Patterns, determinants, and management of freshwater biodiversity in Europe

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Summary

Fresh water is a threatened resource, albeit its unique importance for human well-being. However, independent of human utility considerations, freshwater ecosystems and species have an ethical, intrinsic value of their own. Globally, freshwater ecosystems and their biodiversity are exposed to multiple human stressors, often leading to irreversible alterations of the morphology, hydrology, and ecology of these systems. Understanding human-environment interactions provide insights into the consequences of environmental change on freshwater biodiversity. Such insights play a fundamental role in informing conservation decisions, policy makers and the general public, but also biodiversity related research agendas and policies. Because there are considerable gaps in understanding large-scale spatio-temporal dynamics of freshwater species in response to anthropogenic stressors, in this thesis, I analyzed large-scale freshwater diversity patterns in geographic Europe and evaluated the multifaceted processes that cause biodiversity change. Moreover, I quantified the effects of anthropogenic stressors and natural, geo-climatic drivers on the contemporary patterns of European freshwater biodiversity and evaluated the generality in biodiversity response. Additionally, I analyzed current river basin management strategies – using the Danube River Basin as a case study – in order to support the development and implementation of effective future conservation and management strategies.

A comparison of the European freshwater fish fauna (Chapter 1) of the mid-19th century with the contemporary patterns revealed profound, continent-wide changes in the composition of species assemblages, creating taxonomic homogenization (i.e. increase in similarity of species assemblages) among river catchments. The results allowed appraising the opportunities and limits of the calculation of taxonomic similarity change. Translocated species (i.e. species originating from Europe, but not native to the respective study river catchment) were identified as the main drivers of taxonomic homogenization. Indeed, many translocated species, with a native range above a specific threshold (i.e. number of occupied catchments), immediately contributed to taxonomic homogenization when introduced elsewhere, even if they were introduced to a single new catchment. However, translocated species with a range size below the specific threshold attenuated taxonomic homogenization, as most exotic species (i.e. species originating from outside Europe) did. In contrast to the established view, it became evident that the prevention of intended or unintended species introduction will not lower the rate of taxonomic homogenization per se: many species actually cause taxonomic differentiation despite their range gain, but still considerably contribute to taxonomic change with potential negative effects on ecosystem functions and services.

Variance partitioning of the effects of anthropogenic stressors and natural, geo-climatic drivers on contemporary distribution patterns of European freshwater biodiversity (Chapter 2) revealed that anthropogenic stressors explained a consistently low degree of variation in biodiversity response patterns (i.e. species richness, taxonomic distinctness, endemicity) of the five groups of European freshwater species studied (i.e. fish, odonates, amphibians, birds, molluscs). However, geo-climatic conditions explained a higher proportion of the variation of biodiversity, suggesting a strong influence of geo-climatic gradients on contemporary biodiversity patterns. Geo-climatic conditions primarily affected species with specialized habitat use and a restricted range of occurrence, but had minor effects on species with high dispersal capacities. The distinct joint effects of geo-climatic and anthropogenic factors on the variation in biodiversity patterns, and the distinct linkages between socio-economic and natural gradients implied that the geo-climatic conditions are providing the context within which anthropogenic stressors operate. Therefore, a combined analysis of geo-climatic conditions and anthropogenic factors is indispensable to understand biodiversity patterns. In addition to species richness and endemicity, taxonomic distinctness was identified as a useful indicator of biodiversity, as it responded consistently to anthropogenic stressors across several taxonomic groups and at large scale.

Synthesis of information and data on environmental and climate conditions, topography, land use as well as past and contemporary socio-economic and political features of the Danube River Basin (Chapter 3) depicted various large-scale alterations of the nutrient and sediment regime, the morphology and the species composition, with presumably major, adverse consequences for the functioning of river ecosystems in the entire basin. The principal lack of basic information on ecosystem processes, biodiversity and general environmental descriptors as well as the dispersed nature of available information among different institutional levels, scientific institutions and individual scientists were identified as obstacles hindering proper assessment of the environmental status and decision making towards sustainable management. In addition, the conflicts among economic and environmental issues were found to be highly complex, indicating that the management of a transboundary and diverse basin such as the Danube requires the combined efforts of a wide range of disciplines: a balance between use and protection, a better harmonization and improved synergy of presently disparate objectives, and tight links and feedbacks between science and application (Chapter 4). River basin authorities such as the International Commission for the Protection of the Danube River (ICPDR) were identified as important and useful platforms for dialogue and debate of appropriate goals and their implementation, involvement of stakeholders and the public, but also as “translators” of scientific results.

The results of this thesis confirm that most freshwater ecosystems in Europe are far from pristine. Although present scientific knowledge is already sufficient to allow decision makers managing freshwater ecosystems and entire river basins to make competent plans, additional research in better understanding human-environment interactions and predicting the effects of rapid environmental change on the long-term dynamics of freshwater biodiversity is required. Ultimately, further loss of freshwater species and related ecosystem services will only be avoided if tighter synergies among the presently competing targets of e.g. agriculture, food processing, mining industry, navigation, hydro-/thermal power production, flood control and biodiversity conservation are established.

