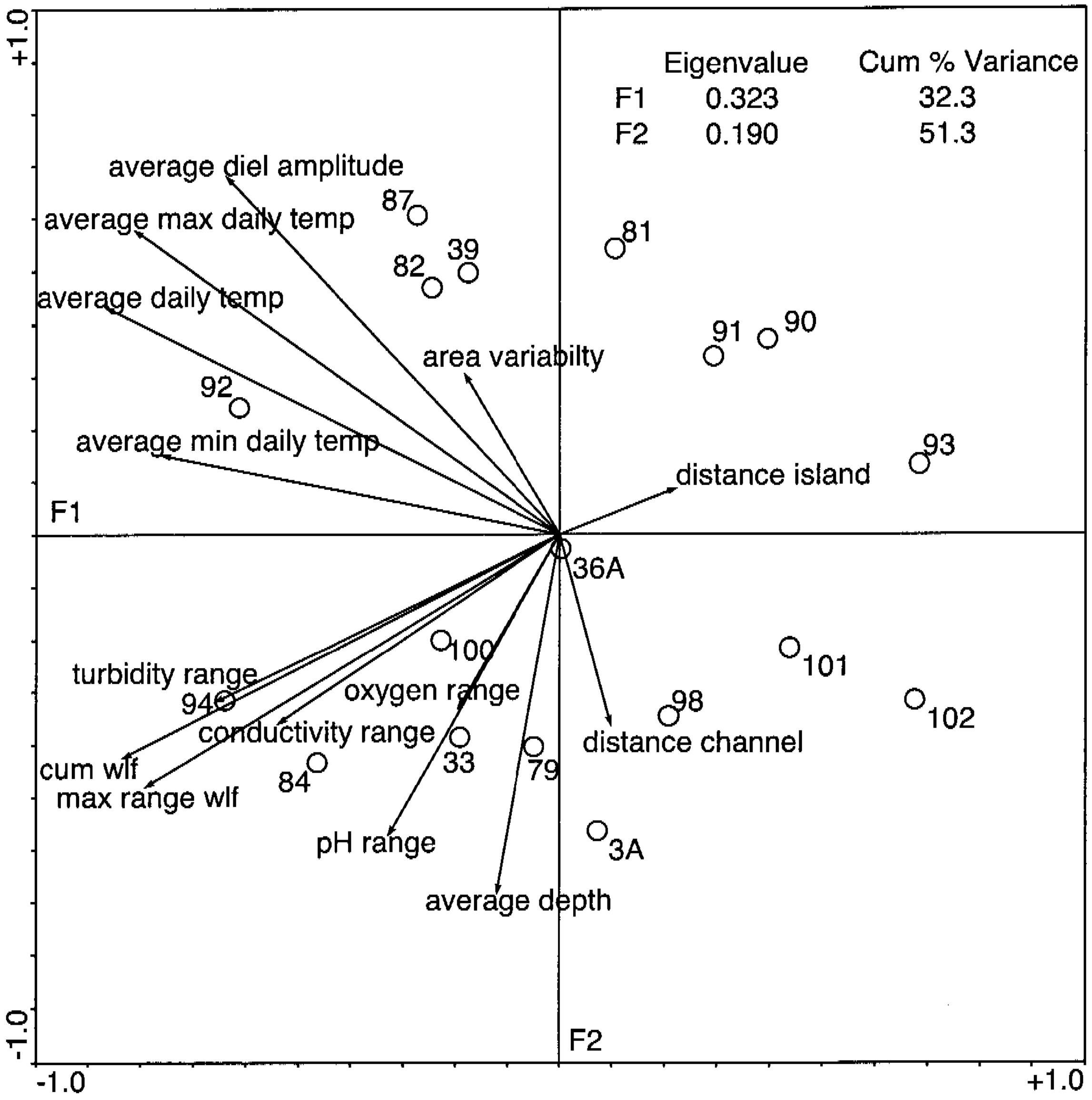


Figure 10. Principal components analysis ordination based on fourteen environmental variables for the ponds. Circles with numbers represent ponds and arrows indicate different variables. The ordination map illustrates the relationship of each variable with the definition of either the F1 or F2 axis and of each sampling point (pond) with respect to the F1 and F2 axes (defined by the variables). Average max daily temp = average maximum daily temperature; average min daily temp = average minimum daily temperature; average daily temp = average daily temperature; cum wlf = cumulative water-level fluctuation; max range wlf = maximum range of water-level fluctuation.

DISCUSSION

The Tagliamento River offers the rare opportunity to investigate ecosystem patterns and processes under semi-natural conditions that can be studied almost nowhere else in Europe (Ward *et al.* 1999). The Tagliamento has a number of attributes that have not been given due consideration in river ecology: (i) an immense corridor of more than 150 km^2, (ii) unconstrained floodplain segments, and (iii) a large number of vegetated islands (Tockner *et al.* 2003). A high diversity of parafluvial ponds is considered as an additional key attribute along the dynamic river corridor that has not yet been studied in detail.

Pond dynamics in space and time

Along the active corridor of the Tagliamento, a maximum of 22 ponds per river-km was quantified (Figure 2). Ponds were absent in human-controlled sections. Therefore, ponds can be considered as very sensitive aquatic habitats that disappear rapidly as a consequence of human impacts such as canalization or flow control. Along the Isar River (Germany), intensive hydrologic engineering has also led to a major decrease in pond density and heterogeneity (Homes *et al.* 1999).

Besides human impacts, changes in the hydrologic and geo-morphological style along the river corridor control pond density and diversity. In the headwater section, a narrow flood plain, a steep channel slope with coarse sediments, and a low alluvial reservoir limit the formation of ponds. An increase in active floodplain width, higher flow rates favor the formation of parafluvial ponds in the middle or braided sections. In the meandering section, an increase of the active channel width combined with a narrow active floodplain corridor, and a higher alluvium results in the formation of fewer but larger ponds (Arscott *et al.* 2000).

Parafluvial ponds differ from woodland ponds, marshy ponds, or prairie ponds. They are very young habitats that are formed and shaped by repeated cut-and-fill processes (Kohler *et al.* 1999; Arscott *et al.* 2002). Indeed, ponds are among the youngest habitats in the Tagliamento channel, with average half-life expectancies of less than seven months (Van der Nat *et al.* 2003). Gravel deposition, as well as erosion, is responsible for the low half-life expectancies of ponds. Hydrologically, parafluvial ponds are closely linked to the main channel. Therefore, water-level fluctuations in the main channel control the number and areal extent of ponds (Figure 5). In the Tagliamento flood plain, an exponential relationship between water level and pond density has been observed (Figure 4). Therefore, even moderate flow fluctuations can have major consequences for both pond density and area.

Pond hydrology and thermal heterogeneity

The two most important factors that control pond diversity are hydrology (source and pathway of water) and temperature (see Figure 10). Hydrologic and thermal differences among ponds can be explained by a combination of flow paths (alluvial and hill-slope ground water), pond location (shading, distance to the channel), and topography (ratio of low-to-high water surface area). For example, a decreasing trend in flow variability from the main channel towards the riparian forest was observed. The "forest ponds" (e.g., 102), which were almost completely shaded, deep, and fed by hill-slope ground water, had almost no water-level fluctuations.

The variability of water level affects area, which again influences surface connectivity (lateral connectivity) between ponds and the channel. Water-level fluctuation, topography, and spatial location of each pond create a heterogeneous pattern of connectivity (Figure 7). During low water level, most ponds are disconnected and expected to function ecologically as (concave) islands. Flood events connect the islands with the river and support the exchange of matter and organisms between lotic and lentic habitats (Drago 1989), a primary factor for ecosystem dynamics and functioning. Connectivity influences, for example, diversity and productivity across different hierarchical scales (Amoros & Roux 1988; Ward & Stanford 1995; Stanford *et al.* 1996; Tockner *et al.* 1999; Ward *et al.*

1999). Hydrologic connectivity, which includes longitudinal, lateral, vertical, and temporal connectivity, as well as complex habitat gradients, are strongly related to high species and life-history-strategy diversity (Amoros & Bornette 2002).

The second most important factor controlling pond diversity is temperature. The investigated ponds provided a diverse array of warm and cold water patches within the active flood plain. In addition to longitudinal patterns in water temperature, lateral (e.g., ponds, backwaters) and vertical (e.g., within the substrate) heterogeneity in temperature is increasingly recognized as a potentially important aspect in habitat conditions in streams and rivers (Poole & Berman 2001; Arscott *et al.* 2002; Claret *et al.* 2002). In the main study area, a lateral thermal difference of up to 17°C at a specific day is as high as along the entire 170-km long river corridor (Arscott *et al.* 2001). Temperature is a primary factor that regulates ecosystem processes and therefore structures biotic communities (Ward & Stanford 1982; Ward 1992). It has a strong influence on life history, species diversity, and abundance levels (Ward & Stanford 1982).

Pond heterogeneity and ecological role

Parafluvial ponds had a wide range in size, shape, and physicochemical properties. An average synchrony among ponds of 0.33 indicates a low temporal coherence of ponds to a common driver (water source, flow path, temperature). Furthermore, the low average synchrony value between ponds and the lotic channel (0.31) indicates that physicochemical parameters are strongly influenced by local factors such as the topographic position of ponds, morphology, and their subsurface connectivity (i.e., ground-water exchanges). An example of local influences was demonstrated using the relationships with specific conductance, which can be used as an indicator of hydrologic connectivity. In instances where specific conductance correlated poorly between ponds and side channel, while water-level fluctuation between ponds and the main channel were highly correlated, the interpretation suggests hydrostatic effects, which indicate a hydrostatic water connection but no water exchange between ponds and channels.

The morphological, topographical, hydrologic, thermal, and physicochemical heterogeneity, which is strongly related to the local environment of each pond leads to a unique pond mosaic (Figure 10). Parafluvial ponds are responsible for much of the variation in chemical conditions and thermal variability across the flood plain (Arscott *et al.* 2000). In contrast, they only cover a tiny portion of total aquatic surface area. In the main study area of the Tagliamento, for example, ponds contribute ~6.0% of the total aquatic surface area at low water level and <1.0% at high water level (Van der Nat *et al.* 2002). Despite this small aerial extent, ponds are expected to play a crucial ecological role. Floodplain ponds can provide habitat for a specific fauna and flora as demonstrated in recent investigations along the Isar (Germany, Homes *et al.* 1999), in the Lužnice flood plain (Czech Republic, Pechar *et al.* 1996), along the Ain and Rhône Rivers (France, Castella *et al.* 1991), or along the Flathead River (Montana, J.A. Stanford and M. Lorang, pers. comm.). The faunal community composition depends on pond age (Schneider & Frost 1996), the frequency of flooding and drying (Castella 1987), on area and spatial arrangement within the landscape (Brönmark 1985; Ward & Blaustein 1994; Oertli *et al.* 2002), on depth and width (Amoros 2001), and on the frequency, duration, magnitude, and timing of flooding and drying (Brooks 2000). This supports our assumption that each pond has an insular nature ("concave island") with a characteristic set of environmental properties. Lastly, many ponds are associated with vegetated islands. Indeed, the presence of vegetated islands enhances the diversity of aquatic habitats (Arscott *et al.* 2000; Gurnell *et al.* 2001; Gurnell & Petts 2002). Therefore, ponds are expected to contribute to a greater invertebrate diversity within the active floodplain channel.

CONCLUSIONS

The present study characterized and quantified the spatiotemporal dynamic that characterizes parafluvial ponds. Basically, all ponds are strongly related to the hydrologic regime of the channel. However, the morphology, topography, and the physicochemical properties of each pond form a heterogeneous pattern in space and time. Thereby, each pond contributes to the overall habitat diversity of the flood plain. The longitudinal investigation not only showed ponds as part of the corridor, but also emphasized the sensitivity of ponds to anthropogenic impacts. Therefore, parafluvial ponds can be used as sensitive indicators, similar to vegetated islands (see Tockner *et al.* 2003), of the integrity of entire river corridors.

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CHAPTER 3

THE IMPORTANCE OF PARAFLUVIAL PONDS FOR RIVERINE INVERTEBRATE DIVERSITY: A STRUCTURAL AND FUNCTIONAL PERSPECTIVE

Ute Karaus and Klement Tockner, submitted

Parafluvial ponds are discrete lentic water bodies in the active zone of riparian corridors. They are very sensitive landscape elements that disappear first as a consequence of morphological change and flow control. The contribution of parafluvial ponds to biodiversity has been almost completely ignored in river ecology. In an island-braided segment of the Tagliamento River (NE-Italy), the structural and functional (i.e., biological trait) diversity of aquatic invertebrate communities in parafluvial ponds and in the lotic channel was investigated. Detailed investigations of physicochemical conditions and invertebrates were carried out over a five-month period following a major spring flood in 2001. Seventy-two percent of a total of 91 taxa were restricted in their occurrence to ponds, 10% to the channel. A high proportion of taxa was classified as rare that occurred in <10% of ponds. Taxa richness significantly decreased with increasing environmental variability. Co-inertia analyses revealed no clear pattern between environmental conditions and biological traits of macroinvertebrates, which indicated the early successional stage of most parafluvial ponds. The present study confirmed a disproportionate contribution of parafluvial ponds to overall riverine biodiversity.

INTRODUCTION

Parafluvial (*sensu* Fisher *et al.* 1998) ponds are discrete lentic water bodies within the active zone of river corridors (Frissell *et al.* 1986; Karaus *et al.* 2005). Their formation depends on cut and fill alluviation, scouring by the presence of large wood and vegetated islands, an abundant sediment supply, and a natural flood regime (Arscott *et al.* 2000; Ward *et al.* 2002). They are primarily fed by alluvial groundwater although other sources can be important (rain and river water). Parafluvial ponds occupy a small portion of the floodplain area, however, they substantially contribute to total aquatic habitat diversity (Drago 1989; Homes *et al.* 1999; Arscott *et al.* 2000; Van der Nat *et al.* 2002; Karaus *et al.* 2005). High habitat diversity (i.e., spatial heterogeneity) was mainly caused by a wide range in area, temperature, and hydrologic conditions (Karaus *et al.* 2005). In addition, temporal variability of environmental properties is expected to be different in individual ponds (Karaus *et al.* 2005).

Spatial habitat heterogeneity determines the composition and distribution of communities (Palmer 1992; Tilman 1994; Palmer 1995; Malmqvist 2002). Southwood (1977; 1988) proposed that habitat conditions ("habitat templet"; spatial and temporal variation of the habitat) filter characteristic life history strategies (combination of biological traits) that enable the survival of species in a given habitat. Based on Southwood's habitat templet theory, Townsend and Hildrew (1994) developed the River Habitat Templet, which is related to temporal variability (disturbance frequency) and spatial heterogeneity (refugia availability). This concept predicts that organisms in habitats with high temporal variability and low spatial heterogeneity are more resilient and resistant than organisms in less heterogeneous and variable habitats (Townsend & Hildrew 1994; Townsend *et al.* 1997). Several investigations have confirmed the proposed relationship between species traits and habitat use (Schlosser 1990; Scarsbrook & Townsend 1993; Statzner *et al.* 1994; Poff & Allan 1995; Mérigoux *et al.* 2001; Snook & Milner

2002). However, there is no comprehensive information on biological trait pattern in parafluvial ponds. In the present study, we used a set of biological traits to characterize parafluvial ponds. High spatial heterogeneity and temporal variability of environmental conditions among parafluvial ponds is assumed to be reflected in a divers array of biological traits.

The faunal composition of lentic water bodies such as vernal ponds, forested wetland ponds, prairie ponds, artificial ponds, and small lakes has been extensively studied (e.g., Batzer *et al.* 1999; Brooks 2000; Schwartz & Jenkins 2000; Brönmark & Hannsson 2002; Oertli *et al.* 2002). The main factors that controlled their communities included pond age (Schneider & Frost 1996), area and spatial arrangement within the landscape (Brönmark 1985; Ward & Blaustein 1994; Oertli *et al.* 2002), pond morphology (Amoros 2001), and the frequency, duration, magnitude, and timing of flooding and drying (Castella 1987; Brooks 2000). Very limited information, however, is available on the community composition of lentic water bodies (parafluvial ponds) along active river corridors (Homes *et al.* 1999).

In the present study, we focused on the diversity of benthic macroinvertebrates in parafluvial ponds. The primary aim was to investigate the relationship between pond heterogeneity and benthic communities. We hypothesized that (1) pond fauna substantially differs from that in the channel; (2) individual ponds are colonized by distinct benthic communities (i.e., high environmental heterogeneity in ponds results in distinct benthic communities); (3) environmental variability of ponds controls taxa diversity (i.e., more stable ponds have higher taxa diversity than more variable ones); (4) individual biological traits of benthic invertebrates are related to ponds arrayed along an environmental variability gradient (i.e., organisms in variable ponds exhibit mainly biological traits that are required to cope with harsh environmental conditions).

STUDY AREA

The Tagliamento is a large gravel-bed river in north-eastern Italy (Friuli-Venezia Giulia; 46°N, 12°30´E; Figure 1A). It starts at 1195 m a.s.l. in the Carnian Alps and flows 170 km to the Adriatic Sea. The catchment covers 2580 km^2 with more than 70% located in the Alps. The mountainous section of the catchment consists of limestone and Flysch deposits, and the Friulian plain is filled with Tertiary and Quaternary sediments. The Tagliamento has an average discharge of ~90 m^3/s, whereas 2-, 5- and 10-year floods are estimated to be 1100, 1600 and 2150 m^3/s, respectively (Petts *et al.* 2000). High flow is caused by snowmelt (spring) and heavy rainfall (autumn) with discharge maxima of ~4000 m^3/s (Ward *et al.* 1999). The near pristine character of the Tagliamento is evidenced by its complex channel morphology, dynamic flood regime, and a longitudinal sequence of constrained, braided, and meandering sections.

The main study area was a 1 km^2 island-braided flood plain in the middle section of the river corridor (river km 79.8 – 80.8; 135 m a.s.l.; Figure 1B). The flood plain consists of channels, lentic water bodies (backwaters and ponds), gravel bars, vegetated islands, and the fringing riparian forest. The local climate has an Alpine character with high precipitation (annual discharge: 2000 mm) and a mean maximum air temperature of 17.6°C. For detailed information on the catchment and the main study area see Ward *et al.* (1999), Gurnell *et al.* (2000), Arscott *et al.* (2000) and Tockner *et al.* (2003).

METHODS

In the main study area, all permanent ponds with a surface area >2 m^2 and a water depth >10 cm were surveyed. Temporary ponds were excluded because they contained surface water only during short flow or flood pulses (Karaus *et al.* 2005). In total, 18 ponds and the lotic channel were repeatedly investigated after a spring flood in April (May until October 2001; Figure 1C). Fifteen ponds were located within the active river corridor; 3 ponds at the edge of the riparian forest.

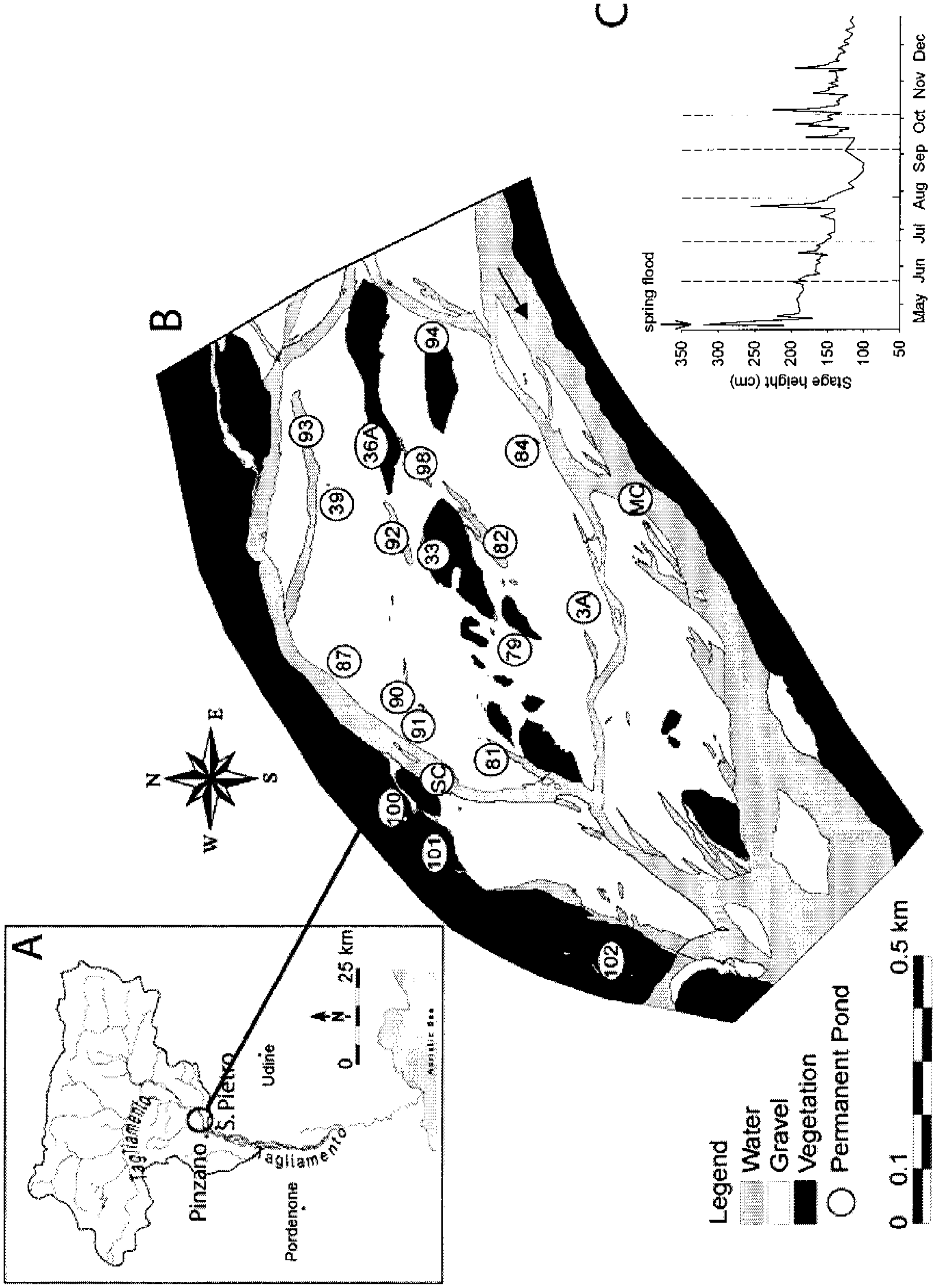

Figure 1. A. Catchment of the Tagliamento River. B. Map of the main study area (April 2002). C. Stage height at river-km 84 (S. Pietro; 1.5 km downstream of our study site). Dashed lines indicate macroinvertebrate sampling dates.

Environmental characterization

For each pond, position, area, and distance to the lotic channel were measured using a differential GPS (TCS 1, Trimble Inc., USA). Water level was determined using graduated staff gauges installed at the deepest point of each of the 18 floodplain ponds. Staff gauges were read manually (totalling 46 dates). A permanent gauging station at a knick point 1.5 km downstream of our investigation site (location name: S. Pietro) served as a reference in the main channel. Daily cumulative water level fluctuations ("wlf"; sum of daily change) were calculated for each pond. Area, shape, and water level of each pond were determined at intervals between 3 to 12 days (totalling 46 times), depending on the relative change of water level in the main channel. Variability of pond area was expressed as the ratio of the area at the highest (216 cm) to the lowest (102 cm) measured water level in the main channel.

Data-loggers (VEMCO Minilog, Nova Scotia, Canada) were installed at the deepest point of each pond to record surface water temperature at hourly intervals. Mean daily temperature (temp dm) and the diel temperature amplitude (temp da; maximum – minimum difference) were calculated to characterize thermal heterogeneity.

Selected physicochemical variables were measured with portable meters at 3 to 12 day intervals (totalling 46 dates). Variables included oxygen (mg/l; Oxi 320, WTW, Germany), pH (pH 340, WTW, Germany), turbidity (nephelometric turbidity units [NTU]; Cosmos, Züllig, Switzerland), and specific conductance ($\mu S\ cm^{-1}$, T_{ref} 20°C; LF 325, WTW, Germany). To minimize diel influences, all ponds were sampled between 8:00 and 11:00 a.m. at the central part of the pond (at the location of the temperature loggers).

In each water body, surface water was collected prior to sampling of benthic macroinvertebrates (totalling five dates). Water was collected in 1 litre polyethylene bottles and kept cool (4°C) prior to analyses. All chemical analyses were performed within four days of sample collection. Analytical methods for ammonia (NH_4), nitrate (NO_3), soluble reactive phosphorus (SRP), dissolved organic carbon (DOC), and sulphate (SO_4) were identical to Tockner *et al.* (1997) and Malard *et al.* (1999).