Zusammenfassung

Süßwasser ist, trotz seiner herausragenden Bedeutung für das menschliche Wohlbefinden, eine gefährdete Ressource. Unabhängig von Nutzungen durch den Menschen haben Binnengewässerökosysteme aber auch einen intrinsischen Wert, d.h. dass neben ökonomischen Werten auch ökologische und ethische Aspekte zu berücksichtigen sind. Weltweit sind Binnengewässerökosysteme und deren biologische Vielfalt (im Folgenden: Biodiversität) mannigfaltigem menschlichen Nutzungsdruck ausgesetzt, der in vielen Fällen irreversible Veränderungen der Morphologie, der Hydrologie und der Ökologie dieser Systeme nach sich zieht. Das Verständnis von Wechselwirkungen zwischen Mensch und Umwelt ist unerlässlich, um Erkenntnisse über die Veränderungen der Biodiversität von Binnengewässern in Folge von Umweltveränderungen zu gewinnen. Diese Erkenntnisse stellen eine unerlässliche Basis zur Entwicklung von Strategien zum Schutz der Biodiversität von Binnengewässern dar; sie sind ferner wichtig, um politische Entscheidungsträger und die Öffentlichkeit zu informieren, sowie um geeignete Forschungsprogramme, Richtlinien und Umweltabkommen zu entwickeln. Nach wie vor bestehen allerdings deutliche Wissenslücken insbesondere im Verständnis von großräumigen, d.h. globalen und kontinentalen Dynamiken (räumlich wie zeitlich) von Biodiversitätsmustern in Reaktion auf menschlichen Nutzungsdruck. Daher war es das Ziel meiner Arbeit, gesamteuropäische Verteilungsmuster der Biodiversität (Arten) von Binnengewässern zu analysieren, sowie die vielfältigen Prozesse zu ermitteln und zu beurteilen, die die Änderung der Verteilungsmuster bestimmen. Zudem habe ich untersucht, wie einheitlich die Wirkung verschiedener Einflussfaktoren (d.h. menschlicher Stressoren und natürlicher, geo-klimatischer Bedingungen) auf die Verteilungsmuster verschiedener Faunengruppen ist. Einen weiteren Schwerpunkt meiner Arbeit bildete die Untersuchung von derzeitigen Flussgebietsbewirtschaftungsstrategien. Anhand des Donaueinzugsgebiets als Fallbeispiel habe ich Herausforderungen und Chancen, aber auch Optionen für die Entwicklung und Umsetzung zukünftiger Bewirtschaftungs- sowie Schutzstrategien diskutiert.

Ein Vergleich zeitgenössischer Verteilungsmuster der europäischen Binnengewässerfischfauna mit historischen Verteilungsmustern aus der Mitte des neunzehnten Jahrhunderts (Kapitel 1) zeigte für den gesamten Kontinent tiefgreifende Änderungen in der Zusammensetzung von Artengemeinschaften, die zu taxonomischer Homogenisierung, d.h. einer Zunahme der Ähnlichkeit der Artenzusammensetzung unter den untersuchten Flusseinzugsgebieten, führte. Die Ergebnisse ermöglichten es, Stärken und Schwächen der Ermittlung von Änderungen der taxonomischen Ähnlichkeit einzuschätzen. Es zeigte sich, dass translozierte Arten (d.h. in Europa heimische Arten, die im jeweils untersuchten Flusseinzugsgebiet historisch nicht vorkamen) maßgeblich zur taxonomischen Homogenisierung beitrugen. Eine große Anzahl der translozierten Arten, deren natives Verbreitungsgebiet über einem spezifischen Schwellenwert lag, d.h. deren Verbreitungsgebiet eine bestimmte Anzahl an Flusseinzugsgebieten überstieg, trugen selbst dann zur taxonomischen Homogenisierung bei, wenn sie in nur ein einziges weiteres Einzugsgebiet eingebracht wurden. Im Gegensatz hierzu schwächten translozierte Arten, deren natives Verbreitungsgebiet unter dem spezifischen Schwellenwert lag, sowie auch die meisten exotischen Arten (d.h. Arten, die aus einem Gebiet außerhalb Europas stammen) die taxonomische Homogenisierung ab. Abweichend von der gängigen Sicht wurde deutlich, dass taxonomische Homo-

genisierung sich nicht durch die Verhinderung von beabsichtigtem oder versehentlichem Verschleppen von Arten verringern wird: viele eingeschleppte Arten tragen zu einer taxonomischen Differenzierung bei, trotzdem sie in ihrem durch die Verschleppung vergrößerten Verbreitungsgebiet die Artenzusammensetzung ändern, was wiederum negative Auswirkungen auf das Funktionieren von Ökosystemen und auf Ökosystemleistungen haben kann.

Die Varianz-Partitionierung von Auswirkungen menschlicher Stressoren und natürlicher, geo-klimatischer Faktoren auf aktuelle Verteilungsmuster der Biodiversität der Binnengewässer in Europa (Kapitel 2) zeigte, dass menschliche Stressoren einen durchgehend niedrigen Anteil der Variation in den Mustern der Biodiversität (bezüglich Artenreichtum, taxonomischer Verschiedenheit und Endemismus) der untersuchten Binnengewässerfauna (d.h. Fische, Libellen, Amphibien, Vögel, Mollusken) erklären. Dagegen erklärten geo-klimatische Faktoren einen höheren Anteil an der Varianz in den Mustern der Biodiversität, was auf einen hohen Einfluss von geo-klimatischen Gradienten auf die Biodiversität schließen lässt. Geo-klimatische Bedingungen wirkten sich besonders stark auf Arten mit kleinem Verbreitungsgebiet und speziellen Lebensraumansprüchen aus, zeigten jedoch einen geringen Effekt auf Arten mit großem Verbreitungsgebiet. Vor allem die ermittelten gemeinsamen Effekte von geo-klimatischen und menschlichen Faktoren auf die Variation in den Verteilungsmustern der Biodiversität, sowie die ausgeprägten Zusammenhänge zwischen sozio-ökonomischen und natürlichen Gradienten, legten den Schluss nahe, dass geo-klimatischen Faktoren den Kontext liefern, innerhalb dessen menschliche Stressoren wirken. Daher ist eine kombinierte Analyse von geo-klimatischen Bedingungen und menschlichen Stressoren unumgänglich, um Verteilungsmuster der Biodiversität zu verstehen. Zusätzlich zum Artenreichtum und zum Endemismus hat sich die Ermittlung der taxonomischen Verschiedenheit als ein nützlicher Biodiversitätsindikator erwiesen, da diese Auswirkungen menschlicher Stressoren über Faunengrenzen hinweg kohärent und auf kontinentaler Ebene anzuzeigen vermag.