Macroinvertebrates

Benthic invertebrates were sampled from all ponds and the channel at monthly intervals. Macroinvertebrates were collected using a D-shaped kick-net (mesh size: 250 μm). In ponds, invertebrates were sampled according to the method of Oertli *et al.* (2002). The number of samples (n) collected within each pond was dependant on pond size (S, in m^2) and calculated as follows:

$$n = 0.885 \text{ x } (2^{\log S}).$$

In the channel, the number of samples (n) was similar to the total number of samples of all ponds combined. Within each water body, all major mesohabitats (bare sediment, large wood, macrophytes, pool and riffle) were sampled according to their relative abundance. For each sample, the net was swept above the sediment-water interface for 30sec. All samples from an individual water body were combined into a composite sample and preserved in 4% formaldehyde (Platts *et al.* 1983). In the laboratory, all invertebrates were identified to the lowest practical taxonomic level using a dissecting microscope.

Biological traits

Ten biological traits were selected to calculate functional diversity of macroinvertebrates (Table 1). Biological traits were chosen according to Townsend and Hildrew (1994) (dependant on available information), who predicted several biological traits shaped by the habitat templet. Traits reflected rapid recruitment (descendents per reproductive cycle, reproductive cycles per year), rapid reproduction in variable habitats (reproduction technique, duration of developmental phases of larvae and eggs), physiological adaptations (i.e., desiccation tolerance, form of resistance, thermal tolerances), resilience (dispersal),

Table 1. Biological traits and modalities (=categories) of aquatic macroinvertebrates used in this study.

Trait	Modalities	Code
Rapid recruitment		
Descendants per reproductive cycle	≤1000	AA
	>1000-3000	AB
	>3000	AC
Reproductive cycles per year	<1 / semivoltin	BA
	1 / univoltin	BB
	2 / bivoltin	BC
	>2	BD
Rapid reproduction in variable habitats		
Reproduction technique (parthenogenesis or sexual)	Single individual	DA
	Male/female	DB
Duration of developmental phases larvae (month)	≤4	EA
	>4-8	EB
	>8-12	EC
	>12	ED
Duration of developmental phase egg (month)	≤2	FA
	> 2-6	FB
	> 6	FC
Desiccation tolerance		
Form of resistance	Eggs, gemmulae, statoblasts	HA
	Cocoons	HB
	Desiccation bags	HC
	Diapause	HD
	None	HE
Temperature fluctuation tolerance	Stenotherm (<15°C)	JA
	Stenotherm (>15°C)	JB
	Eurytherm	JC
Biotic interactions		
Potential size (mm)	≤5	NA
	>5-10	NB
	>10-20	NC
	>20-40	ND
	>40	NE
Functional feeding group	Scraper	QA
	Shredder	QB
	Deposit feeder	QC
	Filterer	QD
	Predator	QE
Resilience		
Dispersal	Aquatic passive	KA
	Aquatic active	KB
	Air passive	KC
	Air active	KD

and biotic interactions (functional feeding group, potential size). The 10 traits were subdivided into categories, hereafter called "modalities" (Table 1). Each taxon was then assigned an affinity to each trait modality using a fuzzy coding procedure (Chevenet *et al.* 1994). This procedure takes into account variations in trait expression. We used a scoring range of 0 to 3, with 0 being no affinity to a trait modality and 3 being total affinity. Information on biological traits was obtained from ~50 primary (e.g., Frömming 1956; Freude *et al.* 1964-1998; Glöer & Meier-Book 1994; Tachet *et al.* 2000) and secondary (e.g., Gardner 1950; Bournaud *et al.* 1992; Usseglio-Polatera 1994; Usseglio-Polatera & Tachet 1994) sources. Where information on a particular trait could not be obtained for a specific taxon, this taxon was assigned "0" for that trait so that it had no influence on the overall results (Chevenet *et al.* 1994). Functional composition of ponds was calculated based on relative taxa abundances. Relative abundance of each taxon was multiplied with the trait affinity (in %), and the proportion of each modality per trait was calculated as described by Charvet *et al.* (2000) and by Statzner *et al.* (2001).

Statistical Analyses

Jackknife estimates

To standardize samples, Jackknife estimates (Jack-1, Heltshe & Forrester 1983) for taxa richness were generated (based on individuals; Programme EstimateS Version 6.0b1 Colwell 2001). All Jackknife estimates were permuted at random 1000 times to produce more accurate estimates for ponds and the channel including standard deviations. Furthermore, Jackknife analyses were used to calculate the total number of expected species (Krebs 1998).

Nestedness

Sites are considered to be nested when species assemblages of species-poor sites comprise a subset of species assemblages in richer sites (Patterson 1987). Nestedness was determined using the Temperature Calculator of Atmar & Patterson (1993; 1995). The calculated "temperature" (T) reflects the degree of order present in presence-absence matrices. It ranges from T=0° (perfectly nested) to T=100° (random). Data were packed in rows (ponds) and columns (taxa) to maximize nestedness. Monte Carlo randomizations (500 permutations) were used to test whether calculated T value was significantly lower compared to a randomly calculated T.

Similarity

Taxa similarity between all pairs of ponds was calculated using Jaccard's similarity coefficient (Krebs 1998). Similarity was used as a surrogate of spatial turnover (beta-diversity).

Environmental variability

Within pond variability was measured using an approach similar to Romanuk's environmental variability index (EVI) (Romanuk & Kolasa 2002). Multivariate ordination of 10 environmental variables (ranges of oxygen, turbidity, pH, specific conductance, DOC, NH_4, NO_3, SRP, SO4, maximal range of water level fluctuation, mean daily temperature, and diel temperature amplitude) was used to define a single "overall" measure of habitat variability for each pond. Ranges were expressed as differences between maximum and minimum values. The resulting matrix was then analyzed with a non-centered principal components analysis. The first component of such an analysis is always unipolar (Noy-Meir 1973) and can be used as a multivariate environmental variability index. Prior to statistical analyses, environmental data were standardized by subtracting the mean and dividing by the standard deviation.

Multivariate analyses

Within-class Co-inertia analysis was used to simultaneously investigate the structure in the environmental and species trait data, and to determine if concordance (i.e., co-structure) between these two independent structures existed (Dolédec & Chessel 1994; Franquet *et al.* 1995). Concordance between environmental and species trait data was determined using a Monte Carlo permutation test (10000 permutations). All multivariate analyses were computed using ADE-4 software (Thioulouse *et al.* 1997).

RESULTS

Species richness patterns and nestedness

A total of 5860 macroinvertebrates from 91 taxa was sampled. Diptera (30%), Coleoptera (23%), and Ephemeroptera (17%) dominated the community. Plathelminthes, Mollusca, Odonata, Rhynchota (Hemiptera), and Megaloptera were restricted in their occurrence to ponds (Appendix, Table 1).

Based on Jackknife estimates, we sampled 72% of the expected total taxa richness in both ponds and the channel. Estimates of species richness produced using Jackknife procedures (standardized for number of individuals), exhibited faster increase of richness in ponds than in the channel (steeper slope; Figure 2). In a random sample of 800 individuals, for example, 57 (SD: 6.8) taxa can be expected in ponds and 32 (SD: 2.1) in the channel. Pond fauna differed from channel fauna. Sixty-six taxa were restricted to ponds, nine to the channel, and 16 occurred in both types of water bodies (Appendix, Table 1).

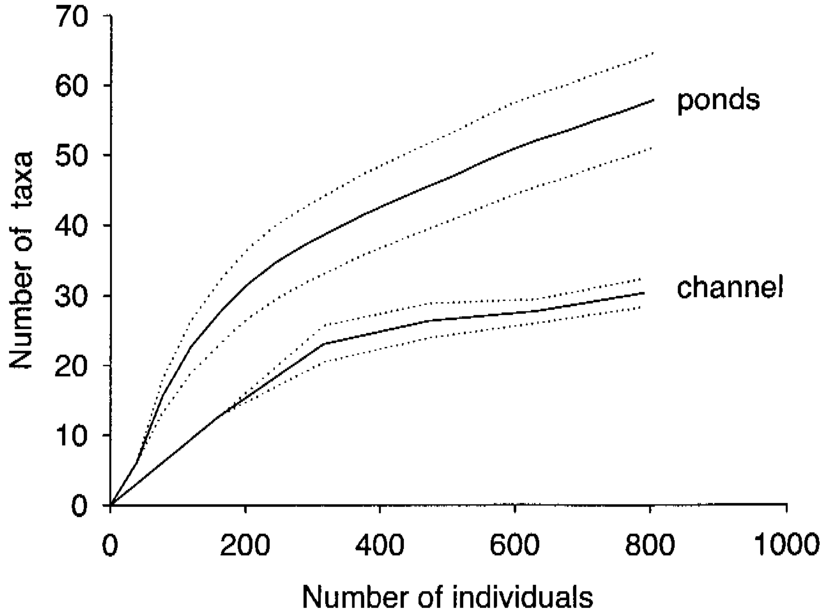

Figure 2. Jackknife estimate curves (±SD) of taxa richness in ponds and in the channel standardized by the number of individuals.

Assemblage structure was nested among the 18 ponds and the channel (T=18.95°) and "temperature" was significantly lower than estimates randomly produced by Monte Carlo simulations ($p < 0.001$). Ponds, however, did not form a nested subset of the channel.

The mean number of taxa per pond (all five sampling dates combined) was 16 and ranged from one (pond 100) to 34 (pond 102). For comparison: the mean number of taxa in the main channel was 15 taxa. Fifty-three percent of all pond taxa were classified as "lentic" taxa, ranging from 0% (pond 100) to 100% (pond 82). A high portion of taxa was classified as rare (Figure 3). Fifty-one percent of all pond taxa occurred in only one pond (not in the same pond; Figure 3). Frequency distribution (% of ponds occupied by each taxon) was significantly related to the relative abundance of taxa ($r^2=0.48$, $p < 0.0001$). Taxa similarity among ponds was low reflecting high spatial turnover (average similarity: 0.24, SD: 0.11). Only 2% of all pond-pairs exhibited a similarity coefficient >0.5.

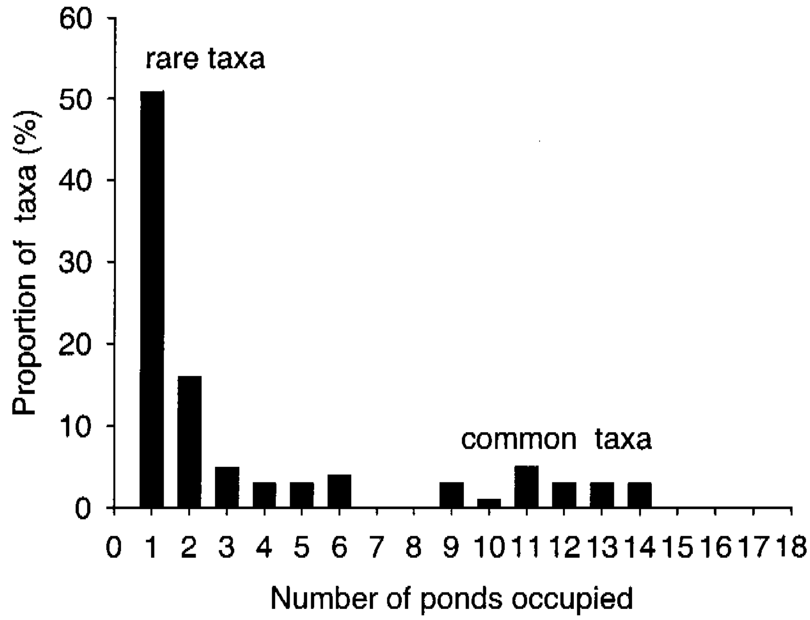

Figure 3. Frequency (%) distribution of all pond taxa (number of ponds colonized by individual taxa).

Environmental variability and species richness

Based on the multivariate environmental variability index, ponds were distributed along the first axis of a non-centered PCA. A significant negative relationship between environmental variability index and taxa richness occurred (r^2=0.31, P < 0.01; Figure 4).

Environmental variability and biological traits

Co-structure between environmental and species trait data sets was highly significant, as confirmed by Monte-Carlo permutation test (P = 0). F1 and F2 axes explained 48% and 28% of the total inertia. SRP, specific conductance, and NH_4 were negatively correlated with F1, while DOC, diel temperature amplitude, and pH were strongly positively correlated with F1 (Figure 5A). Mean daily temperature, turbidity, and water level fluctuations were strongly negatively correlated with F2 (Figure 5A).

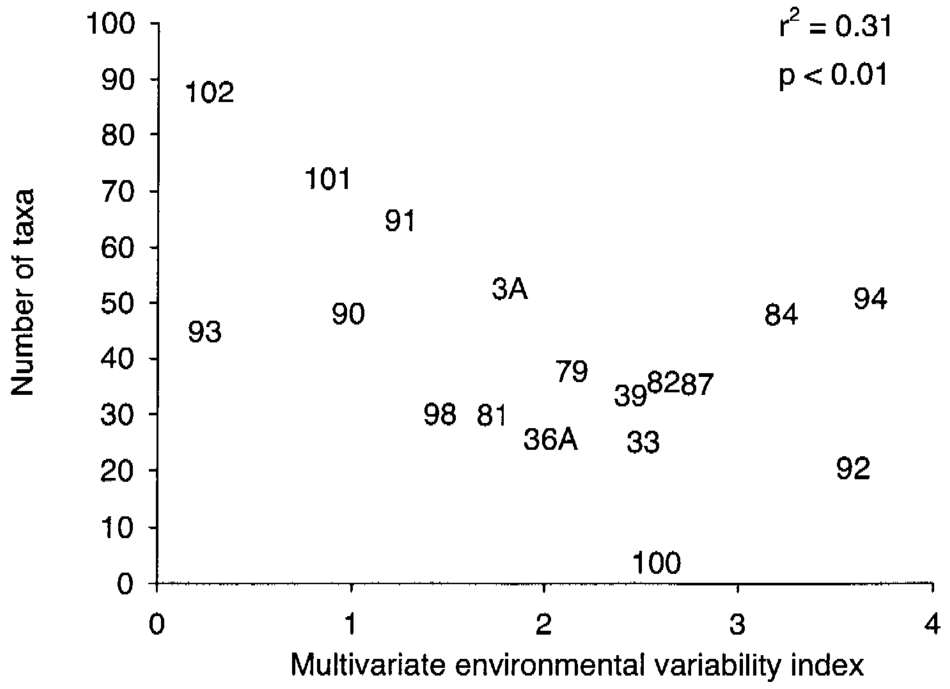

Figure 4. Relationship between environmental variability and pond species richness (pond identity: Figure 1B). High values indicate high variability.

Species traits (code: see Table 1) BB, BC, JA, NB, and QE were negatively correlated with the F1 axis, while EA, NA, and QA were strongly positively correlated with the F1 axis (Figure 5B). AC, FB, FC, HA, and KB were negatively correlated with the F2 axis, while ND was strongly positively correlated with the F2 axis (Figure 5B).

To illustrate the co-structure between biological traits and the environment, species traits and environment scores were plotted together on the F1xF2 ordination axes. The two positions were linked by an arrow (Figure 5C). The length of the arrow is a measure of the strength of the co-structure: the shorter the arrow, the better the agreement between the two structures. The F1 axis separated stable ponds (upper half of the factorial plane) from more variable ponds (lower half of the factorial plane). In May, ponds of a particular type (e.g., stable ponds) exhibited similar environmental conditions. In June and July, however, stable and variable ponds became more separated. In September and October, ponds were again more similar to each other. High affinities to traits that allow survival under harsh environmental conditions such as the ability for a diapause (HD), to resist as eggs, gemmulae, statoblasts (HA), the active dispersal via air (KD), bivoltinsm (BC), and a high number of descendants per year (>1000; AB, AC) occurred mainly on the lower half of the factorial plane (Figure 5B). Traits did not clearly reflect environmental conditions of individual ponds. Traits of highly variable ponds (e.g., 94, 92, 87) included also traits with adaptations to survive in variable environments. However, communities in some variable ponds (e.g., 33, 82) did not show a high affinity to traits with adaptations to survive in variable environments (Figure 5D). Stable ponds exhibited a wider range of traits than more variable ponds.

From May until July, trait diversity in ponds was highest and all ponds were equally distributed on the factorial plane (Figure 5D). In September and October, ponds were clearly separated into two groups, mainly characterized by a high and a low affinity to predators (Figure 5D). Trait diversity was related to environmental heterogeneity (Figure 5C). Highest environmental heterogeneity and trait diversity occurred in June and July, while environmental heterogeneity and trait diversity was lower in September and October (Figure 5D).

A

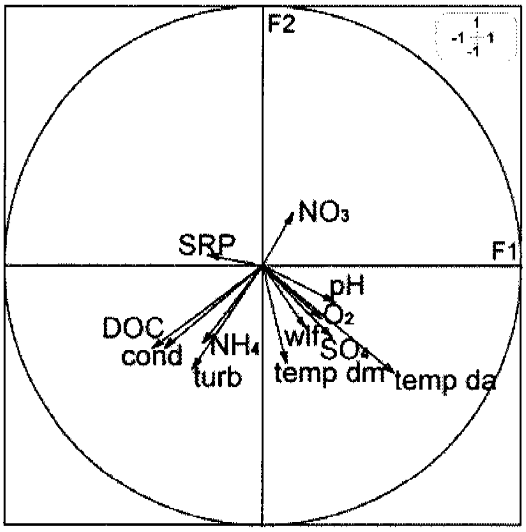

Figure 5. Within-date Co-inertia analysis (CIA; spatial typology).

Figure 5A. Co-inertia scores of environmental parameters. O_2 – oxygen, turb – turbidity, cond – specific conductance, NH_4 – ammonia, NO_3 – nitrate, SRP – soluble reactive phosphorus, DOC – dissolved organic carbon, SO_4 – sulfate, temp da – diel temperature amplitude, temp dm – mean daily temperature, wlf – water level fluctuation.

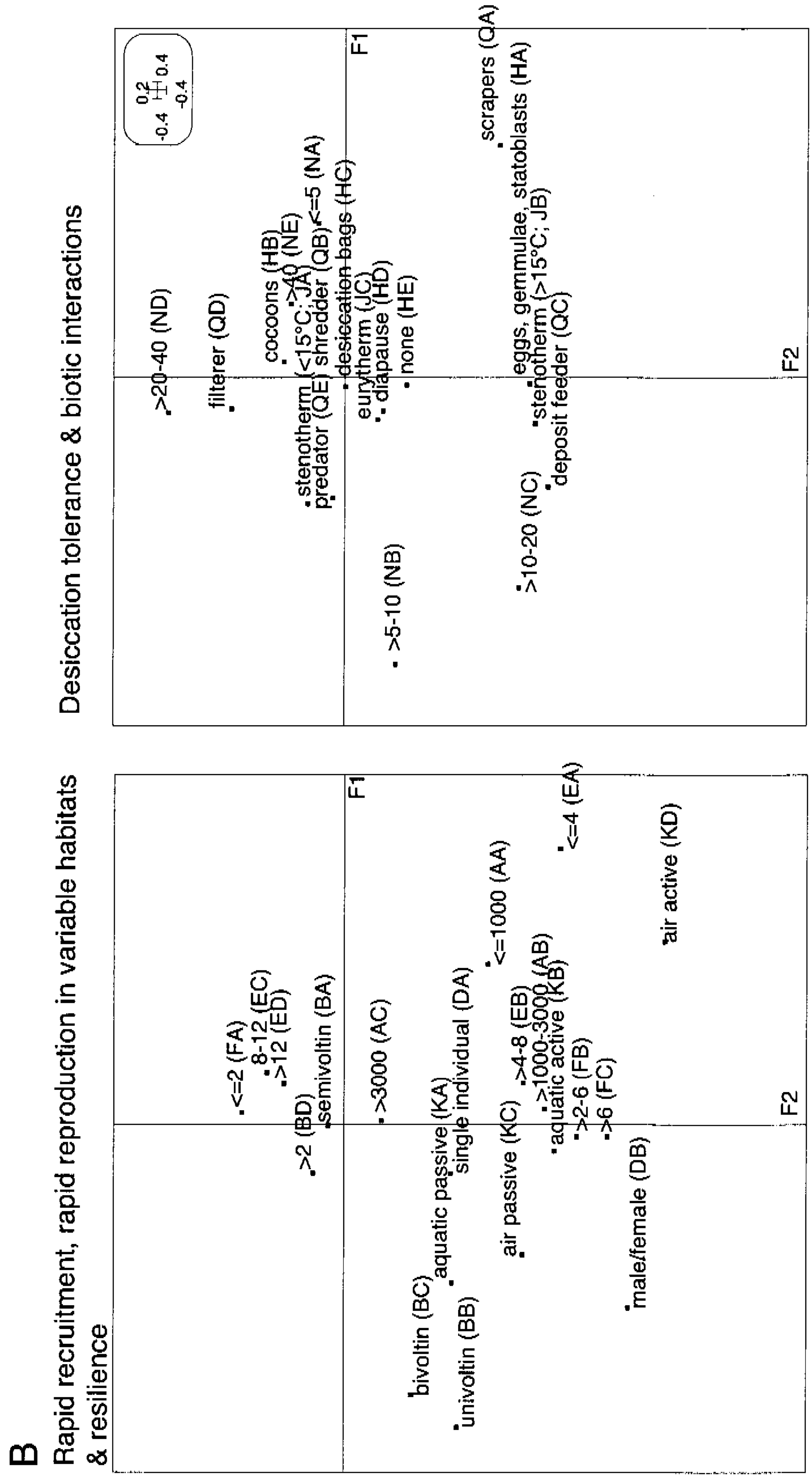

Figure 5B. Co-inertia scores of taxa traits on the F1xF2 factorial map (abbreviations: Table 1).

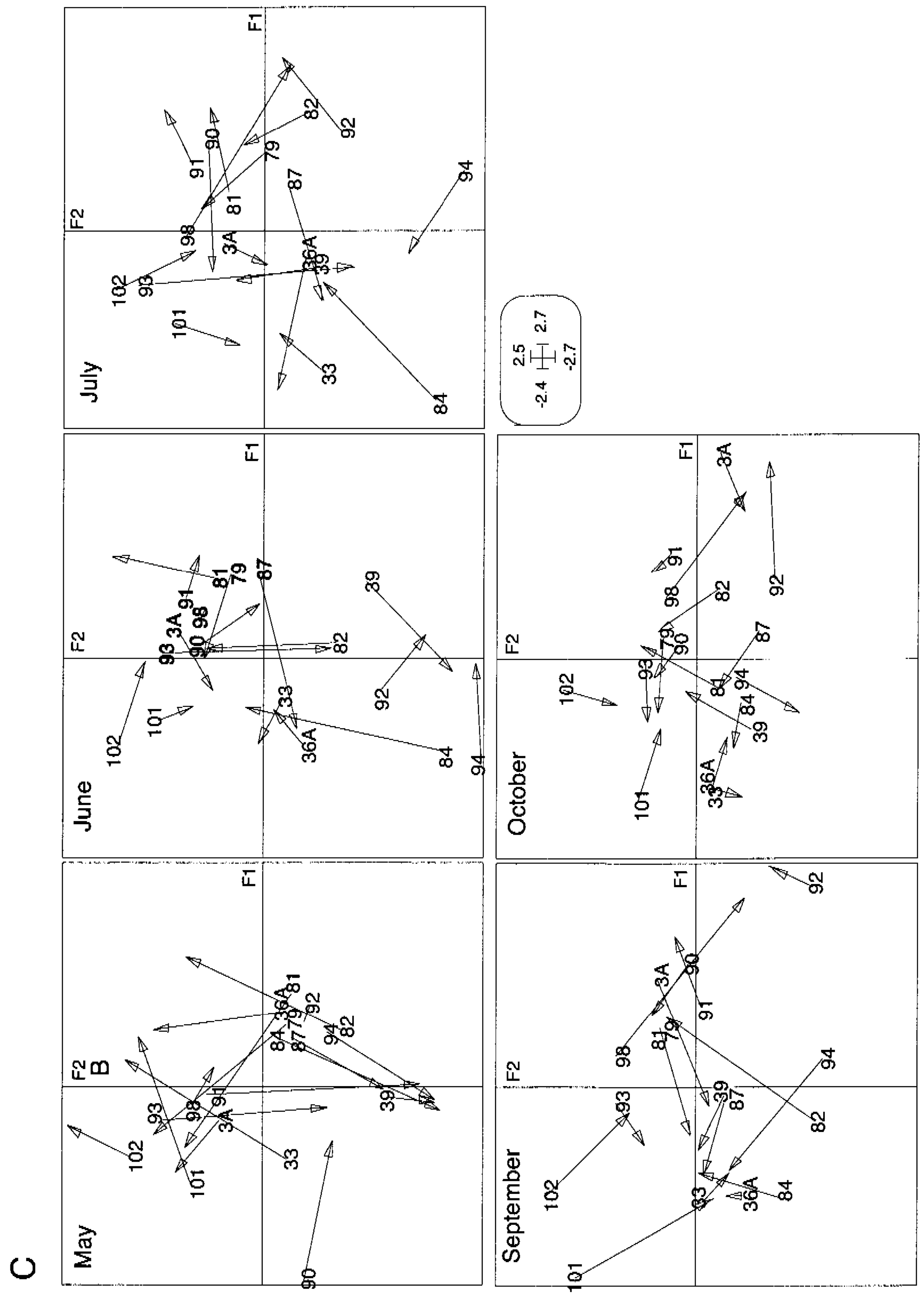

Figure 5C. Co-inertia scores of ponds of environmental and taxa trait data sets onto the F1xF2 factorial maps for each sampling date. Arrows measure the strength of the co-structure between taxa trait and the environment.

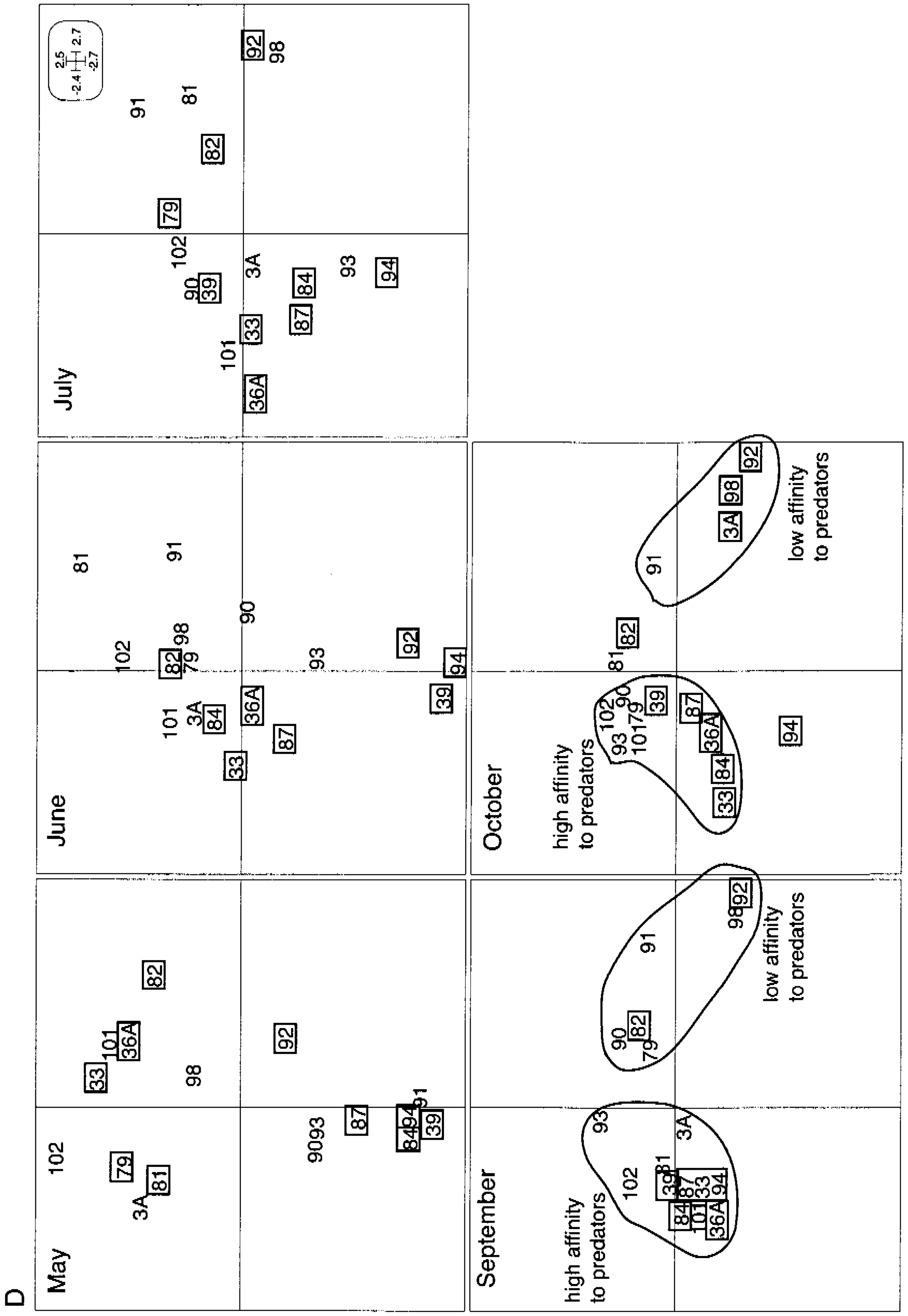

Figure 5D. Co-inertia scores of ponds of taxa trait data sets onto the F1xF2 factorial maps for each sampling date. Framed numbers indicate instable ponds.

DISCUSSION

River research has mainly focused on the lotic channel. Only recently have lentic water bodies also been considered as integral habitats along riparian corridors (Tockner *et al.* 1999; Ward *et al.* 2002), although the importance of lateral water bodies for riverine fish has been acknowledged for a long time (Antipa 1927-28; Welcomme 1979). Parafluvial ponds in particular have been neglected because they disappear first as a consequence of river regulation and flow control (Homes *et al.* 1999). Along the semi-natural Tagliamento corridor, parafluvial ponds are still abundant with up to 39 ponds per river-km (Karaus *et al.* 2005). Within our main study site, ponds formed discrete aquatic habitat patches with a characteristic set of physicochemical variables (Figure 4, Karaus *et al.* 2005).

Species richness pattern and nestedness

A small portion of taxa occurred in both channel and pond habitats. This confirms our first hypothesis that fauna in ponds differs substantially from the channel. The major factor that discriminates invertebrate compositions is supposed to be the lotic-lentic gradient (Boulton & Lloyd 1991; Greenwood & Richardot-Coulet 1996; Brunke *et al.* 2003). Several lotic organisms were also found in parafluvial ponds, which is an indication of dispersal from the channel to ponds (most likely passive dispersal during high flow).

Taxa richness, standardized by Jackknife estimates, was higher in ponds than in the channel (Figure 2). This finding was consistent with studies from the Paraná and the Rhône Rivers (Marchese & de Drago 1992; Richoux 1994). There, invertebrate density decreased from the main channel to secondary channels, whereas diversity increased. Faunal differences between parafluvial ponds and the channel are supposed to be related to different environmental properties. Channels are physically more stable within a geomorphological scale (Frissell *et al.* 1986), which ensures less variable physicochemical conditions. In contrast, each individual pond exhibited distinct physicochemical characteristics depending on local properties such as water supply and pond morphology.

Since local invertebrate assemblages are mainly controlled by local habitat conditions (Douglas & Lake 1994; Downes *et al.* 1998; Minshall & Robinson 1998; Voelz & McArthur 2000), major differences in environmental heterogeneity among ponds may result in diverse pond communities. Low taxa similarity among ponds and the high portion of rare taxa (Figure 3) indicated that each pond comprised a distinct invertebrate community. Most parafluvial pond taxa exhibited a limited spatial distribution (Figure 3). Common taxa, however, included organisms that occurred both in the channel and in pond habitats. Since dispersal ability of insects is inversely correlated with the permanency of a habitat (Roff 1990; Wagner & Liebherr 1992), lotic species may have smaller distributional ranges than species in variable stagnant waters (Ribera & Vogler 2000). In habitats that lack temporal and spatial continuity (e.g., ponds), survival of populations is only made possible by frequent dispersal, while the long-term persistence of a habitat (e.g., channel) makes dispersal less necessary (Ribera & Vogler 2000). Hence, common species are supposed to be initially channel taxa, whereas rare taxa probably originate from farther aquatic habitats (e.g., forest ponds, lakes). This assumption is supported by the nestedness analysis. Pond communities were nested, but they were not a subset of the channel community. Occurrence of channel taxa in ponds can be related to the formation of ponds following a flood event. Ponds, which emerge from channels after a flood event are assumed to provide flow refugia (*sensu* Sedell *et al.* 1990; Lancaster & Hildrew 1993) for channel taxa.

Environmental variability and species richness

Braided rivers are harsh environments located on the descending limb of a harshness-diversity curve (Burgherr *et al.* 2002; Robinson *et al.* 2002; Tockner & Stanford 2002). The present study suggests that species richness in parafluvial ponds was controlled by environmental variability. With increasing variability taxa richness declined (Figure 4). In the Everglade marshes, Kushlan (1976) found that a prolonged period of stable water conditions increased fish richness but favoured alterations of the community, shifting it from a community previously regulated by fluctuating abiotic conditions to one regulated by predation. In very harsh environments, communities are less diverse (Connell 1978; Reynolds *et al.* 1993; Wilson 1994; Reynolds 1995) and tend to be dominated by few "weedy species" (Scarsbrook & Townsend 1993). Moreover, investigations on fishes suggested that community persistence increased with decreasing environmental variability (Ross *et al.* 1985). Invertebrate communities in lotic ecosystems tended to diverge compositionally as habitat variability increased (Death & Winterbourn 1994). This may indicate that highly variable ponds in the Tagliamento increased the probability that proportionately higher numbers of community members failed to function as the environment fluctuated. Hence, high variable ponds were dominated by few taxa.

Environmental variability and biological traits

Biological traits were not clearly related to environmental properties in individual ponds. Stable ponds generally exhibited a high diversity of biological traits, with high and low affinities to traits to survive under harsh environmental conditions. This is in concordance to Townsend and Hildrew (1994), who predicted that biological traits that enable species to cope with variable conditions are also present in stable habitats, along with a variety of other traits. Highly variable ponds (39, 92, 94 in May, Figure 5D) were mainly characterized by traits to survive harsh environmental conditions (Figure 5D). However, some variable ponds (e.g., 33, 82) did not show traits to cope with variable environments (Figure 5D). Previous studies found significant relationships between biological traits and habitat conditions (e.g., Richoux 1994; Tachet *et al.* 1994; Usseglio-Polatera 1994; Poff & Allan 1995; Mérigoux *et al.* 2001). The less distinct relationship between environmental properties and traits in variable parafluvial ponds indicated that filtering of characteristic traits by individual environmental properties was probably overlaid by random colonization processes. Parafluvial ponds are the youngest habitats in the Tagliamento corridor, with half-life expectancies of <7 months (Van der Nat *et al.* 2003), which suggests that they represent early successional stages. Studies about temporary ponds confirmed that early succession of macroinvertebrates is dominated by unpredictable colonization processes (Lake *et al.* 1989; Schneider & Frost 1996). Interspecific competition became more important as succession progressed, since predatory macroinvertebrate populations may require a larger number and diversity of prey. In parafluvial ponds, the dominance of predators increased with time (Figure 5D). In addition to invertebrate species, many vertebrates use parafluvial ponds, in particular amphibians and birds, but their role in structuring macroinvertebrate communities has not been examined.

CONCLUSIONS

The present study clearly underpins the importance of lentic water bodies in maintaining biodiversity along active river corridors. Parafluvial ponds in particular represent habitats in early successional stages that are colonized by a diverse and often rare fauna. Nowadays, these habitats can only be investigated in a few remaining large braided rivers, such as the Tagliamento, since parafluvial ponds are among the first habitats that disappear as a consequence of river management. Similar to vegetated islands, parafluvial ponds can be used as sensitive landscape indicators of the integrity of river corridors. Future research on parafluvial ponds has to focus on the relationship between habitat age, water source, and species identity and richness, on dispersal pathways between the channel and ponds and between water bodies in the active corridor and in the adjacent riparian forest, and on the potential role of parafluvial ponds as flood and drought refugia.

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APPENDIX

Table1. Macroinvertebrate taxa list. "X" indicates the occurrence of taxa in the channel. Numbers correspond to frequency (number of ponds) of occurrence.

Taxa	**Channel**	**Ponds**
Plathelminthes		
Turbellaria		
Planariidae		
Polycelis tenuis/nigra		2
Dendrocoelidae		
Dendrocoelum lacteum Müller		1
Mollusca		
Gastropoda		
Physidae		
Physella acuta Draparnaud		14
Lymnaeidae		
Stagnicola sp.		4
Radix ovata Draparnaud		1
Lithoglyphidae		
Lithoglyphus sp.		1
Bithyniidae		
Bithynia tentaculata Linnaeus		2
Valvatidae		
Valvata piscinalis Müller		1
Planorbidae		
Anisus sp.		1
Planorbarius corneus Linnaeus		1
Viviparidae		
Viviparus sp.		1
Bivalvia		
Sphaeridae		
Pisidium supinum/henslowanum		1
Pisidium sp. 2		2

Taxa	Channel	Ponds
Annelida		
Clitellata		
Hirudinea		
Erpobdellidae	x	1
Glossiphoniidae		1
Oligochaeta		3
Crustacea		
Malacostraca		
Percarida		
Amphipoda		
Gammaridae		
Gammarus sp.	*x*	1
Echinogammarus stammeri Karaman	*x*	12
Niphargidae		1
Isopoda		
Assellidae		
Asellus aquaticus Linnaeus		6
Insecta		
Ephemeroptera		
Ephemerellidae		
Ephemerella ignita Poda	*x*	13
Baetidae		
Cloeon dipterum Eaton		6
Baetis rhodani Pictet	*x*	
Baetis sp. 2	*x*	
Siphlonuridae		
Siphlonurus lacustris Eaton		14
Caenidae		
Caenis horaria Linnaeus		1
Heptageniidae		
Ecdyonurus dispar Curtis	*x*	2
Ecdyonurus venosus Fabricius	*x*	2
Electrogena lateralis Curtis		1
Rhithrogena sp.	*x*	
Ephemerellidae		
Ephemera sp.		1

Taxa	**Channel**	**Ponds**
Odonata		
Anisoptera		
Libellulidae		
Sympetrum striolatum Charpentier		1
Aeshnidae		
Aeshna affinis Vander Linden		1
Zygoptera		
Platycnemididae		
Platycnemis pennipes Pallas		2
Coenagrionidae		2
Lestidae		
Lestes viridis Vander Linden		1
Calopterygidae		
Calopteryx splendens Harris		1
Plecoptera		
Leuctridae		
Leuctra sp.	x	11
Dinocras sp.	x	
Chloroperlidae		1
Rhynchota (Hemiptera)		
Heteroptera		
Corixidae		
Micronectinae		2
Corixinae		1
Megaloptera		
Sialidae		
Sialis morio/lutaria		1
Sialis sp. 2		1
Coleoptera		
Hydroporinae		
Potamonectes griseostriatus de Geer		1
Scarodytes halensis Fabricius		10
Bidessus unistriatus Goeze		2
Laccornis sp.		1
Colymbetinae		
Agabus sp.		1

Taxa	**Channel**	**Ponds**
Hydrophilidae		
Laccobius sinuatus Motschulsky	x	15
Helophorus sp.		1
Hydraenidae		
Ochthebius nobilis		6
Ochthebius sp. 2		5
Haliplidae		
Haliplus confinis Stephens		3
Haliplus obliquus Fabricius		1
Dryopidae		
Dryops sp.	x	11
Elmidae		
Oulimnius sp.		1
Elmis sp.	x	
Limnius sp.		2
Gyrinidae		
Gyrinus sp.		1
Trichoptera		
Rhyacophilidae		
Rhyacophila aurata Brauer	x	
Hydropsychidae		
Hydropsyche pellucidula Curtis	x	
Limnephilidae		
Allogamus auricollis Pictet		1
Consorophylax consors McLachlan		1
Potamophylax rotundipennis Brauer		1
Halesus digitatus Schrank		2
Mesophylax impunctatus McLachlan		2
Mesophylax aspersus Rambur		1
Limnephilus auricula Curtis		1
Stenophylax vibex Curtis		1
Acrophylax zerberus Brauer		1
Micropterna lateralis Stephens		1

Taxa	**Channel**	**Ponds**
Diptera		
Nematocera		
Tipulidae	x	13
Limoniidae	x	12
Limnophila sp.		1
Eloeophila sp.		3
Pseudolimnophila sp.		1
Chironomidae		
Tanypodinae	x	15
Chironominae		
Chironomini	x	15
Chironomus annularius Gruppe		5
Chironomus fluviatilis-Gruppe		1
Chironomus sp. 3		3
Tanytarsini	x	9
Pseudochironomini		1
Orthocladiinae	x	11
Prodiamesa olivacea Meigen		4
Ceratopogonidae		9
Culicidae		2
Simuliidae	x	
Blephariceridae	x	
Tabanidae	x	11

CHAPTER 4

HYDROLOGICAL CONNECTIVITY AND TEMPORAL DYNAMICS OF BENTHIC INVERTEBRATES IN A BRAIDED RIVER (TAGLIAMENTO, NE-ITALY)

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submitted

The importance of hydrological connectivity for the integrity of river floodplain systems has often been emphasized. However, investigations on temporal dynamics of invertebrates across connectivity gradients in natural or near-natural river systems are almost completely missing. In the present study, we investigated seasonal dynamics of environmental variables and benthic invertebrates in nine water bodies across a lateral connectivity gradient over a one-year period in the semi-natural Tagliamento River (NE-Italy). Within each water body, physicochemical variables and the density and diversity of Oligochaeta and Chironomidae were quantified at monthly intervals (April 1999 until March 2000). Concentrations of dissolved phosphorus, invertebrate density, and the composition of Oligochaeta and Chironomidae were significantly related to hydrological connectivity. Frequently connected water bodies exhibited similar environmental conditions and invertebrate communities. Water bodies with low connectivity exhibited higher environmental heterogeneity and harboured a more distinct and diverse community. Community persistence and density were markedly lower in less connected water bodies, probably resulting from environmental conditions and biotic interactions within individual water bodies. Concordance in abundances was lower compared to investigations in other river systems, indicating either the strong influence of flood disturbance on the abundance pattern or specific adaptations (*r*-selected traits) to the harsh

environmental conditions of braided-river systems. Our results demonstrated that hydrological connectivity between the channel and lateral aquatic habitats cannot be reduced to a simple gradient, and emphasizes the importance of hydrological connectivity for the maintenance of a shifting habitat mosaic and, hence, high biodiversity.

INTRODUCTION

Natural rivers and their flood plains form complex, dynamic, and diverse ecosystems (Ward *et al.* 1999b). The active channel and the adjacent flood plain are linked by hydrological and ecological processes; the driving force being the pulsing of flow. It determines the degree of connectivity and the exchange of matter, energy, and organisms across multiple gradients (Junk *et al.* 1989; Ward *et al.* 1999b). Hydrological connectivity is essential to the ecological integrity of river floodplain-systems (Amoros & Bornette 2002; Pringle 2003). Flow and flood pulses (*sensu* Junk *et al.* 1989; Tockner *et al.* 2000) facilitate fragmentation and connection between habitat patches of the river-floodplain system. In the Tagliamento, for example, varying flow caused a complex shifting mosaic of disconnected-connected stages of parafluvial ponds with the lotic channel (Van der Nat *et al.* 2002; Karaus *et al.* 2005). The process of fragmentation and reconnection increases spatiotemporal habitat heterogeneity (Ward *et al.* 1999b). A wide range in connectivity classes, from highly isolated to dynamic side-channels, is necessary to create and maintain the high biodiversity characteristic of river-floodplain systems (Amoros & Roux 1988; Van den Brink *et al.* 1996; Bornette *et al.* 1998; Ward 1998).

The importance of the interaction between the river and its flood plain in maintaining high biodiversity has been recognized for various rivers (e.g., Amoros & Roux 1988; Sheldon *et al.* 2002; Aarts *et al.* 2004; Sommer *et al.* 2004). However, detailed investigations on the lateral organization of aquatic macroinvertebrates across the lateral dimension are scarce (Castella *et al.* 1991; Foeckler *et al.* 1991; Obrdlik & Fuchs 1991; Van den Brink *et al.* 1996; Tockner *et al.* 1999). In a Danube flood plain (Austria), for example, species diversity peaked in water bodies with an intermediate degree of connectivity (Tockner *et al.* 1999). In an alpine pro-glacial flood plain (Val Roseg, Switzerland), however, the most isolated and most stable water bodies contained highest richness (Burgherr *et al.* 2002). In the Lower Rhine, diversity in highly-connected water bodies was diminished due to massive nutrient inputs from the main channel (Van den Brink *et al.* 1994). Moreover, individual groups (e.g., molluscs, fish, amphibians and macrophytes) are expected to peak in diversity at different locations along a connectivity gradient, as demonstrated for the Danube (Tockner *et al.* 1999). In the flood plains of the Rhône (French part) and the Val Roseg (Switzerland), species turnover was highest in fragmented water bodies with low connectivity (Castella *et al.* 1991; Klein & Tockner 2000). However, detailed seasonal investigations on benthic macroinvertebrates across connectivity gradients are almost completely missing (e.g., Garcia & Laville 2001; Burgherr *et al.* 2002). In addition, most studies on the lateral dimension were conducted in regulated river systems.

Seasonal flood pulses are dominant determinants of the community structure along river corridors (Resh *et al.* 1988). However, most investigations on the effect of flood disturbance focused on the main stem (e.g., Cobb *et al.* 1992; Angradi 1997), whereas the impact on different water bodies across a lateral connectivity gradient has mostly been ignored (but see: Bornette *et al.* 1998).

Along the Tagliamento River, a large gravel-bed corridor that escaped major river regulation, ecosystem patterns and processes can be investigated under near-natural conditions. In the present study, we quantitatively investigated benthic communities in a braided river section. The main aim of the study was to examine seasonal dynamics of environmental variables and benthic invertebrates in water bodies arranged across a lateral connectivity gradient. Specific questions included: (i) Do environmental variables and benthic invertebrates reflect the lateral connectivity gradient? and (ii) Is there a coherent temporal trend in benthic invertebrates in different water bodies across the connectivity gradient? We further investigated flood effects on macroinvertebrates within individual water bodies. Our focus was on Chironomidae (Insecta: Diptera) and Oliochaeta, the dominant groups in many floodplain waters.

STUDY AREA

The Tagliamento is a large gravel-bed river located in north-eastern Italy (Friuli-Venezia Giulia; 46°N, 12°30´E; Figure 1A). It rises at 1195 m a.s.l. in the Carnian Alps and flows 170 km to the Adriatic Sea. The catchment covers 2580 km^2 with more than 70% located in the Alps. The mountainous part of the catchment consists of limestone and Flysch deposits; the Friulian plain is filled with Tertiary and Quaternary sediments. The Tagliamento has an average discharge of ~90 m^3/s, whereas 2-, 5- and 10-year floods are estimated to be 1100, 1600 and 2150 m^3/s (Petts *et al.* 2000). High flow is caused by snowmelt (spring) and heavy rainfall (autumn) with discharge maxima of ~4000 m^3/s (Ward *et al.* 1999a). The near pristine character of the Tagliamento is reflected in its complex channel morphology, a dynamic flood regime, and an idealized longitudinal sequence of constrained, braided and meandering sections. In the braided section, the active flood plain is up to 1.5 km wide and characterized by a highly variable presence of vegetated islands (Gurnell *et al.* 2000; Arscott *et al.* 2001; Van der Nat *et al.* 2002).

The main study area is a 1 km^2 island-braided reach in the middle section of the river corridor (river kilometre 79.8 – 80.8; 135 m a.s.l.; Figure 1B). The flood plain consists of channels, lentic water bodies (backwaters and ponds), gravel bars, vegetated islands, and the fringing riparian forest. The local climate has an Alpine character with a high precipitation of 2000 mm per year and a mean maximum air temperature of 17.6°C. For detailed information on the catchment and the main study area see Ward *et al.* (1999a), Gurnell *et al.* (2000), Arscott *et al.* (2000) and Tockner *et al.* (2003).

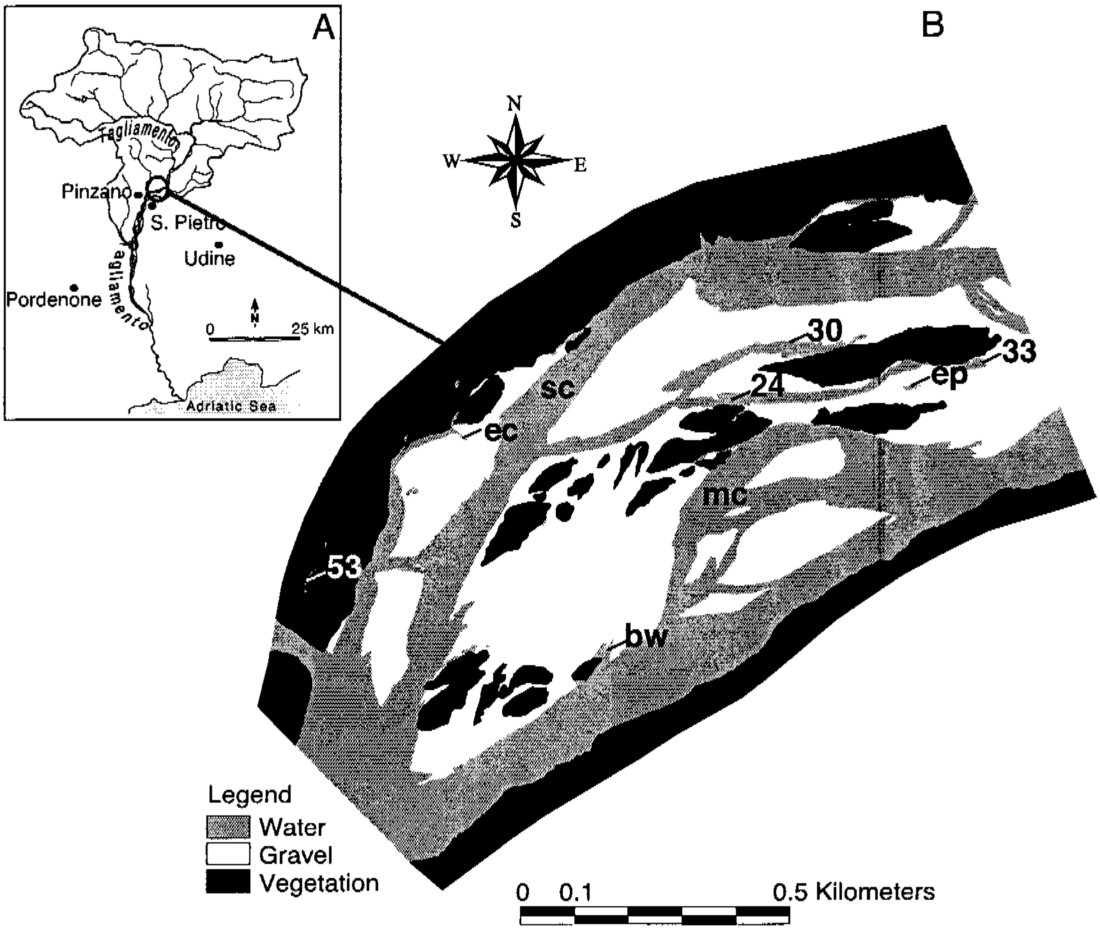


Figure 1. A. The catchment of the Tagliamento River. B. The main study area and location of sampling sites (map: September 1999). Mc=main channel, sc=side channel, ec=ephemeral channel, bw=backwater, ep=ephemeral pond.