Das Zusammenstellen von Informationen und Daten zu natürlichen Charakteristika wie Klima und Umwelt, zur Hydrologie und Landnutzung, sowie historischen als auch gegenwärtigen sozioökonomischen und politischen Besonderheiten des Donaueinzugsgebiets (Kapitel 3) verdeutlichte die vielfältigen, großräumigen Veränderungen des Nährstoff- und Sedimenthaushalts, der Morphologie und der Artenzusammensetzung, mit vermutlich weitreichenden, nachteiligen Konsequenzen für die Funktionsfähigkeit von Ökosystemen im gesamten Einzugsgebiet. Das prinzipielle Fehlen grundlegender Informationen bezüglich ökosystemarer Prozesse, der Artenvielfalt wie auch allgemeiner Umweltdeskriptoren, aber auch die Zersplitterung verfügbarer Informationen auf verschiedene institutionelle Ebenen, wissenschaftliche Institute und einzelne Wissenschaftler erwiesen sich als Hindernisse bei der Ermittlung des Umweltzustandes wie auch der Entscheidungsfindung im Rahmen nachhaltiger Flussgebietsbewirtschaftung. Zudem erwiesen sich die Zielkonflikte zwischen wirtschaftlichen Interessen und ökologischen Aspekten als vielschichtig, was verdeutlichte, dass die Bewirtschaftung eines mehrfach grenzüberschreitenden und derart internationalen und facettenreichen Einzugsgebietes wie der Donau der vereinten Bemühungen vieler Disziplinen bedarf: einer Balance zwischen Nutzung und Schutzmaßnahmen, einer verbesserten Harmonisierung und stärkeren Synergien gegenwärtig unvereinbarter Zielvorstellungen, sowie einer engeren Zusammenarbeit und Rückkopplung zwischen Wissenschaft und Anwendung (Kapitel 4). Flussgebietsverwaltungen, wie zum Beispiel die Internationale Kommission zum Schutz der Donau (IKSD), wurden als wichtige und nützliche Plattformen identifiziert, um geeignete Zielvorstellungen und deren Umsetzung abzustimmen, Interessensgruppen und die Öffentlichkeit einzubinden, und zudem als „Übersetzer“ von wissenschaftlichen Ergebnissen zu dienen.

Die Ergebnisse meiner Arbeit bestätigen, dass die meisten europäischen Binnengewässer und deren Ökosysteme stark durch menschliche Eingriffe überformt sind. Obwohl der gegenwärtige Stand der Forschung ausreicht, um Entscheidungsträger einzelner Ökosysteme und auch ganzer Flussgebiete kompetent zu beraten, besteht weiterer Forschungsbedarf, um die Wechselwirkungen zwischen Mensch und Umwelt besser zu verstehen, und ferner, um Auswirkungen sich rasch ändernder Umweltbedingungen auf die langfristigen Dynamiken der Biodiversität von Binnengewässern zu prognostizieren. Letztendlich wird ein weiterer Verlust der Biodiversität von Binnengewässern und zugehörigen Ökosystemleistungen nur zu verhindern sein, wenn es gelingt, Synergien zwischen derzeit divergierenden Zielvorstellungen von Sektoren wie Landwirtschaft, Nahrungsmittelindustrie, Bergbau, Schifffahrt, Wasser- und Wärmekraftnutzung, Hochwasser- und Biodiversitätsschutz zu stärken.

Introduction

In 1992 in Rio de Janeiro, Brazil, the United Nations Conference on Environment and Development universally acknowledged the importance of biodiversity leading to the "Convention on Biological Diversity" (CBD[1]). The CBD came into force in 1993 with the following objectives: "The conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources, including by appropriate access to genetic resources and by appropriate transfer of relevant technologies, taking into account all rights over those resources and to technologies, and by appropriate funding" (GBO 3, 2010). There are currently 196 Parties to the CBD.

In line with the rationale of the CBD, many environmental laws (e.g. the "Habitats Directive"[2] of the European Council) and Agendas have been set in place, including the commitment of the Parties to the CBD to "achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level as a contribution to poverty alleviation and to the benefit of all life on Earth" (COP 6 Decision VI/26[3], Balmford *et al.* 2005). Despite the fundamental importance of biodiversity, this target not been met (GBO 3, 2010). In order to halt the global loss of biodiversity and to ensure that by 2020 ecosystems are resilient and continue to provide essential services, the parties to the CBD have adopted the "Strategic Plan for Biodiversity 2011-2020" (COP 10 Decision X/2[4]). This agreement on an ambitious and comprehensive roadmap for global biodiversity policy is a strong signal which helped to stimulate important action to safeguard biodiversity. At the international level, but also in the European Union, progress has been made in developing mechanisms for research, monitoring and scientific assessment of biodiversity (GBO 3, 2010). The Strategic Plan states that "the generation of scientific information and the development of indicators relating to biodiversity functioning, status and trends should be promoted and improved, since insufficient scientific information for policy and decision making is an obstacle for the implementation of the CBD".

However, the fact that biodiversity is highly dynamic in space and time is scientifically challenging, since analyzing and understanding patterns of biodiversity and its changes requires studies of often intertwined abiotic and natural processes that moreover act on several spatial and temporal scales.

In the following paragraphs I highlight general characteristics of biodiversity, and the drivers of distribution patterns and dynamics, with a special focus on freshwater ecosystems, since freshwater species are consistently more threatened than their terrestrial counterparts (e.g. Proença and Pereira 2013, Collen *et al.* 2014). I also discuss the significance of in depth analyses of spatial distribution patterns. The knowledge and also the understanding of the processes determining the spatio-temporal dynamics of freshwater species is central to many basic questions in macroecology and conservation biology such as the origin of species or the prioritization of areas for conservation (Orme *et al.* 2006, Collen *et al.*

[1] http://www.cbd.int (verified 18.10.2015)

[2] http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:31992L0043:EN:HTML (verified 18.10.2015)

[3] https://www.cbd.int/decision/cop/default.shtml?id=7200 (verified 18.10.2015)

[4] https://www.cbd.int/decision/cop/?id=12268 (verified 18.10.2015)

2014). The understanding of spatio-temporal dynamics is also needed to inform policy makers, other stakeholders, and the general public, and to design biodiversity-related policies and research agendas. I conclude with the presentation of my research goals.

Concept and definitions of biodiversity

Both, biodiversity-related phenomena and the underlying mechanisms have fascinated ecologists for a long time, but foundations for modern biodiversity research only developed in the 1960s and 1970s (Barthlott *et al.* 2009). Likewise, the term "biodiversity" is relatively recent. Thomas Lovejoy was the first to use "biological diversity" in 1980 (Lovejoy 1980). In 1988, the American Natural Research Council published the book "Biodiversity" (Wilson 1988). However, it was not until 1992, with the launch of the CBD, that the term "biodiversity" left the scientific arena and was introduced to a general audience, such as decision makers and the general public. Nowadays biodiversity is often used synonymously with species richness, but the term encompasses much more; as clearly defined by the CBD: "Biological diversity means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems" (CBD, Article 2). Thus, the definition includes multiple levels of life on earth: it refers to the diversity within species as well as functional interdependences among the genetic, organismic and ecosystem level. Biodiversity is not just something scientists can quantify to inform them about the status of an ecosystem, but is also a strategic concept for the conservation and sustainable use of natural systems and can be used to represent overall naturalness or intactness of life on Earth (Fischer and Young, 2007).