METHODS

A spatially-hierarchical sampling approach was applied that included lotic and lentic as well as permanent and temporary water bodies (Figure 2).

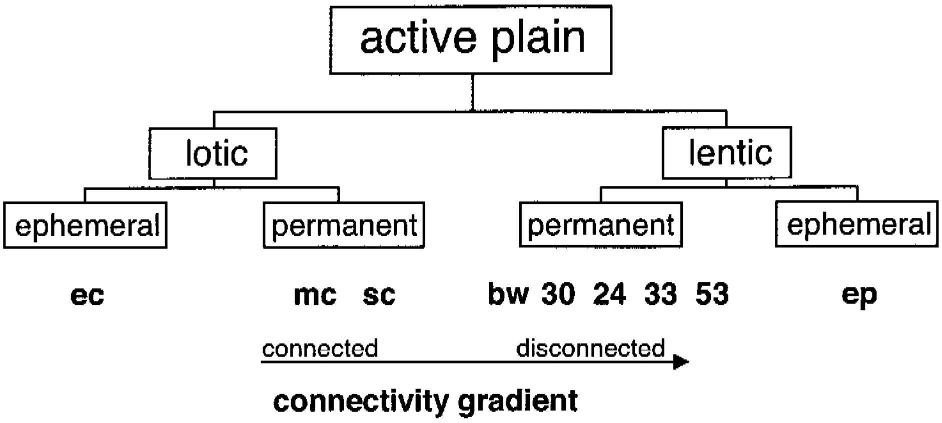


Figure 2. Nested sampling design: water bodies are separated by flow permanency and degree of connectivity. Mc=main channel, sc=side channel, ec=ephemeral channel, bw=backwater, ep=ephemeral pond.

Lotic waters included primary (mc, main channel), secondary (sc), and ephemeral channels (ec). Lentic waters included a backwater (bw), with a downstream connection to the channel, and five water bodies (ponds) that differed in their relative location and distance to the channel (different hydrological connectivity). Water bodies 30 and 33 were embedded into the gravel matrix and located close and far from the channel, respectively. Water body 24 was associated with a vegetated island. Water body 53 was located at the edge of the riparian forest. The ephemeral pond (ep) was a bare-gravel pond. Ephemeral water bodies (ep and ec) dried in some periods during the investigation. The study was conducted at monthly intervals from April 1999 until March 2000 (Figure 3). Five flood events occurred during the study with maximum water levels between 206 cm (August) and 292 cm (end of October).

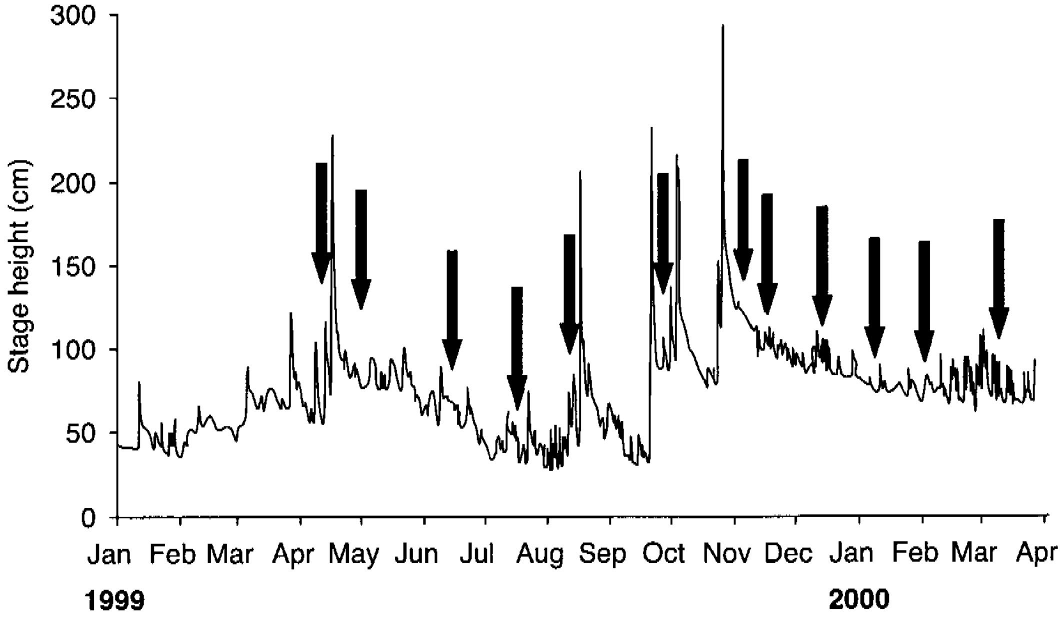


Figure 3. Stage height (cm) from January 1999 until April 2000 at river-km 84 (station S. Pietro). Arrow: sampling date.

Connectivity

Hydrological connectivity depends on the water level of the channel and the position relative to channel height (Hillman & Quinn 2002). Water bodies were grouped according to their degree of hydrological connectivity to the main/side channel (Table 1). The degree of connectivity was defined as the relative duration (% of time) with an up- or downstream surface connection with the lotic channel. Regression analyses were performed to test the relationship between the degree of connectivity, environmental parameters, density and richness of macroinvertebrates, and seasonal species turnover rates.

Table 1. Degree of connectivity, environmental characteristics, invertebrate density and richness in the different waterbodies (mc=main channel, sc=side channel, ec=ephemeral channel, bw=backwater, ep=ephemeral pond) during the 12 study dates. n.d.=no data. Numbers in parenthesis are ranges.

Waterbodies	**mc**	**sc**	**bw**	**30**	**24**	**33**	**53**	**ep**	**ec**
Number of sampling dates	12	12	12	12	12	12	12	7	3
Degree of connectivity (% of time connected to channel)	100	100	75	17	8	0	0	0	25
Physico-chemical variables (mean, range)									
O_2 (mg/L)	10 (8.5-12.6)	11 (8.9-13.1)	9.5 (5.8-13)	9 (7-13)	10 (7.1-13.2)	10 (7-14)	9 (5-14)	10 (8-11)	n.d.
pH	8.2 (8.1-8.25)	8.2 (7.9-8.3)	8 (7.28-8.31)	8 (7-8)	7.9 (7.3-8.1)	8 (8-8)	8 (8-8)	8 (8-8)	n.d.
Specific conductance (µS/cm)	520 (455-569)	521 (476-573)	529 (461-580)	540 (500-614)	532 (483-595)	475 (214-611)	292 (266-350)	517 (480-588)	n.d.
Mean daily temperature (°C)	10 (6.9-14)	13 (11.5-14.7)	11 (7-16)	12 (8-16)	13 (6-20)	11 (5-17)	12 (8-16)	-	n.d.
NH_4 (mg/l)	7 (0-35)	3.5 (0-19)	2.2 (0-12)	2 (0-6)	1 (0-4)	23 (0-111)	2 (0-5)	2 (0-5)	n.d.
NO_3 (mg/l)	673 (639-735)	652 (554-797)	706 (589-814)	634 (559-710)	581 (0-691)	517 (213-678)	975 (833-1162)	730 (665-872)	n.d.
DN (mg/l)	818 (687-945)	782 (598-1016)	885 (734-1024)	774 (702-852)	783 (720-837)	693 (300-936)	1167 (990-1322)	864 (784-1064)	n.d.
PN (mg/l)	19 (3-32)	17 (1-409	16 (6-31)	13 (3-79)	31 (3-254)	39 (7-75)	9 (4-17)	36 (3-179)	n.d.
SRP (mg/l)	1.5 (0-6)	0.7 (0-4)	1.8 (0-5)	1 (0-2)	0.9 (0-2)	1 (0-2)	0.4 (0-2)	0.2 (0-1)	n.d.
DP (mg/l)	4 (0-12)	2.3 (0-8)	4 (0-9)	2 (0-4)	1.8 (0-5)	2 (0-3)	1 (0-3)	1 (0-2)	n.d.
PP (mg/L)	6.8 (3-18)	6.5 (1-16)	4.4 (0-12)	1 (0-6)	0.6 (0-3)	7 (1-26)	1 (0-4)	2 (0-7)	n.d.
DOC (mg/L)	1.6 (0.8-4.4)	1.4 (0.5-3.4)	1.5 (0.6-3.6)	1 (0.4-3)	1.9 (0.5-6)	2 (1-4)	2 (1-6)	1 (1-2)	n.d.
TIC (mg/L)	35 (33-39)	34 (32-38)	35 (32-43)	32 (19-37)	35 (32-42)	31 (18-37)	37 (4-43)	33 (29-35)	n.d.
POC (mg/L)	1.3 (0.2-4.6)	0.9 (0.1-2.5)	0.4 (0.1-2)	0.2 (0.06-1)	0.2 (0.06-0.39)	1 (0.1-3)	0.2 (0.1-0.3)	0.4 (0.1-1)	n.d.
FBOM (g/m^2)	0.7 (0.3-1.4)	1.3 (0.2-2.4)	1 (0.2-4.7)	1 (0.09-2)	1 (0.2-1.2)	3 (1-7)	1 (0.2-2)	0.2 (0.1-0.3)	n.d.
CBOM (g/m^2)	0.4 (0-0.6)	0.6 (0.2-1)	0.8 (0.1-5)	1 (0.007-3)	0.5 (0-1.1)	3 (0.3-8)	1 (0.04-2)	0.2 (0.05-1)	n.d.
Invertebrates (mean±SD)									
Density (total; ind/m^2)	1118±1423	1212±999	970±1109	65±104	100±188	30±47	174±158	83±94	27±29
Density (Chironomidae; ind/m^2)	800±898	854±898	650±832	48±98	75±171	21±35	51±36	38±41	14±11
Density (Oligochaeta; ind/m^2)	24±65	66±191	40±67	2±4	1±1	1±3	14±21	1±3	1±1
Species richness (Chironomidae)	31	39	49	26	23	16	30	12	7
Species richness (Oligochaeta)	11	9	17	6	4	5	19	3	3

Environmental characterization of water bodies

The position of each water body was measured using a Global Positioning System (dGPS, TCS 1, Trimble Inc., USA). Surface water temperature was recorded at hourly intervals using temperature data-loggers (VEMCO Minilog, Nova Scotia, Canada). Data loggers were lost in all habitats during the October flood. Therefore, a data gap existed from 22 September until 03 December 1999 (main flood season). Average daily temperature (av daily temp) and average diel amplitude (maximum – minimum difference; temp da) were calculated to characterize thermal heterogeneity. Physicochemical variables were measured at monthly intervals from April 1999 until March 2000 prior to the sampling of benthic macroinvertebrates. Variables included oxygen (O_2; mg/l; Oxi 320, WTW, Germany), pH (pH 340, WTW, Germany), and specific conductance (spec cond; $\mu S\ cm^{-1}$, T_{ref} 20°C; LF 325, WTW, Germany). To minimize diel influences, all water bodies were sampled between 8:00 and 11:00 a.m. Surface water was collected in polyethylene bottles and kept cool (4°C) until analyses. Water was filtered through pre-combusted Whatman GF/F filters to separate particulate (suspended solids, particulate carbon, nitrogen and phosphorus) from dissolved components. Filters were frozen until analysis. All analyses were performed within four days of sample collection. Analytical methods for soluble reactive phosphorus (SRP), ammonia (NH_4), nitrate (NO_3), particulate nitrogen and phosphorus (PN, PP), total dissolved phosphorus (DP), dissolved nitrogen (DN), dissolved and particulate organic carbon (DOC, POC), and total inorganic carbon (TIC) were identical to Tockner *et al.* (1997) and Malard *et al.* (1999).

Benthic macroinvertebrates and benthic organic matter

Benthic invertebrates were quantitatively sampled at monthly intervals from April 1999 until March 2000. In lotic water bodies, samples were collected by randomly placing a Hess sampler (415 cm^2; mesh size: 100 μm) on the substrate and stirring the substrate with a metal rod for 10 sec to a depth of 5 cm (three replicates per site and date). In standing water habitats, a diaphragm pump apparatus was used to collect benthic invertebrates from the surface within the enclosed Hess-sampler (see: Arscott *et al.* in press). Ten litres were pumped from each Hess sample by holding the intake immediately above the sediment surface and by disturbing the surface with a rod for 10 sec to a depth of 5 cm (three samples per site and date). Samples were preserved in 4% formaldehyde. In the laboratory, all invertebrates were counted and sorted. Chironomidae and Oligochaeta were identified to the lowest taxonomic level, mostly to species.

After removal of all invertebrates, coarse (>1.0mm) and fine (>0.1-1.0mm) benthic organic matter (CBOM, FBOM) was determined. The two size fractions were dried at 60°C, weighed, ashed at 500°C (4 hrs), and re-weighed.

Statistical Analyses

Multivariate Analyses

Differences in environmental parameters were analysed by a between-site principal components analysis (bsPCA). This method is well-suited to distinguish spatial effects (Dolédec & Chessel 1987). The bsPCA seeks axes representing the center of gravity among all groups or subspaces and focuses on the between group-differences, in this case the spatial variation. Data of October and November were excluded, because no temperature data were available. Ephemeral water bodies (ep and ec) were excluded because of the difficulty to incorporate data gaps in multivariate analysis. A principal components analysis (PCA) was applied to classify water bodies based on Chironomidae and Oligochaeta. Prior to statistical analyses, environmental data were standardized by subtracting the mean and dividing by the standard deviation; faunistic data were $\log_{10}(x+1)$ transformed to ensure normality and homogeneity of variances (Sokal & Rohlf 1995). All multivariate analyses were computed using ADE-4 software (Thioulouse *et al.* 1997).

Jackknife Estimates

To standardize samples, Jackknife estimates (Heltshe & Forrester 1983) for taxa richness were generated for individual water bodies (based on individuals, Colwell 2001). All Jackknife estimates were permuted at random 1000 times to produce more accurate values and to generate standard deviations.

Similarity

The faunal similarity (Oligochaeta and Chironomidae) between individual water bodies and the main channel was calculated using Jaccard's similarity coefficient (Krebs 1998).

Turnover, persistence, and temporal concordance of benthic invertebrates

To understand temporal changes in community structure, three quantitative measures were applied. First, we calculated Pearson's correlation coefficients to assess turnover (i.e., the extent of species replacement) patterns in density and diversity of invertebrates among water bodies. The second metric, persistence, is a measure of whether the same species are present from one month to the next. According to Meffe & Minckley (1987), persistence measures were calculated from an index of species turnover rates (T) as follows:

$$T = \frac{(C + E)}{S1 + S2}.$$

C and E are the number of species that colonized or were extirpated between sample periods, while S1 and S2 are the number of species present in each sample period (Järvinen 1979). Turnover rates of all sampling dates were averaged and the index of persistence was calculated as 1 – mean T. This index ranged from 0 (no persistence) to 1 (complete persistence). Third, temporal stability of the relative abundance rankings were examined. Constancy in species rank abundances in time was tested using Kendall's W (Sokal & Rohlf 1995), a nonparametric procedure that tests for overall concordance among multiple samples. The magnitude of the concordance value indicates how constant the assemblage has been over time (0=no concordance; 1=concordance).

RESULTS

Environmental variables across a lateral connectivity gradient

Based on environmental variables, seven permanent water bodies were ordinated using a between-site principal components analysis (bsPCA; Figure 4). The first two axes explained 47% and 22% of the total variance. Specific conductance, PN, and average daily temperature were negatively, and NO_3 and DN positively, correlated with the F1 axis. BOM and NH_4 were positively correlated with the F2 axis (Figure 4A). Water body 33 exhibited the highest temporal variation. Main and side channels, the backwater, and water body 30 were poorly separated by the bsPCA (Figure 4). Concentrations of DP, PP, POC, and pH decreased with decreasing connectivity, although the relationship was only significant for DP ($r^2=0.77$, $P<0.01$).

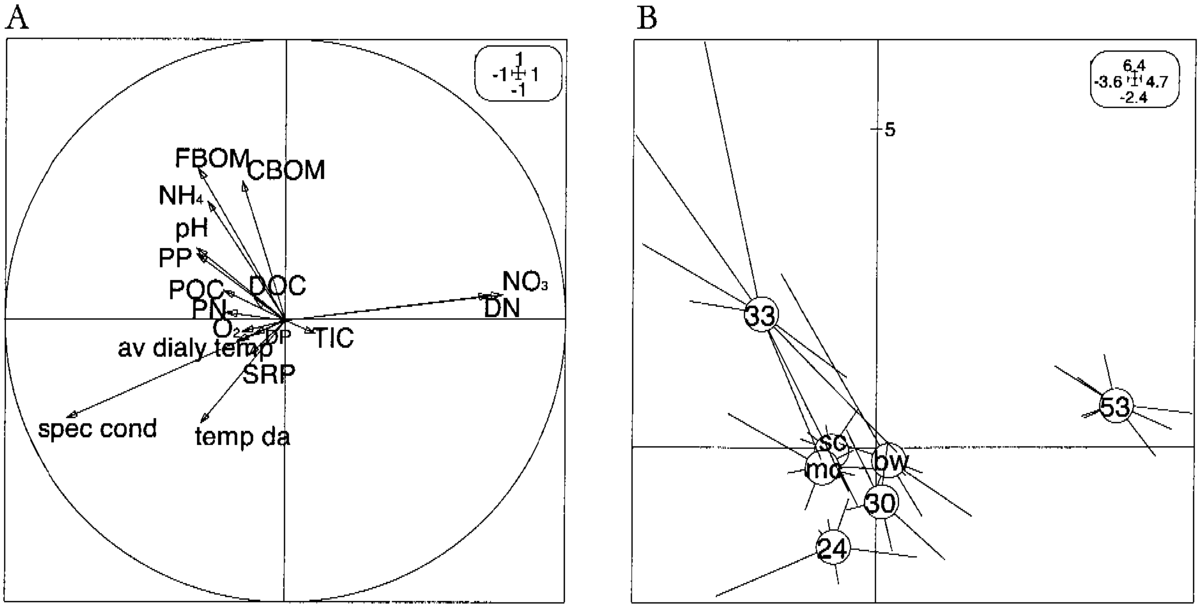


Figure 4. Between-site principal components analysis (bsPCA) on the site/date-by environmental variable matrix. Environmental-variable specific relationships (A) with F1 and F2 dimensions of the between PCA and site scores (B), grouped by water body. Environmental abbreviations are reported in methods. See text for % variance explained. In the factor map, circles (waterbody identification) represent the average score for a water body and are connected by lines to actual scores for each month (May-February, excl. October & November). Mc=main channel, sc=side channel, bw=backwater.

Benthic invertebrates across a lateral connectivity gradient

Lowest seasonal invertebrate density (all water bodies combined) occurred between September and November (<100 ind/m^2), highest density between January and March (>1000 ind/m^2). Density of total invertebrates, Chironomidae, and Oligochaeta decreased significantly with decreasing connectivity (from lotic main and side channels to isolated water bodies; $r^2=0.97$; $P<0.002$; $r^2=0.98$; $P<0.001$; $r^2=0.95$; $P<0.005$; Table 1). Chironomidae (65%), other Diptera (17%), Oligochaeta (7%), and Crustacea (6%) dominated the community. A total of 82 Chironomidae and 35 Oligochaeta were identified (Appendix, Table 1). The mean number of Chironomidae taxa per site and date ranged from 7 (ec) to 49 (bw, Table 1). Oligochaeta richness ranged from 3 (ec, ep) to 19 taxa (water body 53, Table 1). Standardized richness, based on Jackknife procedures and standardized by number of individuals increased along the connectivity gradient. In a random sample of 100 individuals (Oligochaeta and Chironomidae combined), one can expect a lateral increase from 3 (mc) to 41 (water body 53) taxa (Figure 5).

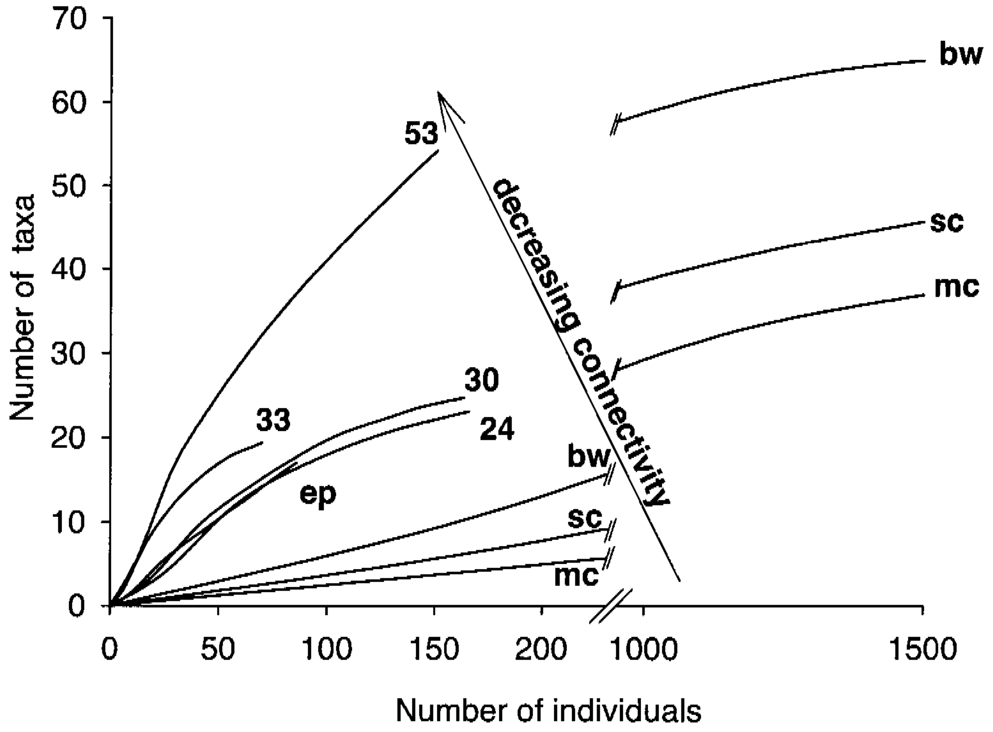
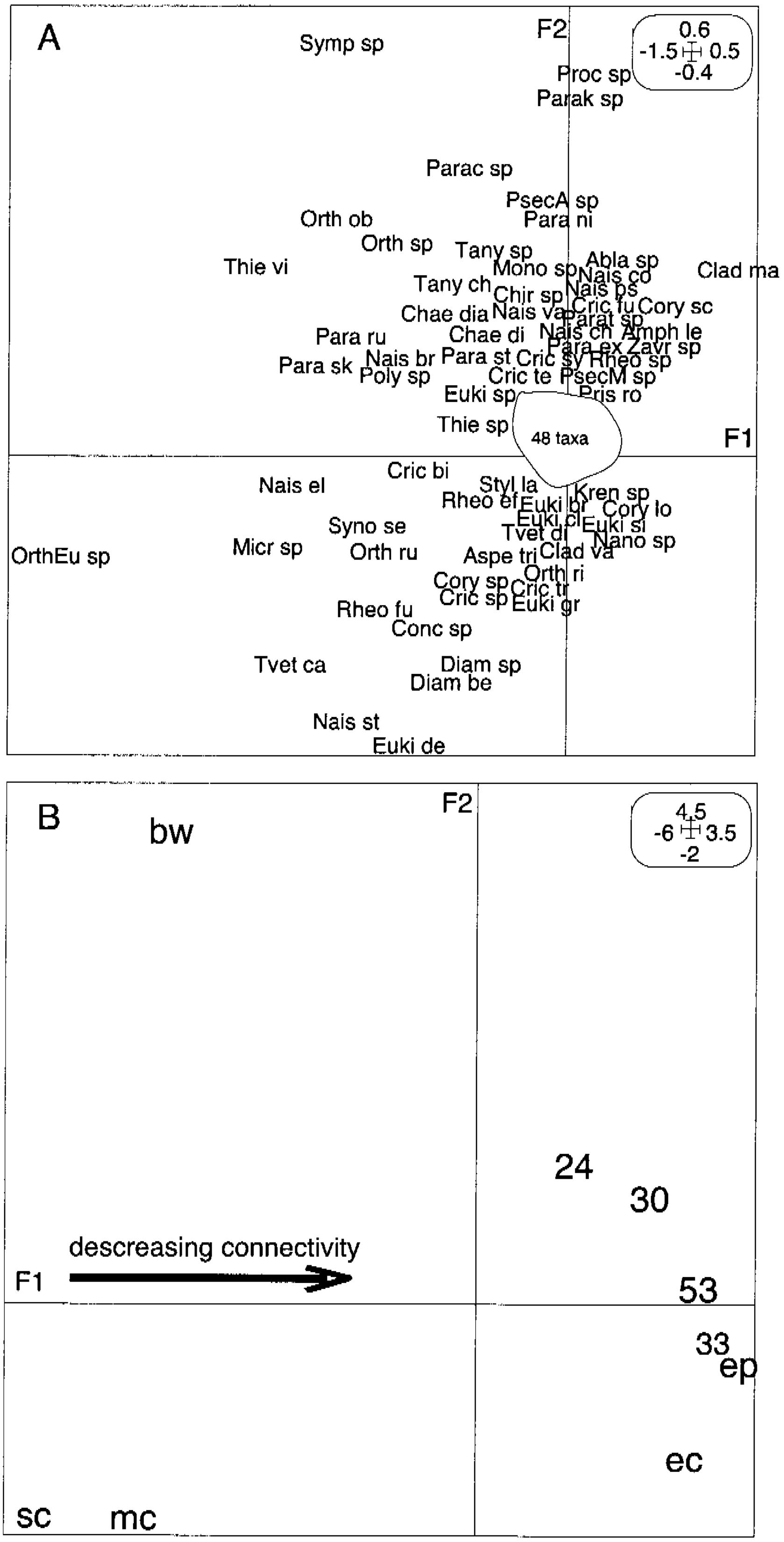


Figure 5. Jackknife estimates of taxa richness for individual water bodies standardized by number of individuals. Mc=main channel, sc=side channel, ec=ephemeral channel, bw=backwater, ep=ephemeral pond.

Community similarity between the main channel and individual water bodies was low and ranged from 0.10 (water body 33) to 0.48 (sc) for Chironomidae, and from 0.14 (water body 24 and ep) to 0.48 (bw) for Oligochaeta. Faunal similarity to the main channel significantly decreased with decreasing degree of connectivity (Chironomidae: $r^2=0.8$, $p<0.025$ and Oligochaeta: $r^2=0.6$, $p<0.05$).

Based on benthic invertebrate composition, the first two axes of a PCA explained 59% and 16% of the total inertia. All water bodies were strongly positively (water bodies 24, 30, 53, ep and ec) or negatively (mc, sc and bw) related to the F1 axis (Figure 6). Three groups of water bodies were distinguished: (1) channels (mc & sc), (2) the backwater, and (3) lentic water bodies with low connectivity (Figure 6). The ordination of water bodies indicated gradual changes in taxonomic composition along the F1 axis, which corresponded to a significant correlation between scores of the F1 axis and degree of connectivity ($r^2=0.93$, $p<0.0001$; Figure 6).

Figure 6. Principal components analysis (PCA) of 117 Oligochaeta and Chironomidae taxa. A: Positions of taxa on the PCA F1xF2 plane (Codes: Appendix). B: Position of waterbodies on the factorial plane based on 117 taxa. Numbers indicate water bodies; mc=main channel, sc=side channel, ec=ephemeral channel, bw=backwater, ep=ephemeral pond.


A
F2
0.6
-1.5
0.5
-0.4
Symp sp
Proc sp
Parak sp
Parac sp
PsecA sp
Para ni
Orth ob
Orth sp
Tany sp
Thie vi
Mono sp
Abla sp
Nais co
Clad ma
Tany ch
Chir sp
Nais ps
Cric fu
Cory sc
Chae dia
Nais va
Parat sp
Para ru
Chae di
Nais ch
Amph le
Para ex
Zavr sp
Para sk
Nais br
Para st
Cric sy
Rheo sp
Poly sp
Cric te
PsecM sp
Euki sp
Pris ro
Thie sp
48 taxa
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Cric bi
Nais el
Styl la
Rheo ef
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Kren sp
Cory lo
Euki cl
Euki si
Syno se
Tvet di
Nano sp
OrthEu sp
Micr sp
Orth ru
Aspe tri
Clad va
Orth ri
Cory sp
Cric tr
Cric sp
Euki gr
Rheo fu
Conc sp
Tvet ca
Diam sp
Diam be
Nais st
Euki de
B
bw
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4.5
-6
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24
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descreasing connectivity
F1
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33
ep
ec
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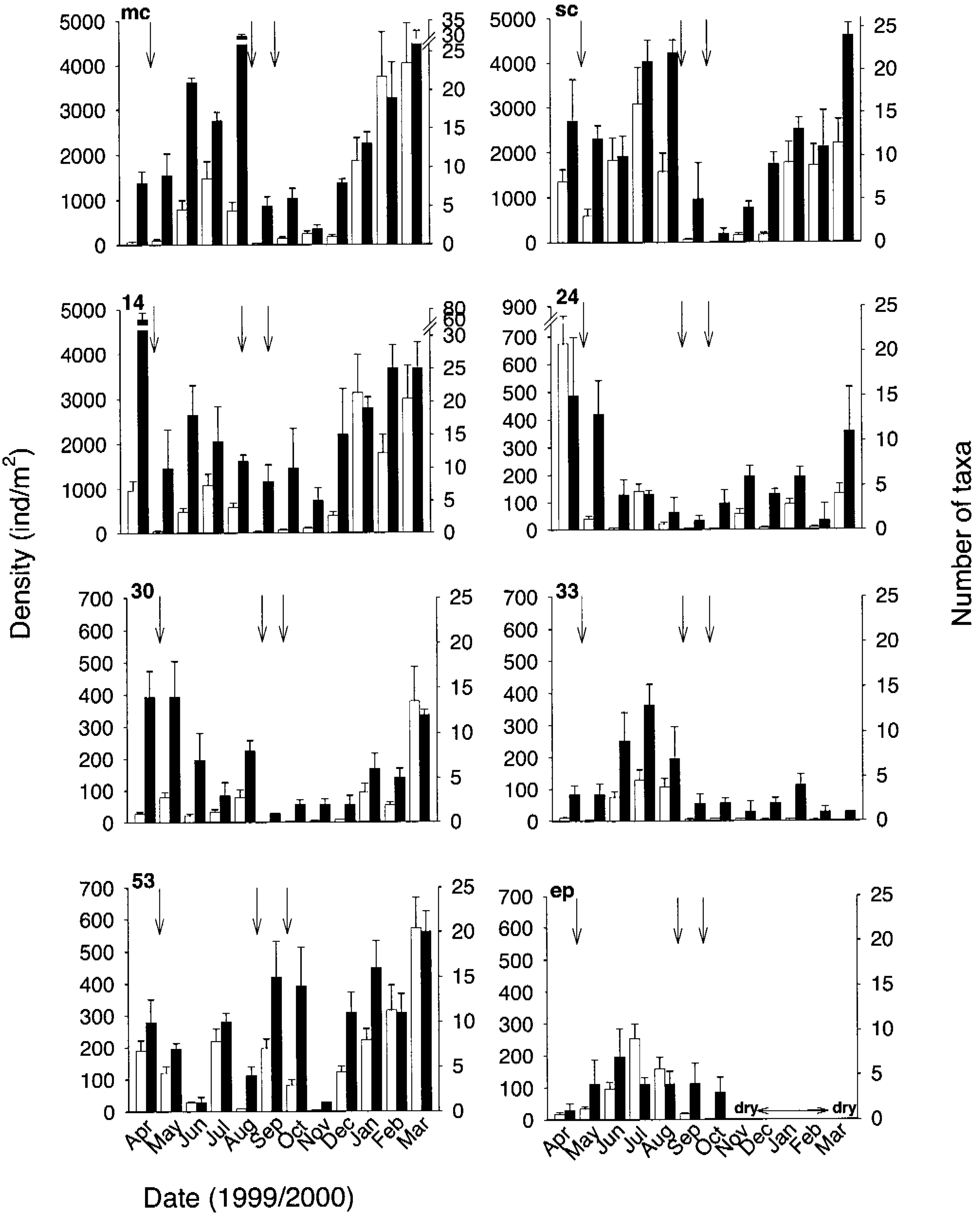
mc


mc
sc
14
24
30
33
53
ep
Density (ind/m^2)
Number of taxa
0
1000
2000
3000
4000
5000
0
100
200
300
400
500
600
700
900
0
5
10
15
20
25
30
35
60
80
dry
dry
Apr
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Date (1999/2000)

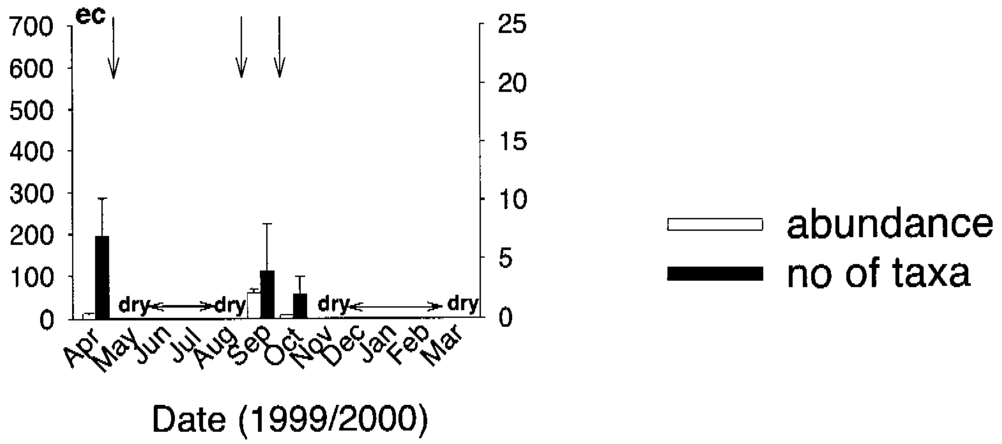

Figure 7. Seasonal dynamics of invertebrate density (ind m^{-2}) and species richness (Oligochaeta and Chironomidae) in all water bodies across a connectivity gradient (April 1999 until March 2000; n=3 per date and site). Arrow: flood event. Mc=main channel, sc=side channel, ec=ephemeral channel, bw=backwater, ep=ephemeral pond.

Turnover, persistence, and temporal concordance of benthic invertebrates

Invertebrate density and richness exhibited distinct seasonal fluctuations, with individual water bodies behaving differently in time (Figure 7). Temporal coherence, calculated as Pearson's correlations between each pair of water bodies, revealed similar temporal density patterns in the main channel and in the backwater (r^2=0.82), and in the ephemeral pond and in water body 33 (r^2=0.97). Temporal trends in richness were coherent only in main and side channel habitats (r^2=0.80), and in water bodies 24 and 30 (r^2=0.82) (Figure 7). In all water bodies, between 54% (mc) and 81% (water body 30) of the taxa were replaced during the investigation period, with a tendency of higher temporal taxa turnover in less connected water bodies (Figure 8).

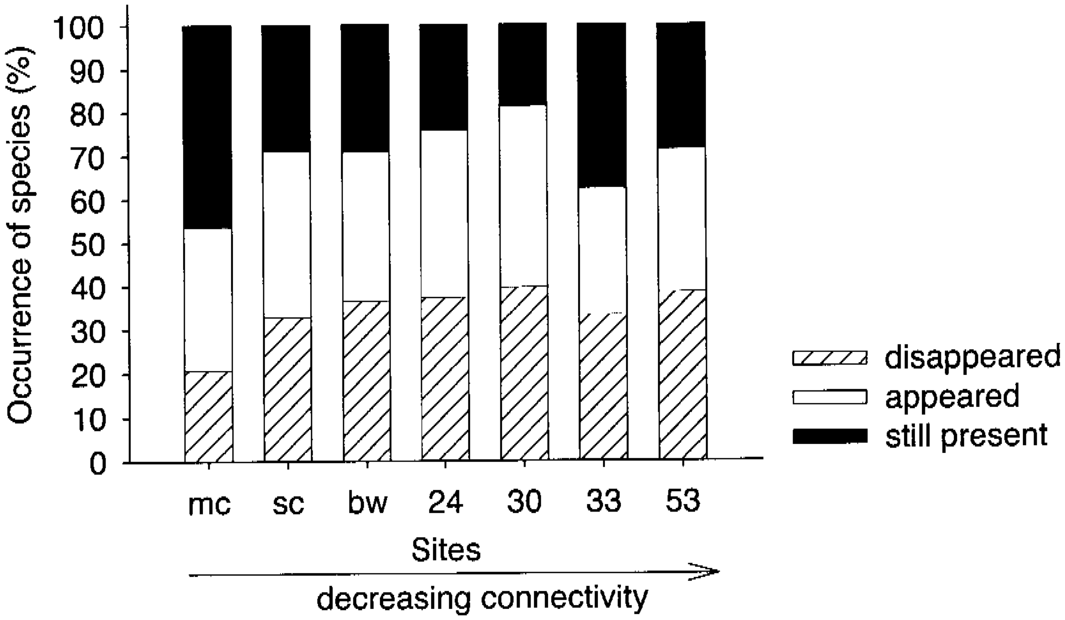

Figure 8. Taxa turnover averaged over the entire sampling period in all permanent water bodies. Taxa turnover expressed as proportion (%) of taxa present in two subsequent months and taxa that appeared and disappeared between two subsequent sampling dates. Mc=main channel, sc=side channel, ec=ephemeral channel, bw=back water, ep=ephemeral pond.

Persistence was lowest in water body 53 and in the ephemeral pond (0.31) and highest in the main channel (0.61) (Table 2). Invertebrate species abundance rankings (expressed by Kendall's W) exhibited a significant temporal change in all water bodies except in ephemeral water bodies (Table 2). Concordance values ranged from 0.10 (ep) to 0.34 (mc).

Flood events had strong influences on invertebrate density and taxa diversity (Figure 7). During the spring flood, taxa density was diminished between 36% (water body 53) and 96% (bw) (Figure 7). In contrast, density in main and ephemeral channels as well as in water body 30 increased 2 to 3-fold during the spring flood (Figure 7). The flood event in September reduced density by 77% (water body 24) to

Table 2. Summary of community change analyses for invertebrate communities in individual water-bodies across a lateral connectivity gradient. W=Kendall's rank concordance values; significance (*, P<0.05; based on Chi-square analyses) indicates a strong temporal change in density. Mc=main channel, sc=side channel, ec=ephemeral channel, bw=backwater, ep=ephemeral pond.

	Water body	No of study dates	Persistence	W
Decreasing connectivity ↓	mc	12	0.61	0.34*
	sc	12	0.42	0.15*
	bw	12	0.46	0.31*
	ec	3	0.26	0.28
	30	12	0.32	0.16*
	24	12	0.42	0.18*
	33	12	0.43	0.26*
	53	12	0.31	0.11*
	ep	7	0.31	0.10

99% (water body 30, Figure 7). However, density in water body 53 increased (25-fold) after the flood. Taxa richness in individual water bodies followed similar temporal trends (Figure 7). After spring and autumn floods, density and richness increased to pre-flood values either within five months (e.g., sc, mc, 30) or did not reach pre-flood density or taxa richness during the sampling period (e.g., 24, 33) (Figure 7).

DISCUSSION

To our knowledge, this is the first study that quantitatively investigated benthic communities across a river-floodplain gradient over an entire annual cycle. This aspect allows us to link spatial and the temporal species richness patterns in a highly dynamic river system.

Environmental variables and invertebrates across a lateral connectivity gradient

Environmental variables are often linked to hydrological connectivity. In the present study, however, only DP was significantly related to the degree of hydrological connectivity (Table 1). This finding was in contrast to other studies: in the Danube (Austria), for example, nutrient concentrations peaked in connected water bodies due to high inputs from the main channel (Heiler *et al.* 1995; Schiemer *et al.* 1999; Hein *et al.* 2004). In the Rhône (France), however, concentrations were highest in isolated water bodies due to nutrient-rich groundwater inputs from adjacent agricultural areas (Amoros & Roux 1988). In the Val Roseg flood plain, specific conductance increased with decreasing connectivity (Burgherr *et al.* 2002).

Antagonistic effects of hydrological connectivity were also reported in other invertebrate investigations. In the present study, macroinvertebrate density significantly decreased with decreasing connectivity, whereas taxa richness (area-based) was not related to connectivity. Standardized taxa richness (density-related) even increased significantly along the connectivity gradient (Figure 5). Similar results were reported along the Garonne River (France), where disconnected sites exhibited highest diversity (Garcia & Laville 2001). At the Rhine and Meuse Rivers (Netherlands), macroinvertebrate diversity was highest in moderately dynamic (i.e., intermediate connected) and in isolated lakes (Van den Brink *et al.* 1996). Studies at the Rhine (Germany), the Lower Salzach (Germany), the Danube (Austria), and at the Paranà (Argentina) Rivers found highest diversity of invertebrates in water bodies with an intermediate degree of connectivity (Foeckler *et al.* 1991; Obrdlik & Fuchs 1991; Tockner *et al.* 1999; Drago *et al.* 2003). Similarly, in a wetland of the Central Platte River (USA), a quadratic relationship between taxa richness of emerging insects and annual hydroperiod (frequency and magnitude of inundation) was found (Whiles & Goldowitz 2001).

These contradicting results indicate that hydrological connectivity between the river and its flood plain cannot be reduced to a single phenomenon (Amoros & Bornette 2002). As a river-floodplain system forms a hierarchical patch mosaic, each patch-element is controlled by the structural conditions within which the system is set (e.g., geomorphology of a stream segment, flow characteristics), but also by the structural characteristics (local conditions) within each patch-element (Poole 2002). Therefore, the effect of hydrological connectivity and its influence on environmental conditions and biodiversity is dependant on both local and regional factors. The effect of regional factors (e.g., flow and sediment regime) varies depending on the position of the system within the river corridor. In high energy and dynamic flood plains, as in braided flood plains with very high habitat turnover rates, the most stable habitats contain the most species (U. Karaus, unpublished data). In contrast, low-energy flood plains with relatively stable habitats (e.g., meandering systems), the most dynamic water bodies may harbour highest species richness (i.e., disturbance-mediated resetting of biological control). In addition, local conditions within each habitat interact with hydrological connectivity and result in different conditions among water bodies. Flow velocity, for example, can be quite different in individual water bodies (Bornette & Amoros 1996). This can result in different organic matter accumulations, plankton densities, or primary production rates.

In the present study, connected water bodies were more similar to each other and exhibited primarily lotic conditions, a clear indication of main channel control. Disconnected water bodies, however, formed more unique habitats, with each water body being controlled by the interplay of connectivity and the specific local conditions (Figure 4). Similar results were reported from flood plains along the Danube (Hein *et al.* 2004) and the Rhône (Bornette *et al.* 1998). Along the Rhône, environmental conditions (e.g., nutrient content) in disconnected water bodies were primarily controlled by local conditions such as by adjacent land use and successional stage of the water body. Since species diversity is related to habitat conditions (see: Vinson & Hawkins 1998), different local conditions may result in different species diversity patterns. Therefore, intermediate connectivity in river-floodplain systems not necessarily results in highest levels of biodiversity.

Hydrological connectivity had a major influence on the composition and distribution of Chironomidae and Oligochaeta (Figure 6). Connected water bodies (mc and sc) were characterized by rheophilous and stenotherm taxa such as *Nais elinguis*, *Rheocrictopus fuscipes*, and *Tvetenia calvescens*. Backwater species exhibited affinities to both lotic and lentic conditions (e.g., *Paratrichocladius rufiventris* or *P. skirwithensis*). Water bodies with a low degree of connectivity were characterized by stagnophilous species, such as *Nais communnis* and *Nais pseudoobtusa.* Similar species-specific preferences for lentic, semi-lotic and lotic habitats were reported by Van den Brink *et al.* (1996) for the Lower Rhine.

Based on invertebrate density, two groups of water bodies could be distinguished: (i) connected water bodies with relatively high densities and (ii) disconnected water bodies, where density was an order-of-magnitude lower than in the first group (Table 1). There were no major differences in BOM that may explain these large differences. Differences in densities can be explained by different dispersal pathways in connected and disconnected water bodies. Hydrological connections between water bodies are the most important dispersal pathways for invertebrates. Many studies found drift to be the most important source for colonists, contributing >80% of invertebrate movement (e.g., Matthaei *et al.* 1997; Gayraud *et al.* 2000). High connectivity among individual water bodies was also reflected in a high similarity of both environmental conditions (Figure 4) and the benthic community composition. In contrast, less connected water bodies have to be primarily colonized by air (egg deposition), that is strongly influenced by stochasticity (Tokeshi 1999). This fact was reflected by lower taxa similarity between main channel and less-connected water bodies.

Turnover, persistence, and temporal concordance of benthic invertebrates

Density and diversity of invertebrates were highly variable in space and time (Figure 7). In the main channel, persistence of Oligochaeta and Chironomidae was moderately high, implying that there was moderate faunal change during the sampling period. For the main channel of the Danube similar persistence values were reported (Adams 1984; Fesl 2002). No values exist for Oligochaeta. The remaining water bodies of the Tagliamento had lower persistence values, indicating higher temporal turnover rates. Particularly in less connected water bodies, highest taxa richness is expected to be reached at low densities (Figure 5), which is also an indication for unstable communities. Low community persistence can result from distinct environmental fluctuations (Death & Winterbourn 1994; Therriault & Kolasa 2000). The disappearance of rare taxa is especially more likely when the environment is highly variable (Death & Winterbourn 1994). Townsend *et al.* (1987) found highest persistence in streams in southern England with cool temperature and a small annual temperature range. In the present study, low community persistence in water bodies 24 and 30 can result from high thermal heterogeneity (Figure 4). Water body 33 exhibited a high physicochemical variability (Figure 4). Low community persistence in water body 53, a forested pond with very high species richness, however, can not be explained by environmental variability. There, biotic interactions may have a major influence on community persistence. Biotic interactions also could be an explanation for the low persistence values of the side channel and the backwater: the backwater and the main and side channels were similar in density, community composition and physicochemical conditions; the community persistence of side channel and the backwater, however, was lower than in the main channel.

Concordance in rank abundance was low compared to similar studies in temperate areas (Weatherley & Ormerod 1990; Richards & Minshall 1992; Death & Winterbourn 1994). In the present study, two possible reasons for low concordance are (i) the dominance of Chironomidae, and (ii) the overriding effect of flash floods on invertebrates. Many Chironomidae posses *r*-selected traits (small body size, high fecundity, short generation time) that allow them to persist under harsh conditions (Petr 1970; Turcotte & Harper 1982; Armitage *et al.* 1995; Miller & Golladay 1996; Townsend *et al.* 1997; Frouz *et al.* 2003). Braided rivers are, in particular, harsh environments with high habitat turnover rates, low productivity, low organic matter input, and highly variable environmental conditions (temperature, flow variation) (Tockner *et al.* in press). With *r*-selected traits, therefore, the influence of harsh environmental conditions such as flood events may become less important (Poff 1992). It is not surprising that Chironomidae dominate the macroinvertebrate community in most dynamic rivers. Unsynchronized emergence patterns, for example, allow macroinvertebrates to cope with highly fluctuating flow regimes.

Floods caused major invertebrate reductions in most water bodies (Figure 7). The increase in density and taxa richness in some water bodies following the spring flood could be a result of higher colonization rates during summer. Duration of post-flood recolonization differed among water bodies (Figure 7). In less-connected water bodies, recolonization rates were low and did not reach pre-flood levels during our investigation period (water body 53 was an exception), probably a consequence of reduced dispersal pathways. Key questions besides potential dispersal pathways are: Where do the macroinvertebrates recolonize from? What are the major refugia from where recolonization starts? Invertebrates may survive (and recolonize from) in dead zones (Lancaster & Hildrew 1993b, a), woody debris dams (Palmer *et al.* 1996), and the hyporheic zone (e.g., Williams & Hynes 1974; Palmer *et al.* 1992; Matthaei *et al.* 1999). In our study, water bodies at the edge of the riparian forest (e.g., water body 53) and within the riparian forest were assumed to function as possible refuge habitats during floods. In contrast to all other water bodies, the number of individuals and taxa increased after the autumn flood (water body 53, Figure 7). In this waterbody, recovery following a flood can occur horizontally by dispersal from less disturbed areas such as the edge of the flood plain. Additional recovery strategies can be the recolonization by aerial stages, egg hatching from refugia (e.g., hyporheic zone), and drift from less affected areas such as tributaries (e.g., Wallace 1990; Mackay 1992; Lancaster & Belyea 1997; Collier & Quinn 2003). However, a confirmation of suggested recovery sources of invertebrates requires detailed investigations.

The present study suggests that hydrological connectivity influences environmental conditions and macroinvertebrate communities in multiple complex ways. Riverscape management and restoration strategies should therefore not focus on a single degree of connectivity or single taxonomic groups. It must sustain or restore the natural flow regime and geomorphologic dynamics to increasing the natural range of hydrological connectivity and high spatiotemporal habitat heterogeneity characteristic for dynamic river-floodplain systems.