In my research I addressed compositional (structural), functional (trait) and phylogenetic aspects of biotic assemblages. I used presence/absence data of species and calculated the species richness, i.e. I determined whether a species occurs at a location or not and quantified the distribution of species within a community. I also assessed whether the species are endemic (have a restricted range), threatened (vulnerable of endangerment in the near future), translocated (European species introduced beyond its native distribution range) or exotic (species coming from outside Europe). In one study (Chapter 2) I quantified the proportion of endemic species in an assemblage ("endemicity" based on Crisp *et al.* 2001 and Linder 2001) and also the average phylogenetic relatedness of species in an assemblage ("taxonomic distinctness" according to Pienkowski *et al.* 1998, Clarke and Warwick 1999). In another study (Chapter 1), I quantified how the similarity in species composition of river catchments has changed over time (in- or de-crease in similarity, which corresponds to "taxonomic homogenization" or "taxonomic differentiation", respectively; Legendre and Legendre 1998, Koleff *et al.* 2003), assessed the relative species turnover over time via a newly developed index, and collected information on the body size of some species.

Biodiversity patterns, dynamics and extinction rates

Several concepts focus on the potential causes of variation of biodiversity patterns. The landscape filter concept (Poff 1997) explains the structure of communities at different spatial scales being determined by different environmental or landscape filters; these filters restrict which species "fit" and are able to pass the filters (in a certain abundance) based on their traits. Other concepts frequently applied in macro-ecological studies highlight the influence of natural drivers such as (i) area/habitat heterogeneity, (ii) climate/energy and (iii) history (e.g. Pearson and Boyero, 2009, Oberdorff *et al.* 2011, Leprieur *et al.* 2011). Area/habitat heterogeneity refers to the positive relationship between the species richness and size as well as the habitat heterogeneity of a given ecosystem. It assumes that the larger and more diverse an ecosystem is, the higher its biodiversity, due to area-dependent species speciation and extinction rates (Mac Arthur and Wilson 1967, Guégan *et al.* 1998, Losos and Schluter 2000, Davies *et al.* 2006). Temperature, precipitation and evapo-transpiration influence the amount of energy available in a system. This energy determines available resources for e.g. primary production but also controls and supports the physiological limits of species (Wright 1983, Turner 1987, Hawkins *et al.* 2003, Evans *et al.* 2005, Mittelbach *et al.* 2007, Field *et al.* 2009). Major historical events such as the retreat of the glaciers of the Pleistocene until about 10 000 years ago and the degree of maturity of systems which has been reached via recolonization since such events are assumed to continue shaping patterns of contemporary species richness (Whittaker 1977, Mittelbach *et al.* 2007, Reyjol *et al.* 2007, Araújo *et al.* 2008, Leprieur *et al.* 2011, Baselga *et al.* 2012, Tisseuil *et al.* 2012).

Moreover, legacy effects of long-lasting but also abandoned land use practices continue influencing current environmental conditions and contemporary biodiversity patterns (Harding et al 1998). Additionally, anthropogenic stress impacts natural biodiversity patterns (MEA 2005, Dudgeon *et al.* 2006, Vörösmarty *et al.* 2010, Feld *et al.* 2014). Anthropogenic stress intensity varies regionally and multiple stressors act in a synergetic, antagonistic or additive way on biodiversity. Furthermore, climate change will continue to change local and regional biodiversity (e.g. Walther *et al.* 2002, Parmesan and Yohe 2003).

Regardless of the concept employed to explain biodiversity, biodiversity is constantly changing due to natural and human drivers (Magurran and Dornelas, 2010). Species extinction and formation are natural processes. Analyses of fossils are able to mirror the evolution and the in- and de-crease of taxonomic diversity over time. Species disappearance has occurred recurrently at a constant low rate through geological time, with relatively long periods of stability alternating with short-term extinction events. Mass extinctions (defined as the loss of at least 75% of all existent species within a limited time interval at the geological scale) have, in contrast, been rare events in Earth's history, which interrupted the natural, background rate of extinction.

Despite large uncertainty due to data restrictions and differences in the criteria of assessments, there are explicit signs that the scope and rate of species loss we are facing today is human driven with a unprecedented decrease of two orders of magnitude higher than the background extinction rate (Jenkins 2003, Naiman and Dudgeon 2011, Proença and Pereira 2013). Systems can tolerate higher-than-background extinction rates for some time, although it is unknown what levels or types of biodiversity loss may possibly trigger non-linear or irreversible changes to the Earth system (Steffen *et al.* 2015).

Valuing biodiversity

Ecosystems produce services which are critical to human well-being, such as pollination of crops, carbon sequestration, nutrient cycling or water supply. The estimated economic values of ecosystem services critical to human welfare reach at least twice the global gross national product; freshwater systems account for about half of this value (MEA 2005, Costanza 2014 and references therein). Loss of biodiversity could greatly reduce the services that humans obtain from ecosystems (MEA 2005). The planetary boundaries framework, which aims to define a safe operating space for humans based on intrinsic biophysical processes that regulate the stability of the Earth system, identified the loss of biodiversity components at global and large ecosystem levels as an important control variable and core boundary (Biodiversity Intactness Index, BII, Scholes and Biggs 2005, Steffen *et al.* 2015). If biodiversity is substantially changed in its integrity, it is expected to undermine the resilience of the Earth system as a whole (Mace *et al.* 2014, Steffen *et al.* 2015). The planetary boundary concept, its definitions as well as the proposed boundaries are subject of intense scientific debate, since there is still limited insight into the relationship between species richness, ecosystem processes and related services. For example, it is unclear how much biodiversity should be retained for securing ecosystem functions and services (Dudgeon 2010, Brook *et al.* 2013, Proença and Pereira 2013). Recently published reviews show that the biodiversity-ecosystem processes relationship is mostly studied in experimental set-ups, which are too simplistic and conducted over too short time spans to allow translation to the real world (Mace *et al.* 2014). However, although the causalities between pressures and biodiversity loss as well as between biodiversity and ecosystem functions are not yet well established, it is evident that environmental conditions often change rapidly and in unanticipated ways. It may therefore be the case that in future, species and their functional traits that may seem complementary or redundant now, may be needed to guarantee ecosystem functions in a changing environment (Vörösmarty *et al.* 2010, Allan *et al.* 2011, Isbell *et al.* 2011). The protection of those species would be in line with the precautionary principle, a management concept which aims to inform decisions under uncertainty (Alcamo *et al.* 2003).