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APPENDIX

Table 1. Oligochaeta and Chironomidae taxa (ind/m^2) list in the sampled water bodies (mc=main channel, sc=side channel, ec=ephemeral channel, bw=backwater, ep= ephemeral pond) and taxa code used in the multivariate analysis.

	code	mc	sc	bw	24	30	33	53	ep	ec
Oligochaeta										
Aelosoma sp.	Aelo sp	0.3								
Amphichaeta leydigii Tauber	Amph le			3				3		
Aulodrilus pluriseta Piguet	Aulo pl							1		
Cernosvitoviella sp.	Cern sp		1	1				1		
Chaetogaster diaphanus Gruithuisen	Chae di	3		8						
C. diastrophus Gruithuisen	Chae dia	2	1	3						
C. setosus Svetl.	Chia se					0.3		0.3		
Cognettia sphagnetorum Vejdovsky	Cogn sp							0.3		
Eiseniella tetraedra Savigny	Eise te							1		
Enchytraeidae	Ench	2		0.3						
Haplotaxis gordioides Hartmann	Hapl go							0.3		
Limnodrilus hoffmeisteri Claparède	Limn ho						0.3			
Lumbriculus variegatus Müller	Lumb va							1		
Nais barbata Müller	Nais ba			0.3						
N. bretscheri Michaelsen	Nais br	22	0.3	5		1				
N. christinae Kasparzak	Nais ch	1		6			2	1	1	1
N. communis Piguet	Nais co	2		14			2	8	3	0.3
N. elinguis Muller	Nais el	6	22	53		5	1			1
N. pseudoobtusa Piguet	Nais ps			5				9		
N. simplex Piguet	Nais si							1		
N. stolci Hrabe	Nais st	45	14	1		1				0.3
N. variabilis Piguet	Nais va	0.3	0.3	5		1		1		
Nais sp.	Nais sp			1						
Potamothrix bedoti Piguet	Pota be							6		
Pristina foreli Piguet	Pris fo					1				
Pristinella rosea Piguet	Pris ro			2	0.3			1	1	
Pristinella sp.	Pris sp	0.3						3		
Psammoryctides barbatus Grube	Psam co		1							
Rhyacodrilus coccineus Vejdovsky	Rhya co			0.3						
Rhynchelmis tetratheca Michaelsen	Rhyn te			0.3						
Specaria josinae Vejdovsky	Spec jo							0.3		
Stylaria lacustris Lamarck	Styl la	4		0.3				0.3		
Stylodrilus heringianus Claparède	Styl he							2		
Stylodrilus sp.	Styl sp				0.3					
Trichodrilus sp.	Tric sp	0.3	0.3		0.3		0.3			
Chironomidae										
Ablabesmyia sp.	Abla sp			6		2	1	7	1	
Apsectrotanypus trifascipennis Zetterstedt	Aspe tri		13					1		
Apsectrotanypus/ Macropelopia sp.	Aspe sp					0.3				
Brillia modesta Meigen	Bril mo		1					1		
Chironomus sp.	Chir sp			5			0.3			

	code	mc	sc	bw	24	30	33	53	ep	ec
Cladotanytarsus mancus Walker	Clad ma			5	9	12	39		65	
C. vanderwulpi Edwards	Clad va		7							
Conchapelopia / Helopelopia sp.	Conc sp	17	75	1	3	2	1	2		
Corynoneura coronata Edwards	Cory co			1				1		
C. lobata Edwards	Cory lo									4
C. scutellata Winnertz	Cory sc			3		1		2	1	
Corynoneura sp.	Cory sp		28		1					
Cricotopus albiforceps Kieffer	Cric al			0.3				0.3		
C. bicinctus Meigen	Cric bi	8	13	9			0.3			
C. fuscus Kieffer	Cric fu			4				9		
C. sylvestris Fabricius	Cric sy			2		0.33				
C. tremulus Linnaeus	Cric te	3		5						
C. trifascia Edwards	Cric sp	2	6							
Cricotopus sp.	Crico sp		27					2		
Cryptochironomus sp.	Cryp sp						1			
Cryptotendipes sp.	Crypt sp						2			
Diamesa bertrami Edwards	Diam be	57	5	0.3						
Diamesa sp.	Diam sp	12	13					1		
Dicrotendipes sp.	Dicro sp							1		
Eukiefferiella brevicalcar Kieffer	Euki br		3							
E. clypeata Kieffer	Euki cl	2								
E. devonica Edwards	Euki de	79	15							
E. gracei Edwards	Euki gr	4	3							
E. minor Edwards	Euki mi	1								
E. similis Goetghebuer	Euki si		3							
Eukiefferiella sp.	Euki sp		13	5		0.3				
Heleniella ornaticollis Edwards	Hele or	0.3		0.3	1	2		1	1	
Heterotrissocladius marcidus Walker	Hete ma							0.3		
Kiefferulus tendipediformis Goetghebuer	Kief te						2			
Krenosmittia sp.	Kren sp	1								
Micropsectra sp.	Micr sp	43	757	25	12			1		
Microtendipes pedellus de Geer	Micr pe					5		1		
Monodiamesa sp.	Mono sp			6						
Nanocladius parvulus Kieffer	Nano pa			0.3					0.3	
Nanocladius sp.	Nano sp	3								
Orthocladius obumbratus Johannes	Orth ob	9	115	123	164					0.3
O. rivulorum Kieffer	Orth ri	1	8							
O. rubicundus Meigen	Orth ru	4	85	5						
Orthocladius (Euorthocladius) sp.	OrthEu sp	3594	257	1116						4
Orthocladius sp.	Orth sp	9	35	68	9	6		1		
Paracladius sp.	Para sp		1				0.3			
Paracladopelma camptolabis Kieffer	Para ca							0.3		
Paracladopelma sp.	Parac sp	12		68	3					
Parakiefferiella triquetra Pankratova	Para tr							0.3		
Parakiefferiella sp.	Parak sp			23	14	4				
Paramerina sp.	Param sp			0.3		0.3				
Parametriocnemus stylatus Kieffer	Para st	14		8	0.3	1				
Paratanytarsus sp.	Parat sp			5			3			
Paratendipes sp.	Parate sp						9			
Paratrissocladius excerptus Wagner	Para ex			3				1		

	code	mc	sc	bw	24	30	33	53	ep	ec
P. nivalis Goetghebuer	Para ni		6	1	8	55		0.3		1
P. rufiventris Meigen	Para ru	2	38	49	1					
P. skirwithensis Edwards	Para sk	14	25	41						
Phaenopsectra sp.	Phae sp						1	1		
Polypedilum sp.	Poly sp	6	22	4	2	1	4	1	0.3	
Procladius sp.	Proc sp		1	76	5	1	8	18	6	
Prodiamesa olivacea Meigen	Prod ol							3		
Psectrocladius sordidellus Zetterstedt	Psec so			0						
Psectrocladius (Allopsectrocladius) sp.	PsecA sp			19						
Psectrocladius (Monopsectrocladius) sp.	PsecM sp			2						
Psectrocladius sp.	Psec sp								1	
Psectrotanypus sp.	Psect sp							0.3		
Pseudorthocladius sp.	Pseu sp				1	1			2	
Rheocricotopus effusus Walker	Rheo ef		7		0.3	1				
Rheocricotopus fuscipes Kieffer	Rheo fu	23	17	2						0.3
Rheocricotopus sp.	Rheo sp			1	2					
Rheosmittia sp.	Rheos sp					0.3				
Stictochironomus sp.	Stic sp						1			
Sympotthastia sp.	Symp sp	12	128	564	73	13	0.3		0.3	
Synorthocladius semivirens Kieffer	Syno se	76	3	15		0.3		1	1	
Tanytarsus chinyensis Goetghebuer	Tany ch		6	1		3	1			
Tanytarsus sp.	Tany sp	7	9	52	1		7	36	3	
Thienemanniella vittata Edwards	Thic vi	38	314	362	1	2		1		1
Thienemannimyia sp.	Thie sp	3	7	6				4		
Tvetenia calvescens Edwards	Tvet ca	113	192	12		0.3				1
Tvetenia discoloripes Goetghebuer	Tvet di	5								
Zavrelimyia sp.	Zavr sp			2				11		

CHAPTER 5

THE CONTRIBUTION OF LATERAL AQUATIC HABITATS TO MACROINVERTEBRATE DIVERSITY ALONG RIVER CORRIDORS

Ute Karaus, Helene Guillong & Klement Tockner, submitted

The lateral dimension of biodiversity along river corridors has been given scant attention in river ecology. Therefore, the objective of the present study was to quantify the distribution and diversity of lateral aquatic habitats and their associated macroinvertebrate communities along three river corridors (Tagliamento, Thur, and Rhône) in the Alps. A nested sampling design was applied. Along each corridor, 1-km long segments were surveyed at 10-km distances (14 to 17 sections per corridor). Within each segment, the main channel, parafluvial ponds, backwaters, and tributaries were sampled for Ephemeroptera, Plecoptera and Trichoptera (EPT-taxa). Overall, 159 EPT-taxa were identified in 119 composite samples, which was between 73% and 77% of the total expected richness along each corridor. Lateral habitats contributed >50% to total corridor species richness. Diversity was hierarchically partitioned to quantify the relative proportion contribution of individual samples, habitats, and corridors to overall diversity (three river corridors). Among-sample and among-corridor diversity components contributed most to total EPT-taxa richness, while <15% was due to within-sample and among-habitat diversity components. The present study clearly emphasises the importance of lateral aquatic habitats for maintaining high aquatic biodiversity along river corridors. Consequently, these habitats need to be fully integrated in future conservation and restoration projects; particularly since these

are the first habitats that disappear as a consequence of river regulation and flow control.

INTRODUCTION

Biodiversity in river corridors is structured along longitudinal, lateral and vertical dimensions (Ward 1989). Various concepts predicting species diversity along river corridors have been developed (Vannote *et al.* 1980; Statzner & Higler 1986; Ward & Stanford 1995; Stanford *et al.* 1996). The river continuum concept (RCC, Vannote *et al.* 1980) proposed maximum biodiversity in middle reaches where environmental heterogeneity is expected to be maximized. Statzner and Higler (1986) suggested that maximized biodiversity is linked to hydraulic changes associated with geomorphological transition zones. In extension of the serial discontinuity concept (SDC), Ward & Stanford (1995) included the interactions between the river channel and its flood plain (i.e., lateral dimension). They proposed greatest diversity in transition zones between constrained and braided sections and in the meandering reach. Stanford *et al.* (1996) suggested a more complex and extended model, which predicts maximum diversity in floodplain reaches and lowest diversity in geomorphological transition zones.

Most concepts have been developed for single-thread rivers. Studies on the lateral organization of aquatic macroinvertebrates were restricted to individual floodplain segments (e.g., Amoros & Roux 1988; Castella *et al.* 1991; Foeckler *et al.* 1991; Obrdlik & Fuchs 1991; Van den Brink *et al.* 1996; Tockner *et al.* 1999; Arscott *et al.* 2003). Although backwaters, parafluvial ponds and tributaries are recognised as key elements of the river "discontinuum" (e.g., Vannote *et al.* 1980; Minshall *et al.* 1985; Perry & Schaeffer 1987; O'Leary *et al.* 1992; Homes *et al.* 1999; Rice *et al.* 2001; Solari *et al.* 2002; Benda *et al.* 2004), their contribution to biodiversity at the corridor scale (regional-scale diversity) has not been tested yet.

In addition, most diversity studies - not only in rivers - focused on alpha-diversity (i.e., local-scale diversity), neglecting hierarchical organization of biodiversity (e.g., Noss 1990; Ward & Tockner 2001). Relationship between scale of investigation and processes that influence species diversity is the basis of the distinction between inventory diversity (α-, γ- & ε-diversity) and differentiation diversity (β-diversity) (Magurran 2004). Studies on beta-diversity (i.e., species turnover along environmental gradients), for example, can be crucial to the understanding of environmental factors that are responsible for observed diversity patterns in both aquatic and terrestrial ecosystems (Bornette *et al.* 2001; Ward & Tockner 2001; Pineda & Halffter 2004). Moreover, processes that operate over a range of scales likely influence the structure of communities along riparian corridors. However, mechanisms at one spatial scale might have larger relative effects on community structure than mechanisms that operate at another scale (Shmida & Wilson 1985; Wagner *et al.* 2000). Identification of such critical scales is of great importance for the successful conservation of riverine biodiversity.

In this study we focus on diversity of aquatic macroinvertebrates along river corridors by including the lateral dimension. Principal objectives are (1) to quantify the relative contribution of main channel, backwater, parafluvial pond and tributary habitats to river corridor diversity and (2) to study the hierarchical structure of biodiversity along river corridors. Based on this study, we discuss potential implications for conservation and management of river ecosystems. Emphasis was given on the insect orders Ephemeroptera, Plecoptera and Trichoptera (EPT). EPT-taxa form an important component of the benthic community of lateral aquatic habitats (Arscott *et al.* in press). Furthermore, they are frequently considered in basic research as well as for biomonitoring of aquatic ecosystems (e.g., Marchant *et al.* 1995; Hewlett 2000; Cereghino *et al.* 2003).

STUDY AREAS

Three Alpine river corridors were investigated for aquatic habitats and benthic macroinvertebrates (Figure 1). The Tagliamento drains into the Adriatic Sea, the Thur via the Rhine River into the North Sea, and the Rhône into the Western Mediterranean Sea. The three river corridors are comparable in their geomorphology and catchment size, although they differ in their anthropogenic alteration (e.g., water abstraction, channelization). The Tagliamento is the least modified, the Rhône the most impacted river.

Tagliamento

The Tagliamento is a large gravel-bed river located in north-eastern Italy (Friuli-Venezia Giulia; 46°N, 12°30´E; Figure 1). It rises at 1195 m a.s.l. in the Carnian Alps and flows 170 km to the Adriatic Sea. The catchment covers 2580 km^2 with more than 70% located in the Alps. The Tagliamento has an average discharge of 90 m^3/s, whereas 2-, 5- and 10-year floods are estimated to be 1100, 1600 and 2150 m^3/s (Petts *et al.* 2000). High flow is caused by snowmelt (spring) and heavy rainfall (autumn) with discharge maxima of ~4000 m^3/s (Ward *et al.* 1999); minimum discharge is 20 m^3/s. The near-pristine character of the Tagliamento is reflected in its complex channel morphology, a dynamic flood regime, and an idealized longitudinal sequence of constrained, braided and meandering sections. For detailed information on the catchment and the main study area see Ward *et al.* (1999), Gurnell *et al.* (2000), Arscott *et al.* (2000), and Tockner *et al.* (2003).

Thur

The Thur is a gravel-bed river located in north-eastern Switzerland (Figure 1). It rises in the alpine region at 2502 m a.s.l. and flows 135 km to the Upper Rhine (345 m a.s.l.). The catchment area covers 1750 km^2. Major parts of the upper catchment are in the pre-alpine zone. Average discharge is 47 m^3/s, with minimum and maximum values of 2.2 m^3/s and 1130 m^3/s, respectively. The Thur is channelized between the lower end of the pre-alpine zone (river-km 59) and its confluence with the River Rhine (river-km 135) (Uehlinger 2000).

Rhône

The Swiss part of the Upper Rhône River originates from the Rhône glacier at 1763 m a.s.l. and flows 166 km to the Lake Geneva (374 m a.s.l., Figure 1). The catchment area covers 5220 km^2 (Loizeau & Dominik 2000). Average annual discharge is 182 m^3/s with a minimum and maximum discharge of 34 m^3/s and 1370 m^3/s, respectively (Bundesamt für Wasser und Geologie 2003). The Upper Rhône River is channelized from river-km 45 to Lake Geneva. Numerous hydroelectric dams have been constructed on the main stem and on tributaries, which strongly modify the flow characteristics of the river (hydropeaking). Dam operations cause rapid variations in discharge and water level fluctuations (>100 cm per day) (Loizeau & Dominik 2000).

METHODS

Sampling design

A nested design was used in this study (*sensu* Ward & Tockner 2001). In spring 2002 (March until May), at approximately mean annual discharge, and before most EPT-larvae emerge, lateral habitat-heterogeneity and the diversity of EPT-taxa were investigated along the three river corridors. Along each corridor, one-km long segments were surveyed at 10-km distances starting at river-km 5. Within each segment the main channel and lateral aquatic habitats (i.e., backwaters, parafluvial ponds, and tributaries) were mapped (Table 1).

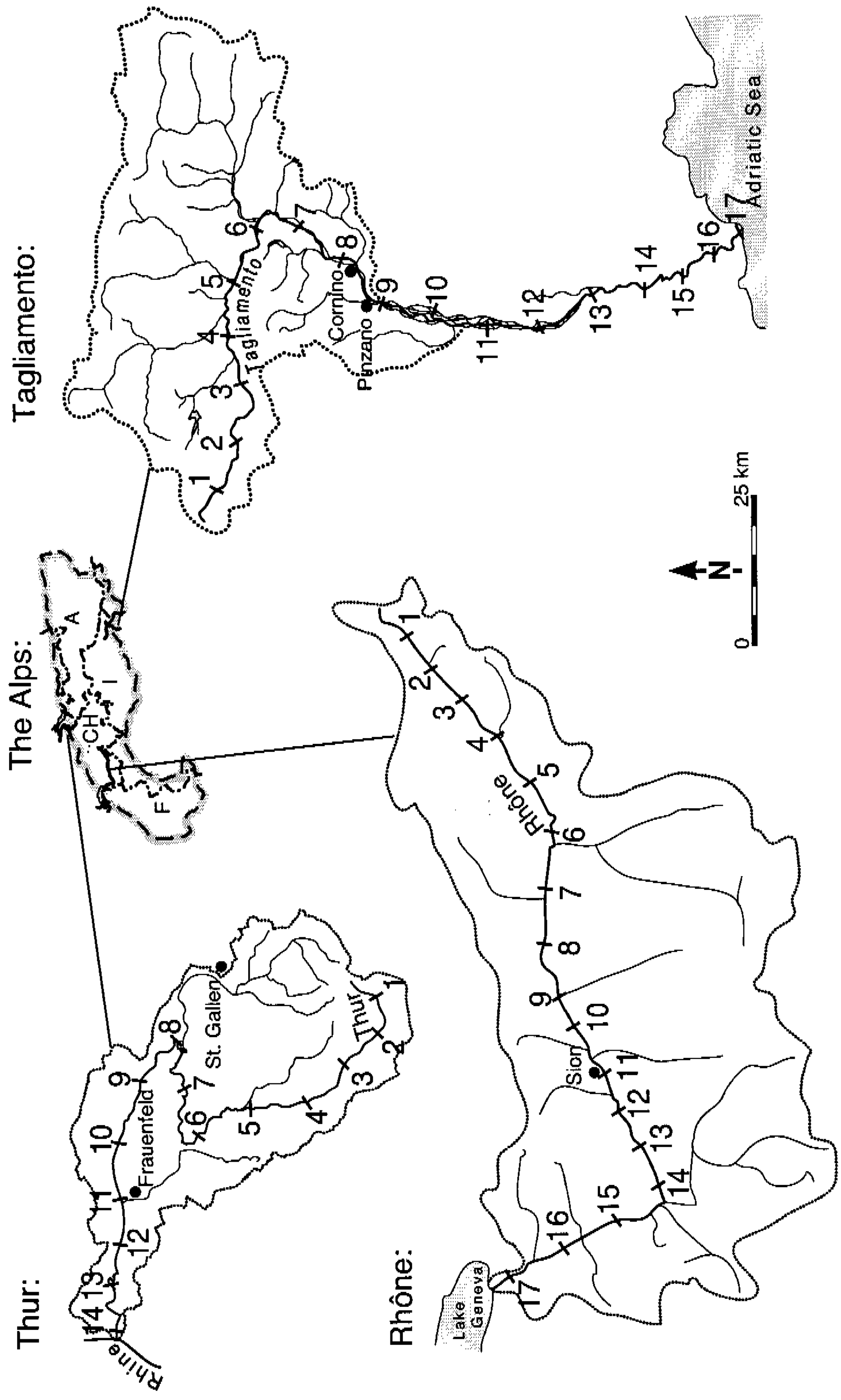

Figure 1. Catchment of the Tagliamento, the Thur, and the Rhône Rivers and location of individual sampling segments along each corridor (numbers; 1-km long segments each 10 km).

Table 1. Total number of composite samples (mc = main channel, p = pond, bw = backwater, t = tributary).

	mc	**p**	**bw**	**t**	**Total**
Tagliamento	15	9	10	5	**39**
Thur	14	5	5	13	**37**
Rhône	17	3	6	17	**43**
Total	**46**	**17**	**21**	**35**	**119**

Backwaters were defined as habitats with a permanent downstream connection to a lotic channel but with local conditions being lentic-like and often with fine sediment deposits. Parafluvial (*sensu* Fisher *et al.* 1998) ponds were disconnected lentic waterbodies within the active zone of the corridor (*sensu* Frissell *et al.* 1986). A tributary was defined as the smaller and the main channel as the larger of two intersecting channels (*sensu* Benda *et al.* 2004). We sampled tributaries upstream from their confluence with the main stem.

Macroinvertebrate sampling and treatment

Along the three river corridors, the main channel, ponds, backwaters, and tributaries were systematically surveyed. Lentic aquatic habitats (ponds and backwaters) were sampled subsequent to the mapping. In segments with >5 lentic habitats, five habitats per type were randomly selected. If <5 habitats were present, all were sampled. Semi-quantitative samples in all aquatic habitats were collected using a D-shaped kick-net (mesh size: 250 μm). To ensure that ecological data gathered from different aquatic habitat types could be directly compared, samples were collected from 50 m^2 area of the aquatic habitat type (Williams *et al.* 2004). Per segment, a total area of 50 m^2 in main channel, ponds, backwaters, and tributaries was sampled for 15 min. Duration of sampling was calculated according to the total area of the chosen aquatic habitat type (example: two ponds with an area of 100 m^2 (pond 1) and 300 m^2 (pond 2) occur in a hypothetical segment. In pond 1 an area of 37.5 m^2 is sampled in 11 min and in pond 2 an area of 12.5 m^2 is sampled for 4 min). Microhabitats within individual aquatic habitat types (e.g., large wood, shallow shore areas, pool-riffle sequences) were sampled proportional to their area. Sub-samples from each aquatic habitat type of each segment were combined into a composite sample and preserved in 4% formaldehyde. In the laboratory, all EPT individuals were identified to the lowest practical taxonomic level, mostly to species level.

Data Analyses

Jackknife estimation of species richness

To standardize samples, jackknifed estimates (Jackknife-1, Heltshe & Forrester 1983) of taxa richness were generated for each individual habitat type (Programme EstimateS Version 6.0b1, Colwell 2001). Data were standardized both by number of samples and number of individuals. For each aquatic habitat type, jackknifed estimates were permuted at random 1,000 times. Furthermore, Jackknife analyses were used to estimate the total expected number of species for each individual river corridor (Krebs 1998).

Nestedness

Communities are considered to be nested when species-poor sites comprise a subset of species assemblages in richer sites (Patterson 1987). Nestedness was determined using the Temperature Calculator of Atmar and Patterson (1993; 1995). The calculated "temperature" (T) reflects the degree of order in presence-absence matrices. It ranges from T=0° (perfectly nested) to T=100° (random). The data were packed in rows (samples) and columns (taxa) to maximize nestedness. Monte Carlo randomization (1000 permutations) was used to test whether the calculated T value of the matrix was significantly lower than the T value of a randomly calculated matrix.

Diversity measures

Based on the nested sampling design, different components of diversity (*sensu* Magurran 2004) were determined (Table 2). Alpha (α) and gamma (γ) diversity are direct measures of species richness that differ in their hierarchical nature (spatial scale). Two types of beta (β) diversity were used. (1) Harrison's beta-1 (β_1) (1992) has been calculated to determine the distinctness of species composition (spatial species turnover) at three different scales (Alps, corridor, habitat types; see Table 2) and among aquatic habitat types within each segment (within segment β_1). The scale "Alps" combines the three river corridors Tagliamento, Thur and Rhône; "corridor" means Tagliamento, Thur, or Rhône; the scale "habitat type" comprises main channel, pond, backwater, and tributary; the scale "sample" includes all individual samples taken during this study (see Table 1). Beta-1 is based on Whittaker's β-diversity (Whittaker 1977) and has been modified in order to compare transects of unequal size:

$$\beta_1 = \frac{\left(\frac{S}{\alpha - 1}\right)}{(N - 1)} \times 100$$

where N is the number of sites, S the regional species diversity and α the mean alpha-diversity. Beta-1 ranges from 0 (complete similarity) to 100 (complete dissimilarity). (2) Lande's beta-diversity (1996) was calculated in order to partition total diversity ("Alps") (Veech *et al.* 2002). Lande's β-diversity determines the diversity among sites (i.e., the mean number of species not found in each of the samples or habitats). Diversity can be partitioned into its components (alpha, beta and gamma) to evaluate the influence of each diversity component to total diversity. Lande (1996) found that inventory and differentiation diversity can be partitioned by the equation:

$$\gamma = \alpha + \beta$$

where γ is the number of species in the corridor and α is the mean species richness of individual samples or habitats. Beta can be estimated as follows:

$$\beta = \gamma - \alpha.$$

This provides a measurement based on the number of species that is comparable with α-diversity. Therefore, diversity components at each hierarchical level can be calculated as $\beta_\mu = \gamma - \alpha_\mu$ at the highest level with m = highest level and $\beta_{i+1} = \alpha_i - \alpha_{i+1}$ for each lower level with i = any level beneath the highest level m. Then, the additive partitioning of diversity is:

$$\gamma = \alpha_1 + \sum_{i=1}^{m} \beta_i \,.$$

Based on this equation, total diversity along the corridors can be expressed as the proportional contribution of diversity at each hierarchical level (Table 2). In the present study, β_i of three different hierarchical levels was calculated (β_C, β_H, β_S; Table 2).