Independent of economic evaluations and human utility considerations, species and natures do have an ethical, intrinsic value of their own (e.g. The UN World Charter for Nature 1982[5], CBD, Naiman *et al.* 2002).

Importance and unique features of freshwater ecosystems and its biodiversity

Freshwater is one of the most essential natural resources and freshwater ecosystems are used by humans for as long as we have existed as a species, e.g. for extraction of drinking and irrigation water and minerals, waste disposal, transportation, power production, harvest of plants, fish, game and sites for settlements, farms and industries (Strayer and Dudgeon 2010, Kummu *et al.* 2011).

Freshwater ecosystems such as rivers, lakes, ponds, groundwaters and wetlands are mosaic or linear elements of the landscape equivalent to landscape elements like fields, forest, roads or cities (Wiens 2002). But freshwater ecosystems are unique. They are highly dynamic: they expand, contract and vary in patch composition and configuration in response to changes in hydrologic flow regimes which results in fast succession (Malard *et al.* 2002). As the lowest topographic points of a landscape they collect and integrate processes of the catchment they are located in (landscape “receivers”) and as such they are functional parts of surrounding landscapes to which they are connected by flows, exchanges of materials, organisms, or energy (Hansen and di Castri 1992, Wiens 2002, Dudgeon *et al.* 2006). Moreo-

[5] http://www.un.org/documents/ga/res/37/a37r007.htm (verified 18.10.2015)

ver, flowing waters are "transmitters": they convey materials (water, dissolved and particulate matter) to downstream areas and are affected by upstream processes (Ward 1989).

The insular nature of freshwater habitats has led to the evolution of many species with a small geographic range, often encompassing only a single lake or catchment (Strayer and Dudgeon, 2010). This high endemism results in high species turnover (β-diversity) among lakes or catchments (Revenga *et al.* 2005, Dudgeon *et al.* 2006). The features listed above explain why freshwaters are so productive and why their biodiversity is richer than would be expected from the area covered by freshwater habitats. Inland water covers just 0.8% of the Earth's surface area (areal extent is likely to be higher if all sizes of freshwater systems and wetlands are considered), but they contain about 10% of all known animal species and 1/3 of all vertebrate species (Balian *et al.* 2008, Downing 2009, Strayer and Dudgeon 2010 and references therein). But high endemism does not only contribute to high species diversity; it is also an indicator of species with a reduced ability to migrate across the landscape and to re-establish extirpated local populations.

Thus, features responsible for high freshwater biodiversity entail its vulnerability.

Anthropogenic threats to freshwater ecosystems and its biodiversity – global and European facts and figures

Freshwater ecosystems are among the most threatened ecosystems, their biodiversity is declining even more rapidly than in terrestrial systems (Loh *et al.* 2005, Dudgeon *et al.* 2006, Darwall *et al.* 2009, Collen *et al.* 2014).

Freshwater ecosystems are not only vulnerable as described above but are also exposed to a complex mixture of human stressors. Humans capture significant proportions of freshwater runoff, trap sediments, fragment rivers, cause eutrophication and pollution, overexploit fish, introduce intentionally or accidentally non-native species and cause qualitative and quantitative losses of riparian zones and freshwater habitats (Tockner *et al.* 2009). As a consequence, humans have transformed the global water cycle and freshwater ecosystems and also the physical, biogeochemical and biological processes of freshwater. This transformation has taken place to an extent that not only compromises the value of freshwater as a habitat for organisms but also for human resource use and development needs (Dudgeon *et al.* 2006, Alcamo *et al.* 2008, Vörösmarty *et al.* 2010).

In Europe, deforestation of floodplains, wetland drainage and early agriculture were the first modifications to rivers about 6000 years ago; followed by human activities such as alterations of channels, small dams, and river bank protection. Large dams started to spread in the 20th century (Benke 2009). Today, few European rivers are free-flowing, and about 50% of the primary wetlands and 95% of the riverine floodplains are lost (Tockner *et al.* 2009). According to Europe's first River Basin Management Plans (RBMPs), 56% of European rivers, 44% of lakes, and 25% of groundwater bodies failed to achieve the "good" status targets of the Water Framework Directive (WFD). Assessments for the IUCN Red List indicate 44% of European freshwater molluscs and 37% of fish species as threatened (Freyhof and Brooks 2011). While the role of single stressors such as strong organic pollution and acidification of freshwaters are declining and currently affect just 14% and 10% of river water bodies, respectively, Europe's water bodies and water resources are now affected by a complex mixture of stressors resulting from urban and agricultural land use, hydropower generation and climate change (Hering *et al.* 2015 and references therein). The relevance of multiple stressors differs regionally: in Alpine and upland Northern regions hydropower plants have fundamentally changed river and lake hydrology, morphology, sediment transport and connectivity, in the lowland areas of Northern and Central Europe intensive agriculture and flood protection are important drivers of degradation, whilst Mediterranean catchments are impaired by riparian degradation and water scarcity and transitional and coastal waters are affected by eutrophication, pollution, morphological changes and different resource exploitation (Hering *et al.* 2015). In addition, climate change increases the risk of floods, erosion and pollution in wet regions and of droughts in water scarce regions; moreover new pollutants, emerging pathogens, exploitation of the sub-surface for alternative forms of energy, and intensified land use in order to meet biofuel demands might amplify threats (Hering *et al.* 2015 and references therein).

Interactions of these threats or stressors are complex and difficult to predict, and climate change might boost their consequences and also the risk of species extinction. Again, it is the insular nature of freshwater habitats which often make adaptations to climate change by way of compensatory movements into cooler habitats (i.e. northwards or upwards migration) impossible, especially for the many entirely aquatic species that cannot move through the terrestrial landscape (Dudgeon 2007, Dudgeon *et al.* 2011). Even flying insects and amphibians might find their dispersal opportunities limited in human-dominated environments (Dudgeon *et al.* 2011).

Assessment, management, and conversation of freshwater biodiversity – the importance of scale and spatial grain

Conservation priorities and resource allocation frameworks have largely ignored freshwater biodiversity and its ecosystems until most recently, despite the disproportionately high contribution of freshwater ecosystems to overall biodiversity and associated services as well as the significant threats freshwaters are facing. This is mainly because global and European biodiversity assessments have so far rarely included freshwaters (Balmford *et al.* 2005, Holland *et al.* 2012). As a consequence, there is a limited availability of robust data on the status, the distribution and the change of the word's freshwater habitats and species (Balian *et al.* 2008). Knowledge on how (often rapid) changes in biodiversity can be influenced and even reversed is often not available for decision making (Revenga and Kura 2003, Collen *et al.* 2014). Compilations of species inventories or the designation of protected areas require high-quality spatial data regarding patterns of freshwater biodiversity and threat (Garcia-Moreno *et al.* 2014). One of the tools that aim to improve this deficit is the "European Union biodiversity strategy to 2020" with its call for "Mapping and Assessment of Ecosystems and their Services (MAES)" (Action 5 of (2011/2307(INI)[6]). Such efforts are important because analyses suggest that terrestrial and freshwater hotspots rarely overlap (Darwall *et al.* 2011) and moreover the methodology for prioritization of freshwater sites is less developed than for terrestrial and marine systems (Holland *et al.* 2012 and references therein).

Global threats have become a major research area for freshwater scientists in recent decades. In a summary of 368 scientific articles on freshwater biodiversity research published between 2000 and 2010,

[6] http://www.europarl.europa.eu/meetdocs/2009_2014/documents/envi/pr/887/887447/887447en.pdf (verified 18.10.2015)

Stendera *et al.* (2012) highlighted the urgent need for comprehensive large-scale studies in order to gain deeper insights into global and continental biodiversity patterns and ecosystems functioning, a prerequisite for more holistic conservation measures. However, the need for large-scale studies is contrasted by the implementation of mainly small scale experimental studies over short-time periods (Kareiva and Andersen 1988). Albeit studies at both, large- and small-scale, are needed to separate local from regional factors influencing local biodiversity, this mismatch is of concern, since it is increasingly recognized that small scale experiments are impacted by landscape effects and large scale processes (Cooper *et al.* 1998, Bonada *et al.* 2008, Leprieur *et al.* 2008) and results of small scale studies are therefore influenced by a mostly unknown fraction of broad scale effects. Moreover, effects and processes change with scale which hampers the extrapolation of results to broader scales and vice versa. This can lead to situations in which the scale on which management is applied differs from the scale on which ecological information that is supposed to inform such management is collected (Wiens 2002 and references therein).

Adequate scientific studies at different spatial scales and grains as well as the communication of their results, e.g. via tight feedbacks between science and the society, are a prerequisite for consistent policy objectives (Bloesch 2005, Eberhard *et al.* 2009). These policies are urgently needed in order to reverse the alarming trends of freshwater biodiversity loss and to protect ecosystems and their freshwater biodiversity on the long-run.

In my research (Chapters 1 and 2) I used river catchments as the spatial unit to explore the factors and processes shaping patterns of freshwater biodiversity. Boundaries of river catchments represent ecologically defined units, within these units there is a high degree of connectivity between habitats and environment parameters (Tisseuil *et al.* 2012 and references therein). River catchments form a kind of "biogeographical islands", i.e. they are, to a certain extent, independent (Oberdorff *et al.* 1995). Therefore, the use of the river catchment grain is ideal when evaluating factors shaping freshwater diversity patterns and determining how similar these diversity patterns and the effects of processes causing those patters to occur are among different groups of freshwater species (Tisseuil *et al.* 2012 and references therein, Collen *et al.* 2014).

Case study River Danube

About 45 percent of the Earth's land mass lies in trans-boundary river catchments, and many catchments are shared by three or even more countries (Cosgrove 2003). Currently, information on the biodiversity or water use of such rivers is however – even in Europe – often only available at the country level, although it is widely accepted that their management is most appropriately done at the catchment scale (Tockner *et al.* 2009, and also see section above).

In my research (Chapters 3 and 4) I focused on the Danube River Basin, Europe's second largest river basin (ICPDR 2009). Due to its extensive area and diverse habitats, it contains a large number of species. The management of international water resources such as the Danube River, the world's most international river basin (synonymously used with river catchment), however, poses particular challenges since the 19 countries which share the river basin comprise countries with administrative and socio-cultural differences and frequently divergent priorities for water quality management and corresponding legal frameworks. Landscapes as complex as large river-floodplain networks require a comprehensive understanding of the underlying ecological structure-function relationships at various spatiotemporal scales. Hence, tailor-made water management strategies need to be properly selected, designed, and implemented based on sound ecological principles, the best available scientific knowledge, and stakeholder participation (Uitto and Duda 2002, Dudgeon *et al.* 2006, Hein *et al.* 2006, Quevauviller 2010).

Thesis goals and outline

The objective of this thesis is to:

1. examine large-scale freshwater diversity patterns in geographic Europe and to evaluate the multifaceted processes that cause biodiversity change,
2. quantify the effects of anthropogenic stressors and natural, geo-climatic drivers on the contemporary patterns of European freshwater biodiversity and to evaluate the generality in biodiversity response and
3. analyze current river basin management strategies – using the Danube River Basin as a case study – and to discuss future strategies.