Similarity

The mean similarity of EPT-taxa between all pairs of habitat types within each segment was calculated using Jaccard's similarity coefficient (Krebs 1998). An analysis of variance (ANOVA) was applied to test for differences among pairs of habitat types.

Table 2. Hierarchical framework of the sampling strategy of the present study in order to determine the different levels of biodiversity. Alps: Tagliamento, Thur & Rhône. See methods for further explanation.

Level	Scale	Inventory diversity	Differentiation diversity
1	Alps	ε_A	β_{1A}, β_A
2	Corridor	γ_C	β_{1C}, β_C
3	Habitat type	α_H	β_{1H}, β_H
4	Sample	α_S	β_S

RESULTS

Habitat distribution

Along the three corridors, a total of 46 1-km long segments were investigated (Table 1). The number of backwaters and ponds was highest along the Tagliamento and lowest along the Rhône (Figure 2).

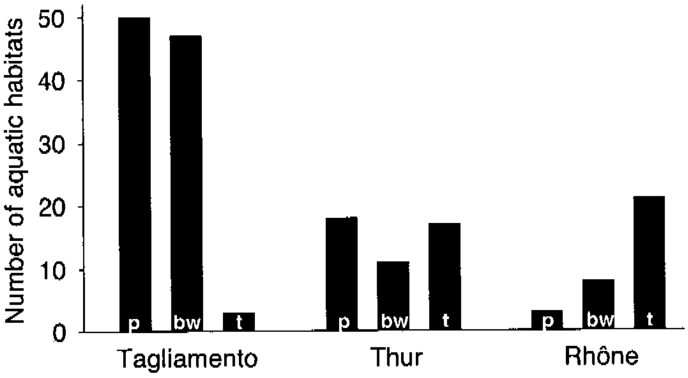

Figure 2. Total number of aquatic habitat types along Tagliamento, Thur and Rhône Rivers. P=pond, bw=backwater, t=tributary (see also Table 1).

The total number of tributaries peaked in the Rhône, with the highest number in headwater segments (Figure 3). Along the Tagliamento, ponds and backwaters occurred mainly in middle, and tributaries in headwater segments (Figure 3). Along the Thur, ponds were most abundant in lower segments (Figure 3).

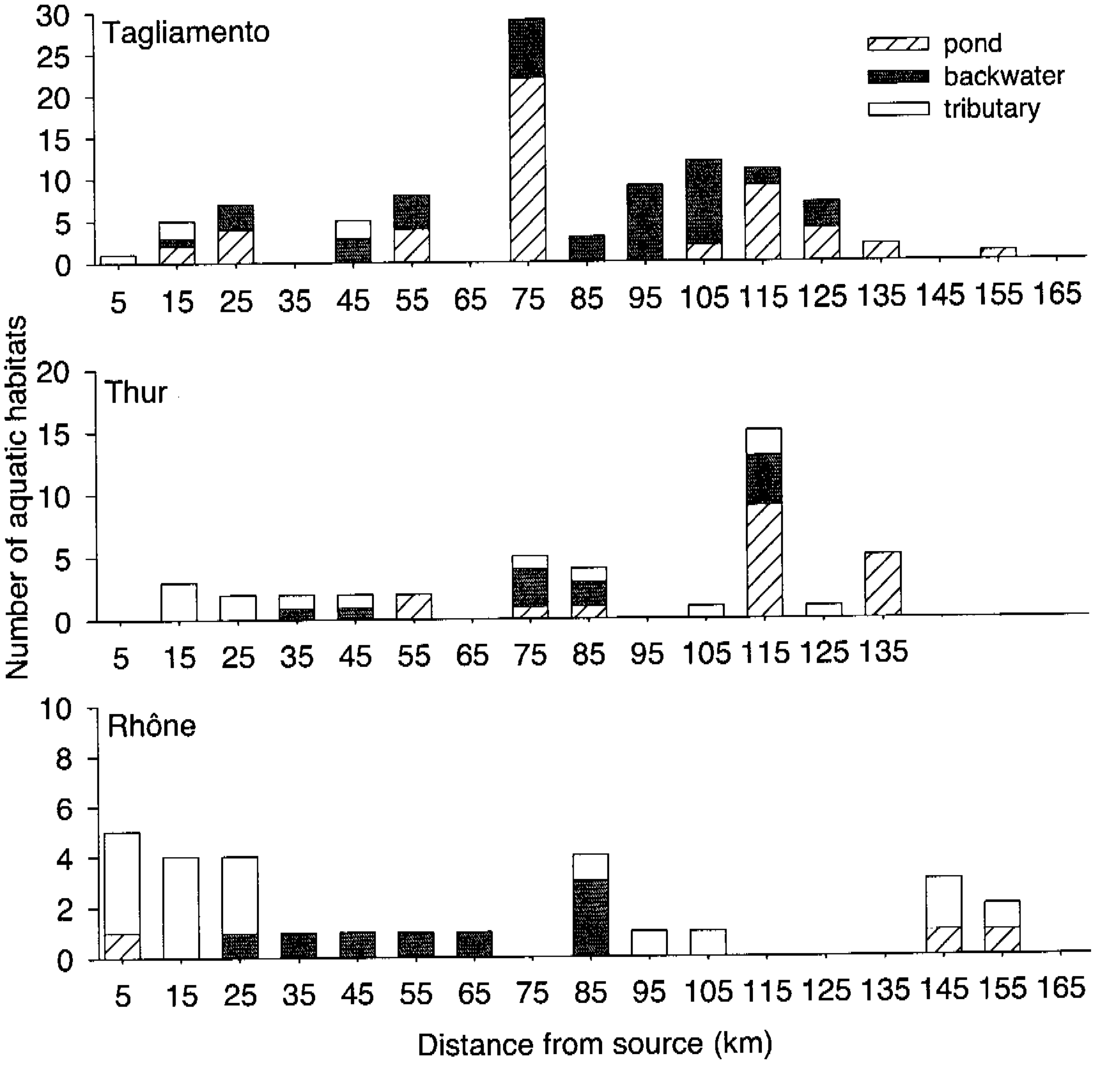

Figure 3. Lateral aquatic habitat distribution along the Tagliamento, Thur, and Rhône.

Species richness patterns

A total of 41918 individuals from 159 EPT-taxa was collected in 119 samples along the three corridors (Appendix, Table 1). Corridor diversity was highest along the Thur (112 taxa), followed by the Tagliamento (78) and the Rhône (65). Based on Jackknife analyses, between 73% (Tagliamento) and 77% (Rhône) of the total expected species richness was sampled. Rare taxa (<1% of total abundance) accounted for 85%, 53%, and 88% of all taxa along the Tagliamento, the Thur, and the Rhône, respectively (Appendix, Table 1).

Estimates of species richness produced using Jackknife procedures, standardized for number of samples and individuals, exhibited a different increase of richness for individual aquatic habitat types (Figure 4). Based on samples, tributaries showed most species (Figure 4A); based on individuals, ponds exhibited a steeper increase in species richness (Figure 4B).

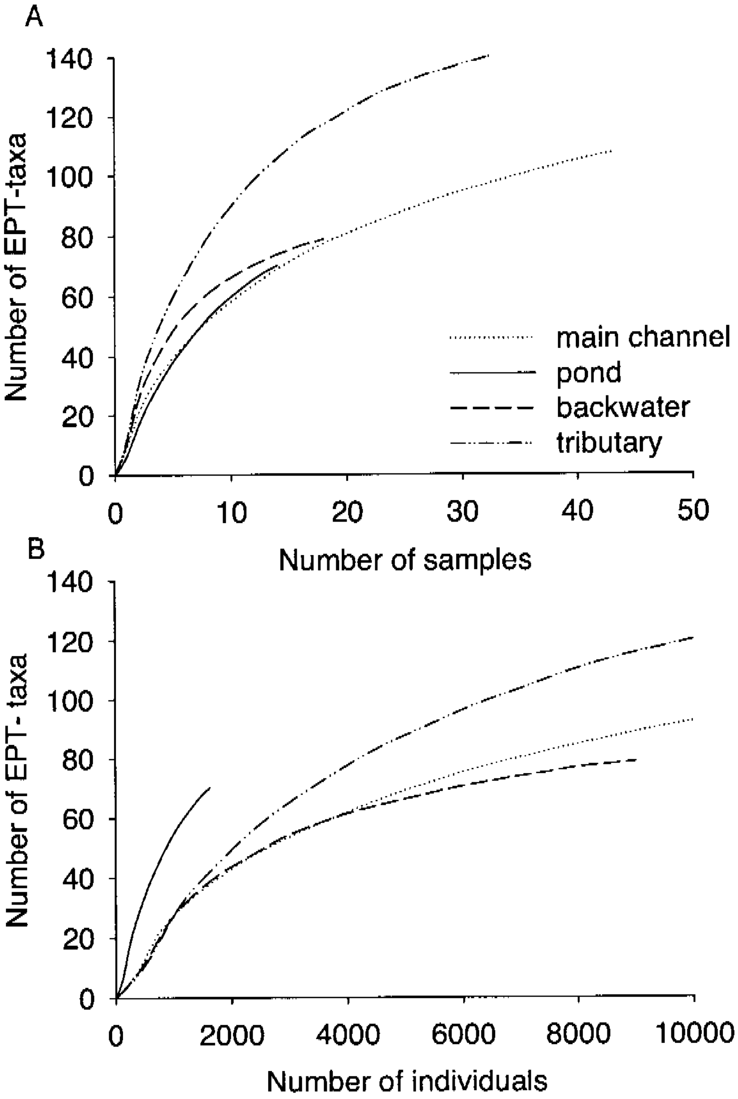

Figure 4. Predicted number of EPT-taxa in individual habitat types based on Jackknife analyses standardized for samples (A; surrogate for area) and individuals (B).

Lateral aquatic habitats (i.e., ponds, backwaters and tributaries) contributed >50% to total EPT-taxa richness, although the relative contribution of habitat types was different along the three corridors (Figure 5). Along the Tagliamento, 14% of total number of taxa was restricted in their occurrence to main channel habitats, 4% to ponds, 23% to backwaters, and 13% to tributaries; along the Thur, 17% was restricted to main channel habitats, 7% to ponds, 3% to backwaters, and 27% to tributaries; and along the Rhône, 12% of taxa was restricted to main channel habitats and 54% to tributaries. Ponds and backwaters were almost completely absent in the Rhône.

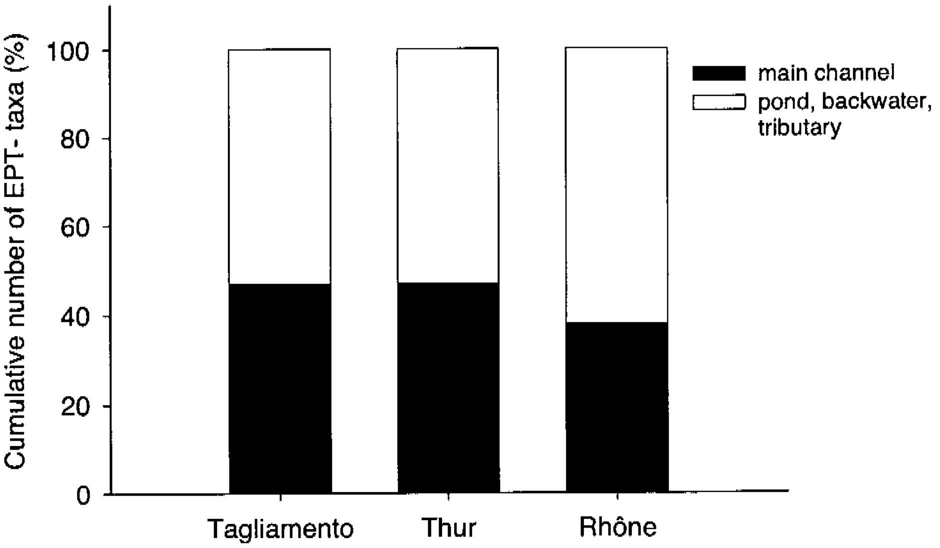

Figure 5. The cumulative relative (%) species richness along the Tagliamento, Thur and Rhône Rivers. Taxa not found in the main channel were cumulatively added.

Longitudinal diversity patterns differed among corridors (Figure 6). Along the Rhône River, diversity peaked in the headwater section. Habitats downstream of river-km 25 added only five new taxa to total corridor diversity. No clear longitudinal patterns occurred along the Thur and Tagliamento. In both rivers, cumulated richness increased continuously along the corridor, with a steeper increase along the Thur (Figure 6).

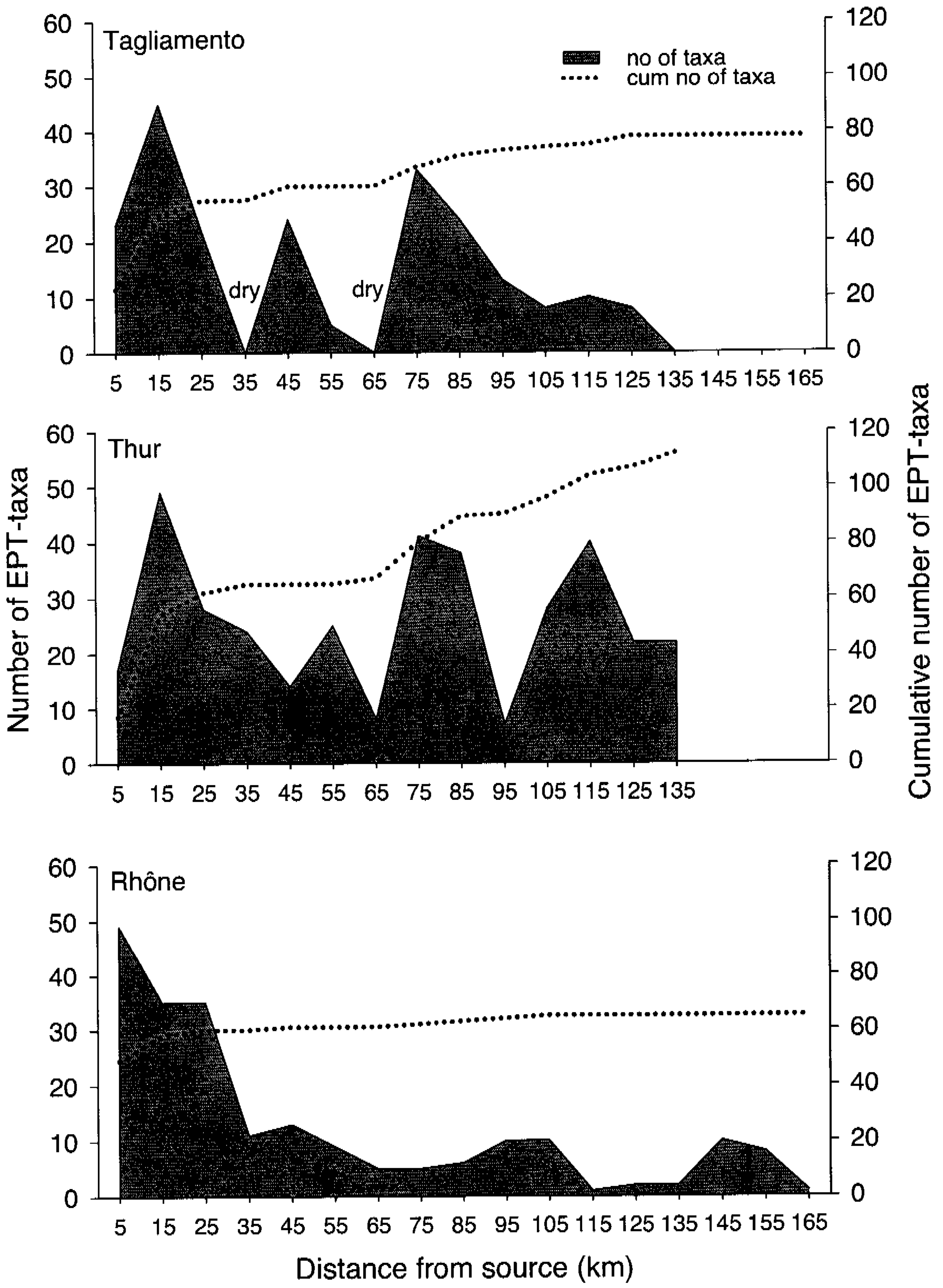

Figure 6. Taxa richness (total no of taxa per segment) and cumulative number (cum no of taxa; dotted line) along the three river corridors.

Nestedness and hierarchical organization

EPT-assemblages were highly nested within each corridor. The calculated temperatures (Tagliamento: 10.1°; Thur: 16.5°; Rhône: 6.6°) were significantly ($p < 0.001$) lower than values randomly produced by Monte Carlo simulations.

Point diversity (α-diversity) was highest along the Thur and lowest along the Rhône (Levels 2-4; Figure 7). Along each corridor, average species richness was lowest in pond habitats (Levels 3 & 4; Figure 7).

Species turnover (β_1-diversity) varied across scales (Figure 7). Turnover rate was highest at the scale "Alps" (Level 1) and lowest at the corridor scale (Level 2).

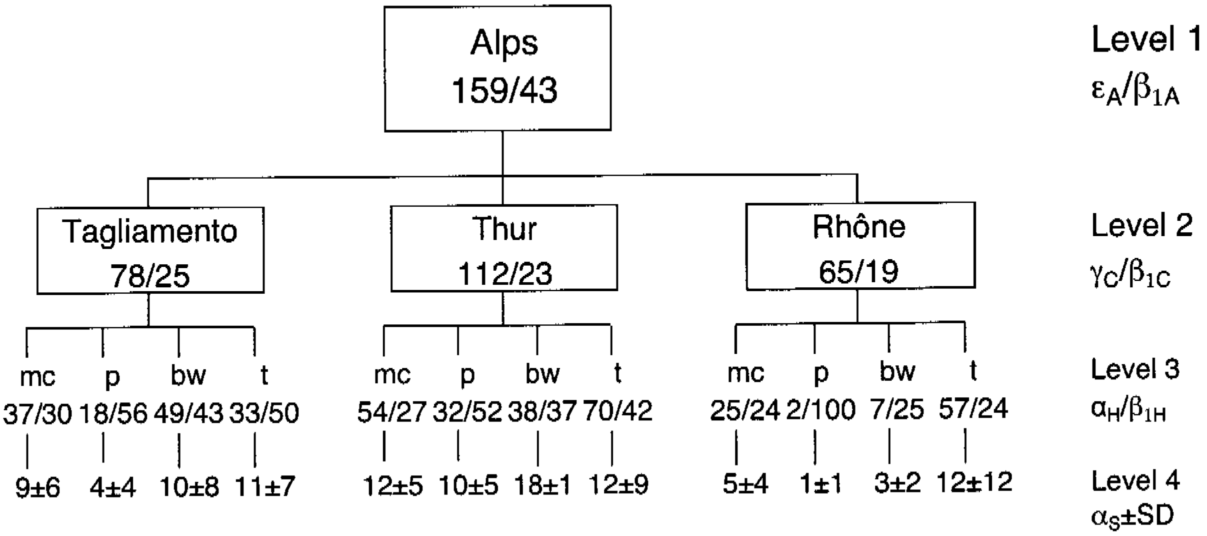

Figure 7. Hierarchical organization of species diversity. Level 1: Alps (ε_A=Alps epsilon; β_{1A}=Alps beta-1); Level 2: corridor (γ_C = corridor gamma ; β_{1C} = corridor beta-1); Level 3: habitat type (α_H = habitat type alpha; β_{1H} = habitat type beta-1); Level 4: individual sample (α_S = sample alpha). Mc=main channel, p=pond, bw= backwater; t= tributary.

Two additional trends could be observed: (1) Turnover rate, or β_{1H}-diversity, decreased (except for ponds) from the near-natural Tagliamento to the highly impacted Rhône (Figure 7). (2) β_{1H}-diversity decreased laterally (main channel<backwaters<ponds and tributaries) along the Thur and Tagliamento. Along the regulated Rhône, the number of backwaters and ponds was too low to detect any lateral trend in beta-diversity. Species-turnover rates among aquatic habitat types within each segment (within segment β_1) were high. Mean values ±SD were 64±16, 63±20, and 59±16 for Tagliamento, Thur and Rhône, respectively.

Total species diversity was partitioned into its hierarchical components. Along the three rivers, among-sample and corridor diversity components (β_S and β_C) contributed most to total EPT-taxa richness, while <15% was due to within-sample and habitat type diversity components (α_S and β_H; Figure 8).

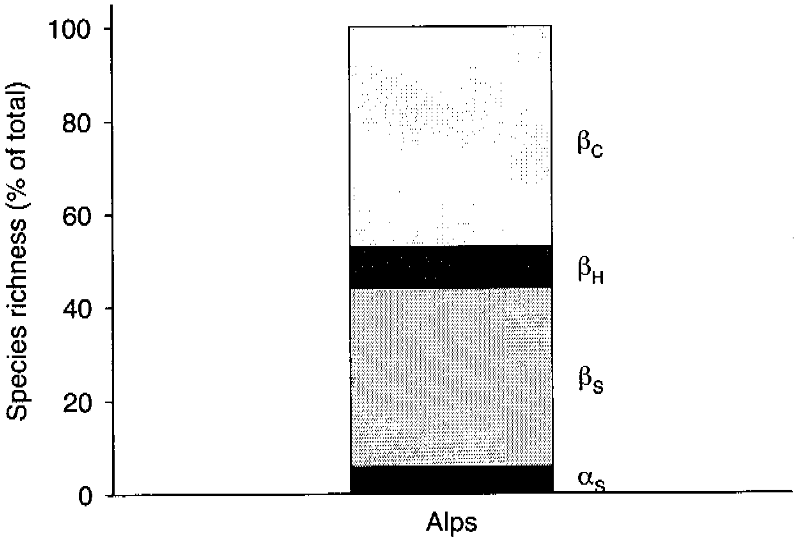

Figure 8. Additive partitioning of observed species richness across three spatial scales. Values are expressed as the percent of the total diversity of EPT-taxa diversity explained by each hierarchical level (see Table 2).

This means that the heterogeneity among individual habitats (i.e., individual samples) explained more of the total species richness than the heterogeneity within individual habitats and among habitat types (i.e., pond, tributary, backwater, main channel).

The average faunal similarity between pairs of aquatic habitat types was low, and differences between pairs were not significant (ANOVA; Table 3).

Table 3. Mean taxa similarity (± SD) between all pairs of aquatic habitat types along the three river corridors (mc=main channel, p=pond, bw=backwater, t=tributary).

	mc-bw	**mc-p**	**mc-t**	**bw-p**	**bw-t**	**p-t**
Tagliamento	0.18 ± 0.09	0.16 ± 0.19	0.15 ± 0.11	0.1 ± 0.11	0.18 ± 0.13	0
Thur	0.22 ± 0.12	0.22 ± 0.14	0.14 ± 0.07	0.17 ± 0.07	0.09 ± 0.09	0.04 ± 0.05
Rhône	0.26 ± 0.1	0.17 ± 0.29	0.18 ± 0.12	-	0.05 ± 0.08	0

DISCUSSION

Habitat and species richness patterns

Species diversity patterns along rivers has been well studied. In particular, it is well known that species are replaced along the river channel due to changes in temperature, sediment structure, and stream metabolism (see Vinson & Hawkins 1998). However, most studies focused on single-thread rivers and excluded lateral habitats. In the present study, we included lateral aquatic habitats along entire river corridors. As a consequence, none of the existing concepts that have been developed to predict biodiversity along river corridors (e.g., Vannote *et al.* 1980; Ward & Stanford 1983; Statzner & Higler 1986) can be supported by our data. Each river exhibited a distinct longitudinal pattern sequence in species diversity (Figure 6), which emphasizes the uniqueness of rivers. Hynes (1975), already proposed that 'every stream is likely to be individual'. Moreover, each habitat type contained a very distinct community, and faunal similarity among individual habitat types was very low (Table 3). The "individuality" of rivers as well as of habitat types, however, has been challenged by anthropogenic impacts. River regulation not only eliminates lateral habitats (see Figures 2 and 3) it also most likely leads to a homogenization of aquatic communities. Along the regulated Rhône, for example, main stem habitats were species-poor; remaining diversity was primarily allocated to tributaries (parafluvial ponds and backwaters were almost completely absent). In tributaries, which are less affected by hydropeaking and canalization, 87% of the present corridor species pool occurred (Appendix, Table 1).