The following manuscripts form the backbone of my thesis:

- Components and drivers of change in European freshwater fish faunas (Chapter 1)
- Responses of the European freshwater biodiversity to anthropogenic stressors and geo-climatic drivers (Chapter 2)
- The Danube River Basin (Chapter 3)
- Managing the world's most international river: the Danube River Basin (Chapter 4)

In **Chapter 1** I quantified the degree of taxonomic change of the European freshwater fish fauna between the year 1840 and today. I disentangled and quantified the underlying components (loss, gain, introduction and extinction of species) and drivers (reasons for introduction and translocation of species) of change. I also investigated how the range loss of migratory species influenced taxonomic change and moreover tested whether the effect of introduced species on the change of taxonomic similarity is determined by their geographic origin (i.e. whether it is a European species that has been introduced beyond its native range or whether it is an introduced species of non-European origin). I developed the Reshuffling Index (RI) in order to represent the sum of all species gains and losses in relation to the historic species inventory. I used entire river catchments (in total 251, each larger than 2,500 km^2) as assessment units.

A quantification of the effects of anthropogenic and geo-climatic factors on the contemporary patterns of European freshwater biodiversity is presented in **Chapter 2**. I used a variance partitioning scheme based on boosted regression tree analysis (BRT) and generalized linear regression modelling (GLM) to quantify the amount of variance in response patterns of five groups of freshwater species (fish, molluscs, amphibians, odonates, wetland birds), explained by (i) anthropogenic stressors (land use and socio-economic descriptors) and (ii) geo-climatic conditions as well as (iii) their shared/interacting influence.

I used three biodiversity metrics (species richness, taxonomic distinctness and endemicity) for each of the five faunal groups. I also evaluated whether the strengths in biodiversity response found are recurrent among the faunal groups and/or the biodiversity metrics. I used entire river catchments (in total 251, each larger than 2,500 km^2) as assessment units.

Chapter 3 was published as a chapter of the book "Rivers of Europe" (Tockner *et al.* 2009) and covers the Danube River Basin. In this chapter I characterized and synthesized the natural features of the main river, 10 major tributaries and the Danube Delta. I not only included information and data on biodiversity, climate and hydrology but also on stressors like land use, pollution, nonnative species introduction or fragmentation by dams and also socioeconomic properties. Additionally, the chapter contains maps and data tables that allow comparison between physical and biological features of the Danube River Basin and other rivers in Europe.

Building on the information and data compiled in Chapter 3, I examined the strengths and weaknesses of current Danube River Basin management strategies, focusing in particular on science-policy interactions. Topics such as the legal framework for Danube River Basin management, current and planned proactive and reactive management actions, public participation as well as recommendations for feedbacks between science and application are addressed in **Chapter 4**.

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Chapter I
Components and drivers of change in European freshwater fish faunas

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NS compiled and analysed the data, conceived the content of and wrote the paper.
The co-authors contributed to the text.

1 Abstract

Aim Human-induced loss of native species and introduction of non-native species have altered the richness and composition of species assemblages worldwide. During the past 15 years many studies have focused on changes in taxonomic similarity and identified numerous yet often contrasting reasons for it. This study aims to quantify taxonomic changes of freshwater fish assemblages between the mid-19th century and today, while explicitly separating its different components and drivers.

Location Geographic Europe, 251 river basins >2,500 km² (total area: 8.3×10^6 km²).

Methods Pairwise catchment comparisons of historic and contemporary fish species inventories, with and without migratory fish, using Jaccard similarity; quantification of relative species turnover using a newly developed Reshuffling Index (RI); determination of the threshold that displays how widespread a species must be (here: number of catchments occupied) to cause homogenization.

Results The European freshwater fish fauna changed profoundly since the mid-19th century. All river catchments exhibited an average net gain of 5.7 species leading to an overall increase in faunal similarity across Europe of 3.1% (4.6% if migratory species are excluded). However, species turnover was much higher than indicated by the net gain. On average, 20% of the historic assemblages became reshuffled. The native catchment range size of an introduced species primarily determines its impact on taxonomic similarity change, irrespective whether it is translocated within or introduced from outside Europe and whether the species is of fisheries importance or not.

Main conclusions The concurrent use of multiple indices allowed to disentangle the main components and drivers of taxonomic change. It became evident that prevention of intended or unintended species introduction will not lower the rate of taxonomic homogenization per se: most species actually cause taxonomic differentiation despite their range gain, but still considerably contribute to taxonomic change with potential negative effects on ecosystem functions and services.

2 Introduction

Freshwater biodiversity is rapidly declining (Riccardi & Rasmussen, 1999; Jenkins, 2003; Dudgeon *et al.*, 2006; Collen *et al.*, 2014). Besides global extinction, the pronounced loss of species at regional and local scales causes concern (Sax & Gaines, 2003). Moreover, the regional loss of native species is often accompanied, and partly outnumbered by the translocation of native species as well as by the establishment of exotic species (Rahel, 2010; Villéger *et al.*, 2011). As a consequence, regional species diversity, i.e. alpha diversity, may increase despite a concurrent loss of native species. Depending on the number and extent of introductions, species similarity across regions may increase too, corresponding to a decrease in beta-diversity. A decrease in beta-diversity is referred to as taxonomic homogenization (Kinzelbach, 1995; Rahel, 2002, 2007).

Taxonomic homogenization might erode biodiversity-related ecosystem functions and services (May, 2011; Isbell *et al.*, 2015), in particular if well-adapted native species are increasingly replaced by cosmopolitan generalists (Rahel, 2007, 2010). Further, global homogenization is expected to accelerate in the near future (Villéger et al 2015).

Homogenization has been reported on various scales: global (Villéger *et al.*, 2011; Toussaint *et al.*, 2014), continental (Rahel, 2002; Guo & Olden, 2014), and regional (Taylor, 2010; Clavero & Hermoso, 2011), from different continents and regions: Canada (Taylor, 2010), Europe (Leprieur *et al.*, 2008), Australia (Olden *et al.*, 2008), Asia (Matsuzaki *et al.*, 2013), and the United States (Guo & Olden, 2014), and for several taxonomic groups: plants (McKinney, 2004, 2005), ungulates (Spear & Chown, 2008), amphibians (Smith, 2006), birds (Lockwood, 2006), and fish (McKinney, 2005; Clavero & Garcia-Berthou, 2006). In contrast, taxonomic differentiation due to non-native species has been reported for vascular plant assemblages across 22 Southern Ocean Islands (Shaw *et al.*, 2010) and especially for freshwater fish in the Afrotropical and Neotropical realms (Villeger *et al.*, 2011) and at lower spatial scales among watersheds within an ecoregion in the US (Rahel, 2010).