Lateral aquatic habitats such as tributaries, backwaters, and parafluvial ponds are among the least-investigated habitat types along river corridors. Although these habitats cover only a small proportion of the total aquatic area (<8% in braided flood plains along the Tagliamento, Van der Nat *et al.* 2003), they contributed >50% to total species richness (Figure 5). In particular backwaters and tributaries contained rich communities that were different from main channel habitats. A modest contribution by parafluvial ponds can partly be explained by our focus on EPT-taxa. By considering other groups such as Mollusca, Crustacea, Odonata or, Coleoptera, we may expect a much higher contribution of lentic habitats (parafluvial ponds, backwaters) to total species diversity (U. Karaus, unpubl. data). Jackknife analyses, standardized by number of individuals, exhibited a steeper curve in ponds compared to other habitat types (Figure 4B). Between-pond heterogeneity is expected to be large, which was confirmed by higher turnover rates among ponds compared to other habitat types (Figure 7). From an ecological perspective, ponds can be regarded as "concave islands" with environmental properties strongly related to local conditions (Karaus *et al.* 2005). Generally, pond invertebrate diversity has been related to a range successional stages, and therefore, to disturbance frequency (Castella 1987; Schneider & Frost 1996; Homes *et al.* 1999) and to hydrological connectivity (Tockner *et al.* 1999).

Tributaries, on the other hand, are not only different from the main channel regarding environmental properties, but also are assumed to enhance the local heterogeneity at the confluence with the main channel (the network dynamics hypothesis, Benda *et al.* 2004). Brown & Coon (1994) reported higher fish density and different community composition in tributaries compared to the channel (Lower Missouri, US). They found a gradient in the faunal assemblage from small tributaries to large river sections, which corresponded to an environmental gradient from shallow streams with coarse substrate to deep rivers with finer sediments. The potential importance of tributaries for main stem communities is virtually unexplored. Tributaries may serve as important refugia for recolonising the main channel after disturbances (e.g., floods, droughts, pollution), and they are important habitats for early life stages of fish and invertebrates (Bruns *et al.* 1984; Rice *et al.* 2001).

In the present study, backwaters also contributed significantly to overall species richness along the three river corridors (Figure 7). They were colonized by a unique and species rich community. Similar differences in taxa richness between backwaters and main-channel habitats were found also in upland streams in Victoria (O'Leary *et al.* 1992). Solari (2002) found high plankton densities in backwaters of the Slado River (Argentina), a consequence of lentic conditions. Lentic conditions, a permanent hydrological connection to the main channel, and increased primary production can enhance species richness within backwaters (Cellot & Bournaud 1986; Schiemer *et al.* 2001). At mean and low discharge, backwaters exhibit lentic conditions, and they primarily accumulate organic matter (Amoros & Roux 1988) In their “Inshore Retention Concept”, Schiemer *et al.* (2001) emphasized the importance of still-water habitats in the active channel for the development of phyto- and zooplankton and fish larvae. Backwaters were identified as important retentive habitats, which contributed to overall river biodiversity and production. However, further studies on local constraints on backwater communities (as well as on tributary communities) - in particular on the potential role of backwaters as refugia during flood events - are required. This is especially intriguing for permanently connected habitats (backwaters and tributaries) where dispersal barriers are presumably absent.

Nestedness and hierarchical organization

River corridors are hierarchically organized and nested ecosystems. In the present study, the nested sampling design allowed to detect differences in species diversity at various spatial scales. As expected, communities were highly nested in all three river corridors. Nestedness is a common attribute of most communities (Wright *et al.* 1998). Aquatic invertebrates, however, have been regarded as an exception, because of their high diversity (Boecklen 1997). Malmqvist & Hoffsten (2000) detected a nested distribution for Ephemeroptera, Plecoptera, Trichoptera, and Simuliidae in Swedish streams and rivers. Nestedness was particularly pronounced in the Rhône River, where communities in the canalized middle and downstream sections formed distinct subsets of the less-impacted and more species-rich headwater reaches. The lower sections along the Rhône - heavily impacted by hydropeaking and river regulation - are very likely sinks for invertebrate species. Most species of the regional pool are expected to be able to disperse over large areas, therefore local conditions primarily determine the presence or absence of species within individual habitats (habitat filters, *sensu* Poff 1997). A lower degree of nestedness (higher system temperature T) in the less impacted Thur and Tagliamento Rivers could result from higher habitat heterogeneity.

In the present study, we applied a quantitative model that allows to partitioning at different spatial scales (see Wagner *et al.* 2000). This approach implies that what we measure as within-community diversity at a higher scale (e.g., corridor scale) is the combined effect of heterogeneity at various lower scales (habitat, river segment). In the present study, high differentiation diversity (beta-diversity) at the broadest spatial scale (Level 1 in Figure 7) reflected distinct biogeographic differences among corridors (i.e., regional control of local diversity). All three rivers flow in different directions. In addition, human impacts were likely to increase differences among catchments.

The low within-corridor turnover (β_{1C}), in contrast to the high within-(β_{1H}) and between-habitat (within-segment β_1) type turnover, assumed that both regional and local factors control benthic communities. The influence of local factors (habitat heterogeneity and biotic interactions) and of regional factors (altitude, river style, land-use patters) on the structure of stream invertebrates has been well documented (see review by Vinson & Hawkins 1998). However, the relationship between regional and local species richness has been rarely investigated for stream invertebrates. Studies on fish diversity showed a strong regional control on local diversity (Hugueny 1995), or an influence by both regional and local factors (Angermeier & Winston 1998). Vaughn (1997) reported a linear relationship between regional and local species richness for river-dwelling mussels, while Heino *et al.* (2003) detected regional species richness as the most influential variable contributing to local species richness. However, it is far from clear whether regional species richness consistently sets the limits to local species richness, or vice versa (Vinson & Hawkins 1998). We may consider the relationship between regional and local species richness as a feedback system where they influence each other. On the one hand, regional species richness sets the upper limit for local species richness; on the other hand, regional species richness is adapted to decrease or increase of local species richness. This implies that the regional species pool is sequentially reduced by environmental filters, which include disturbance regime, dispersal barrier, habitat condition, and biotic interaction (Tonn *et al.* 1990). Each filter operates at a distinctive spatiotemporal scale and leads to a characteristic species community.

Implications for conservation and management

River corridors are among the most threatened ecosystems world wide (Malmqvist & Rundle 2002; Tockner & Stanford 2002). In Europe, for example, ~90% of all former floodplains disappeared or are functionally extinct (Hughes 2003). Nowadays, restoration is a major issue in river management. However, a high proportion of restoration projects fail, mainly because of a fundamental lack of understanding of principal mechanisms that create and maintain biodiversity and biocomplexity along river corridors. Lateral habitats are among the first habitats that disappear as a consequence of river regulation and flow control. Since overall river biodiversity is strongly enhanced by the lateral habitat diversity (see: Figure 5), the formation and rejuvenation of ponds and backwaters needs to be promoted by restoration projects. Furthermore, we also need to more thoroughly understand the importance of tributary confluences as important ecological nodes along river corridors (see Benda *et al.* 2004). Tributaries and their intersections with the main channel may be critical for the resilience of entire river corridors.

At a regional scale, flood disturbance is a key factor promoting biodiversity (Pollock 1998). At a local scale, parafluvial ponds are often associated with dead wood and vegetated islands (Gurnell & Petts 2002; Karaus *et al.* 2005). Hence, dead wood and islands are expected to enhance aquatic habitat diversity (Arscott *et al.* 2000). Furthermore, biodiversity along the three river corridors was strongly nested and hierarchical. This is important since restoration has primarily focused on the reach scale or on individual species and habitats. Clarke (2003) proposed an eco-hydromorphic approach for restoration, which is based on the principle that both morphological and ecological components are closely interlinked and that channel form, system functioning, and species composition result from these interacting processes. A better understanding of the ecology and functioning of lateral aquatic habitats will therefore, support successful river restoration.

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APPENDIX

Table 1. Distribution (total abundance) of EPT-taxa along the three river corridors (mc=main channel, p=pond, bw=backwater, t=tributary). For further explanation see text.

	Tagliamento				Thur				Rhône				
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	Sum
Ephemeroptera													
Baetis alpinus Pictet			3	16				1531				4322	**5872**
B. lutheri Mueller-Liebenau								48				35	**83**
B. muticus Linné			1	2				45					**48**
B. rhodani Pictet			84	114			18	337	138			585	**1276**
B. vernus Curtis			4					99					**103**
Baetis sp. 6	896	3	98	3	2544		19	568	1877		3	362	**6373**
Caenis luctuosa Burmeister			1				15						**16**
C. rivulorum Eaton			4				11						**15**
Caenis sp. 3			1		7	3	27						**38**
Centroptilum luteolum Mueller	8	34	87				1	5					**135**
Centropilum sp. 2					2	8							**10**
Cloeon dipterum Linné					49	52							**101**
Cloeon sp. 2		4											**4**
Ecdyonurus helveticus Eaton												9	**9**
E. picteti Meyer-Dür			3									5	**8**
E. torrentis Kimmins							1	6					**7**
E. venosus Eaton			4	2			7	4					**17**
E. zelleri Eaton			6										**6**
Ecdyonurus sp. 6	679		62	56	76	6	73	14	36			63	**1065**

	Tagliamento				Thur				Rhône				
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	Sum
Electrogena sp.	4	4			3								**11**
Epeorus assimilis Eaton				1				1					**2**
Epeorus sp. 2					65								**65**
Ephemera danica Müller			4			9	1						**14**
Ephemerella ignita Poda	11		1					6					**18**
Ephemerella sp. 2								6					**6**
Habroleptoides confusa Sartori & Thomas	3	2	9	2			5	21					**42**
Habroleptoides sp. 2					4	1							**5**
Habrophlebia lauta Eaton			2				16	6					**24**
Habrophlebia sp. 2					11	11							**22**
Heptageniidae					4						1	39	**44**
Heptagenia sp.	25	367			13				1			32	**438**
Leptophlebiidae			2	1									**3**
Paraleptophlebia sp.					2	1							**3**
Rhithrogena gratianopolitana Sowa, Degrange & Sartori												11	**11**
R. *hybrida* Eaton				7			1	1					**9**
R. *landai* Sowa & Soldán				4									**4**
R. *semicolorata* Curtis				5			32	52					**89**
Rhithrogena sp. 5	5		1	13	677	14	11	93	96			36	**946**
Serratella sp.					28								**28**
Siphlonurus lacustris Eaton			6874	1			18	64					**6957**
Siphlonurus sp. 2	4	56	148		1	459	78	3					**749**

	Tagliamento				Thur				Rhône				
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	Sum
Plecoptera													
Amphinemura sp.	11	4	4	82	56	6	37	26					**226**
Brachyptera risi Morton								5					**5**
B. trifasciata Pictet												2	**2**
Brachyptera sp. 3	9				2								**11**
Chloroperlidae					2				1				**3**
Chloroperla sp.	385	23	64	1	69	33	16	5	1			2	**599**
C. tripunctata Scopoli			34				73	1					**108**
Dictyogenus alpinum Pictet												4	**4**
D. fontium												2	**2**
Dictyogenus sp. 3									11				**11**
Dinocras megacephala Klapalek								2					**2**
Dinocras sp. 2					19	5	5		1				**30**
Isoperla grammatica Poda			1				34	11					**46**
I. lugens Klapálek												124	**124**
I. rivulorum Eaton							4	31			2	74	**111**
Isoperla sp. 3	6	1	2	2	19	9	2	6	41		1	2	**91**
Leuctra alpina Kühtreiber												1	**1**
L. braueri Kempny				1								27	**28**
L. inermis Kempny			1				8	3			93	77	**182**
L. leptogaster/major			29										**29**
Leuctra sp. 5	242	57	85	15	712	293	344	767	1489		3	2661	**6668**

	Tagliamento				Thur				Rhône				
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	Sum
Nemouridae								71				621	**692**
Nemoura marginata Pictet				1									**1**
N. mortoni Ris								1				17	**18**
Nemoura sp. 3	13		14	45	33		5	11	21			82	**224**
Nemurella pictetii Klapalek												46	**46**
Perla grandis Rambur							1	1				1	**3**
Perla sp. 2	2		11		5			3					**21**
Perlidae			1										**1**
Perlodes intricatus Pictet												1	**1**
Perlodes sp. 2					1	1		1	3				**6**
Perlodidae					1								**1**
Protonemura lateralis Pictet												11	**11**
P. nimborum Ris												3	**3**
Protonemura sp. 2	52		4	15	53	1		32	111			1734	**2002**
Rhabdiopteryx alpinus Kühtreiber								1					**1**
R. neglecta Aubert				2									**2**
Rhabdiopteryx sp. 3	9				17				11			99	**136**
Siphonoperla torrentium Pictet							2						**2**
Siphonoperla sp. 2								14				4	**18**
Xanthoperla sp.	1												**1**
Trichoptera													
Agapetus ochripes Curtis								7					**7**

	Tagliamento				Thur				Rhône				
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	Sum
Allogamus auricollis Pictet	4				33		2	2	3168	1	95	137	**3442**
Annitella obscurata McLachlan					1								**1**
Anabolia nervosa Curtis						5							**5**
Athripsodes albifrons Linnaeus					158	3							**161**
Athripsodes sp.							1	15					**16**
Beraeamyia squamosa Mosely	1	1											**2**
Ceraclea dissimilis Stephens					1								**1**
Chaetopterygini/Stenophylacini								3					**3**
Chaetopteryx major McLachlan		2											**2**
C. villosa oder fusca						1							**1**
Crunoecia irrorata Curtis												1	**1**
Cryptothrix nebulicola McLachlan												6	**6**
Cyrnus trimaculatus Curtis			1			1	1						**3**
Drusus biguttatus Pictet					13			1	1			45	**60**
D. discolor Rambur												39	**39**
Drusus sp. 3									2				**2**
Glossosoma conformis Neboiss								15				1	**16**
Halesus digitatus/tesselatus			2		1								**3**
H. rubricollis Pictet					1	2						59	**62**
Holocentropus dubius Rambur					3								**3**
Hydropsyche angustipennis Curtis	2				2								**4**
H. dinarica Marinkovic	6											2	**8**

	Tagliamento				Thur				Rhône				
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	Sum
H. fulvipes Curtis	1												**1**
H. guttata Pictet	4												**4**
H. incognita Pitsch	2							2					**4**
H. instabilis Curtis	8		5	1	8				1			4	**27**
H. pellucidula Curtis	3		1		2								**6**
H. siltalai Döhler					54			7					**61**
H. tenuis Navas				4									**4**
Hydropsyche sp. 10	11		1	6	32			49				2	**101**
Hydroptila martini Marshall			36										**36**
H. sparsa Curtis								312					**312**
Hydroptila sp. 3	75	68	11		59		315	77					**605**
Hydroptila vectis Curtis								1					**1**
Lepidostoma hirtum Fabricius			3		9		2	1					**15**
Limnephilinae			1	2	3		3	1		2		13	**25**
Limnephilus affinis oder incisius						1							**1**
L. auricula Curtis						2							**2**
L. decipiens Kolenati						1							**1**
L. lunatus Curtis		1	1			3							**5**
Limnephilus sp. 5								1					**1**
Lithax niger Hagen												2	**2**
Lype phaeopa Stephens									1				**1**
Lype sp. 2								1					**1**

	Tagliamento				Thur				Rhône				
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	Sum
Melampophylax mucoreus Hagen					1								**1**
Metanoea rhaetica Schmid					5							2	**7**
Metanoea sp. 2								5					**5**
Micrasema morosum McLachlan				1									**1**
Mystacides azurea Linne						1							**1**
Mystacides sp.	2												**2**
Odontocerum albicorne Scopoli					1								**1**
Oecetis sp.						11		1					**12**
Parachiona picicornis Pictet												1	**1**
Philopotamus ludificatus McLachlan								2				18	**20**
Plectrocnemia sp.			1	4				4					**9**
Polycentropus excisus Klapalek	5	11	24	13									**53**
P. flavomaculatus Pictet		1			2	11	7	2					**23**
Potamophylax cingulatus/latipennis/luctuosus			2	2				3				15	**22**
Potamophylax sp. 2	4	1			1			1	2				**9**
Psychomyia pusilla Fabricius					10		1	25					**36**
Ptilocolepus granulatus Pictet												7	**7**
Rhyacophila dorsalis McLachlan								29					**29**
R. *glareosa* McLachlan												3	**3**
R. *hirticornis* McLachlan									2				**2**
R. *intermedia* McLachlan									1			1	**2**
R. *pubescens* Pictet								4					**4**

	Tagliamento				Thur				Rhône				
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	Sum
Rhyacophila s. str. sp.	83		2	26	73	1	3	62	1			11	**262**
R. *torrentium* Pictet	2		1						23			67	**93**
R. *tristis* Pictet				2	6			5				3	**16**
Sericostoma personatum Kirby & Spence	1							7					**8**
S. flavicorne Schneider			1		5	1							**7**
Sericostoma sp. 3												8	**8**
Silo piceus Brauer						1							**1**
Stenophylax vibex Curtis					4								**4**
Tinodes dives Pictet								5					**5**
Tinodes sp. 2								1					**1**
Wormaldia copiosa McLachlan	44											6	**50**
Sum	**2623**	**640**	**7742**	**452**	**4963**	**957**	**1200**	**4553**	**7040**	**3**	**198**	**11547**	**41918**

CHAPTER 6

GENERAL CONCLUSIONS

In the past, rivers were mostly discussed as being either a single channel of flowing water or as the main channel plus the flood plain. During the last decade, research has emphasized the interdependence and perhaps equally integral functioning of the main channel and its adjacent flood plain. However, many patterns and processes regarding river-floodplain systems as holistic units are still not completely understood. Specifically, knowledge about lateral aquatic habitats is limited. The present research focused on the lateral dimension along river corridors.

Aquatic habitats and habitat heterogeneity

The results of the present thesis documented the high contribution of parafluvial ponds, backwaters, and tributaries to overall river habitat diversity. This contribution needs to be emphasized since backwaters and ponds cover only a small portion of the total aquatic surface area (Van der Nat *et al.* 2002). The pulsing of flow in the main channel exerted a major control on parafluvial ponds. Flow pulses resulted in a 'shifting habitat mosaic' mediated by the degree of connectivity between individual ponds and the lotic channel. Both connectivity and fragmentation increase aquatic habitat heterogeneity (Ward *et al.* 1999). Connectivity resets biologically controlled patches, mediates the transfer of energy, matter and organisms between habitat patches, and creates new habitats. Fragmentation results in insular habitats with distinct and locally controlled conditions, and therefore enhances spatial and temporal heterogeneity at the floodplain scale. Ponds differed markedly in their environmental conditions. Therefore, each pond can be regarded as a unique freshwater environment ("concave island"). Large wood and vegetated islands were often associated with ponds. Both structures are assumed to play an active role in enhancing habitat diversity in floodplain rivers by promoting local channel-bed relief, inducing gravel deposition and fine material sedimentation, causing the formation of scour ponds (Gurnell & Petts 2002), and increasing the stability of aquatic habitats (Van der Nat *et al.* 2002). Gurnell & Pett's (2002) hypothesis that highest habitat diversity occurs in island- and bar-braided river segments was supported by our findings along the Tagliamento.

Aquatic habitats and taxa diversity

The results of the present thesis clearly underpin the importance of lateral aquatic habitats for promoting and maintaining biodiversity along active river corridors. The substantial contribution of lateral aquatic habitats to overall biodiversity can be explained as follows:

~ Lateral aquatic habitats increase the overall area of aquatic habitats and therefore the potential number of habitats for colonization.

~ Lateral aquatic habitats increase habitat heterogeneity which enhances environmental complexity and biodiversity (Vinson & Hawkins 1998). In particular, parafluvial ponds with high environmental variability filter species traits and therefore, enhance trait diversity (a surrogate for functional diversity).

~ The patchy nature of habitats (i.e., parafluvial ponds/lateral aquatic habitats) demands to recognize the greater significance of stochasticity in dispersal and habitat colonization during which extinction can occur (Tokeshi 1999). Spatio-temporal stochasticity in dispersal ability and/or habitat colonization keeps species populations at a low level (i.e., high probability of failing to settle successfully on a suitable habitat in the process of dispersal/colonization), and therefore enhances species coexistence and biodiversity.

- The hydrological regime of the semi-natural Tagliamento catchment is dynamic. Hydrological connectivity, mediated by flood and flow pulses, resets biologically controlled patches (e.g., competitive dominants are periodically curtailed and resources are released for inferior species).

Conceptual consideration

Our results support the hierarchical patch dynamics model by Wu & Loucks (1995), which has been applied to lotic ecosystems by Poole (2002) and Thorp *et al.* (in press). In this model, rivers are viewed as patchy discontinua of hierarchically nested and interactive elements. At each scale, individual elements are influenced by the interplay between their context (provided by the encompassing element), the metastructure (i.e., structure, arrangement and juxtaposition of a patch's component elements), and the trans-scale processes that link the structures within the hierarchy (Kay 2000). This view and our results support Hynes' (1975) statement that 'every stream is likely to be individual' and therefore implies the difficulty in predicting the longitudinal progression of environmental and linked biological features (e.g., patterns in biodiversity). However, progressive downstream gradients are observable for some ecosystem attributes such as substrate size and temperature. Several studies proposed geomorphologic and hydrologic characteristics as fundamental properties of rivers (e.g., Rosgen 1994; Church 2002; Thoms & Parsons 2003; Benda *et al.* 2004). Based on these investigations, Thorp *et al.* (in press) suggest dividing the river corridor into hydrogeomorphic patches. These patches result from shifts in hydrologic and geomorphic conditions. Investigations of hydrogeomorphic patch progression along a river corridor would permit predictions of changes in biocomplexity. In conclusion, I agree with Poole's (2002) view that the development of tools and techniques that facilitate a discontinuum view of lotic ecosystems and address both the interactions between streams and their valleys (geomorphologic and hydrologic features) and the unique nature of each lotic ecosystem's patch hierarchy would provide an important step forward in river ecology.

Implications for river restoration and management

Overall, river biodiversity was strongly enhanced by lateral habitat diversity, which requires major consideration in future river restoration and management. Most European rivers and their adjacent flood plains have been altered during the past centuries (e.g., Dynesius & Nilsson 1994). As a consequence, lateral aquatic habitats have almost completely disappeared in European rivers. Therefore, the formation and rejuvenation of lateral aquatic habitats needs to be promoted by restoration projects. Moreover, parafluvial ponds can be used, similar to vegetated islands, as sensitive landscape indicators of the integrity of river corridors.

Flow and flood pulses (sensu Junk *et al.* 1989; Tockner *et al.* 2000) are the main forces maintaining habitat diversity across the active river corridor (Hughes & Rood 2001). The restoration of a natural flow regime with unconstrained flood events as well as large and small water level fluctuations would be an important step to promote more natural rivers and re-create lateral aquatic habitats. Natural flow regimes in combination with the abundance of large wood further affect the formation of vegetated islands (Van der Nat *et al.* 2003). Dead wood and vegetated islands are expected to enhance aquatic (and terrestrial) habitat diversity since they were often associated with lateral aquatic habitats (i.e., ponds and backwaters). This close interdependence among dead wood, islands and parafluvial ponds needs to be considered in river restoration and future management schemes.

Restoration is a major issue in river management. However, a high proportion of restoration projects fail because: (1) there exists a fundamental lack of understanding of the principal mechanisms that create and maintain biodiversity and biocomplexity along river corridors, and (2) restoration has primarily focused on the reach-scale or on individual species and habitats. Since biodiversity along river corridors is strongly hierarchical and nested, a systematic conservation or restoration approach requires whole-catchment planning. The conceptual view of rivers as patchy discontinua of hierarchically nested and interactive elements should therefore be taken into consideration in restoration projects. The eco-hydromorphic approach considers that morphological and ecological components are closely interlinked and that channel form, system functioning and species composition are the result of these interacting processes (Clarke *et al.* 2003).

Perspectives

The research in the present thesis emphasized the complexity of lateral aquatic habitats and biodiversity patterns along river corridors. However, research on lateral aquatic habitats is only beginning. More studies on lateral aquatic habitats are needed to confirm and extend the present findings. In particular, further river systems need to be investigated to detect differences and generalizations of habitat heterogeneity and biodiversity patterns in lateral aquatic habitats. Needs for future research include:

- Comparison of low energy (meandering) and high energy (braided) flood plains to detect differences and/or similarities between temporal community dynamics (e.g., species turnover, community persistence).
- Future research has to focus on dispersal pathways across the flood plain. Riparian forest ponds and aquatic habitats located further from the main channel play a potentially key role and need to be included (see below).
- The potential role of lateral aquatic habitats and riparian forest ponds as flood and drought refugia remains mostly unknown and requires consideration.
- The influence of fishes, amphibians and birds in structuring invertebrate communities in parafluvial ponds and backwaters needs to be investigated.
- The importance of tributaries and tributary confluences as important ecological nodes along river corridors must be further examined. Tributaries

and their intersections with the main channel may be critical for the resilience of river corridors.

- Descriptive research is an important first step to understand ecosystems. However, future research on lateral aquatic habitats needs to apply natural as well as manipulative experiments to complement descriptive research.
- The exchange and co-operation among ecologists, civil engineers and geomorphologists is a pre-requisite for a holistic understanding of river systems and therefore needs to be promoted.

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