This study focuses on freshwater fishes; globally the most species-rich vertebrate group and one of the most threatened components of freshwater biodiversity (Jelks *et al.*, 2008; Freyhof & Brooks, 2011). The main objectives were: Firstly, to quantify the degree of change in i) species richness, ii) number of shared species, iii) taxonomic similarity, and iv) relative species replacement across European river catchments since the year 1840. Secondly, to quantify the relative contribution of translocated (European species introduced beyond their historic catchment range), exotic (introduced species of non-European origin), and diadromous and amphidromous (DiadBrack) migratory species (e.g., Limburg & Waldman, 2009) on taxonomic similarity change. Previous studies on taxonomic change did not consider the obligatory migrants (e.g. Clavero & Garcia-Berthou, 2006; Leprieur *et al.*, 2008; Olden *et al.*, 2008). Historically, DiadBrack species were among the most widespread species in Europe (e.g. Kottelat & Freyhof, 2007; Lassalle *et al.*, 2009); therefore, it is hypothesized that their subsequent range loss or extinction has led to a decrease in taxonomic similarity. Thirdly, to determine the distribution range (here: number of catchments) of a species at which it starts to cause taxonomic homogenization and whether this threshold value differs between translocated and exotic species. Within biogeographic units native species assemblages inherently exhibit a high similarity and thus, it is hypothesised that even a low number of translocations has a high homogenisation effect compared to the introduction of exotic species. Fourthly, it is hypothesized that intentional introductions result in larger range gains of species and therefore increased homogenisation (e.g. Rahel, 2000), while unintentional releases or escapements cause differentiation. Quantifying the different components of taxonomic change advances the scientific knowledge in freshwater fish biogeography, supports conservation strategies and aids the preservation and enhancement of native freshwater biodiversity.

This study covers all main river catchments in geographic Europe using the most comprehensive datasets on historic and contemporary European freshwater lamprey and fish, in the following named fish species (Kottelat & Freyhof, 2007 and unpublished update 2010; see Supporting Information for details). Geographic Europe is part of the Palearctic region, which together with the Nearctic realm is supposed to exhibit the highest degree of taxonomic homogenization of fish assemblages globally (Villéger *et al.*, 2011). The novelty of this study is to differentiate and quantify the key components and drivers that have altered the European fish fauna in the past 170 years.

3 Methods

3.1 Dataset

All 251 European river catchments (see Fig. S1 and Table S2a in Supporting Information) larger than 2,500 km² that directly drain into the sea were selected from the CCM2 River Network (Vogt *et al.*, 2007). Presence/absence data of all European freshwater fish species, including DiadBrack species that regularly migrate into fresh waters, were obtained from GIS-referenced historic and contemporary species inventories (Kottelat & Freyhof, 2007; J. Freyhof, unpubl. data) (Table S1). The historic species inventory refers to the year 1840, a date before major extinctions of native and introductions of exotic species occurred (Wolter & Röhr, 2010; Villéger *et al.*, 2015 and references therein). The "historic species inventory" included all known native species from a catchment, including species that went extinct or were extirpated. In addition, species that were described later but most likely were already present in the year 1840 were included (J. Freyhof, unpublished data). The only exceptions were common carp *Cyprinus carpio* and prussian carp *Carassius gibelio*. Both species were already common throughout Europe long before 1840. For these two species the pre-Medieval catchment range was considered as native range and the documented re-distribution by monks (e.g., Hoffmann, 1994) as translocated range. The contemporary species inventory comprised the present native, translocated native and exotic species and excluded extirpated or extinct species. Stocked but not established (i.e. non-reproducing) species were excluded from the analyses (Tables S1 & S3). However, stocked species that became established in parts of their introduced range were included in the analyses with their entire range (e.g. *Oncorhynchus mykiss, Salvelinus fontinalis, Cyprinus carpio*). Threatened species categorization was based on Freyhof & Brooks (2011).

Catchment ranges, i.e. number of catchments colonised per species, were calculated for i) all historically native, ii) extinct (globally extinct), iii) extirpated (locally extinct, still exists elsewhere), iv) translocated, v) exotic, and vi) contemporary native species (Table S1 and Supporting Information).

3.2 Data analysis

3.2.1 Quantification of change

For each catchment the net change of species richness was calculated as the difference between historic and contemporary species richness. Because net balancing allows the mathematical compensation of species losses by species gains, a reshuffling index (RI) was developed to represent the sum of all species gains and losses in relation to the historic species inventory.

$$RI = (S_{trans} + S_{exot} + S_{ex} + S_{ext}) / S_{hist}$$

With S = number of translocated (trans), exotic (exot), extinct (ex), extirpated (ext), and historically native (hist) species. The RI quantifies the relative species turnover between the historic and contemporary fish assemblage within each catchment. The RI may exceed 100% if the sum of species gains and losses exceeds the historic native species richness.

The Jaccard similarity coefficient (Legendre & Legendre, 1998; Koleff *et al.*, 2003; PRIMER-E 6.1.5 software package) was calculated for all pairwise combinations of the 251 catchments (31,375 combinations in total) to quantify taxonomic similarity. Similarity was calculated for both the historical and the contemporary species inventory. For each catchment pair the difference between historical and contemporary taxonomic similarity was calculated representing the change in similarity since the mid-19th century. The average of all pair-wise comparisons yielded the continental change of taxonomic similarity. Moreover the change in taxonomic similarity was calculated for each individual catchment (Leprieur *et al.*, 2008); also the number of species was quantified that now share catchments (contemporary species inventory) compared to the past (historic species inventory).

All pair-wise similarity analyses have been repeated with a reduced dataset excluding the DiadBrack (Table S1). The difference between the calculated similarity changes with and without considering DiadBrack provides the relative contribution of migratory species to the observed taxonomic changes and enables assessing the impact of DiadBrack losses on taxonomic similarity change.

3.2.2 Components and drivers of change

The continental rate of taxonomic similarity change among catchments was calculated separately for these components: species exhibiting range loss (extinct and extirpated species combined) and species exhibiting range gain (translocated and exotic species, individually and combined). These analyses allowed disentangling the underlying components of changes in taxonomic similarity.

Drivers, i.e. the primary objectives to introduce new species, were compiled based on Welcomme (1988), Kottelat & Freyhof (2007) and J. Freyhof (unpubl. data). Drivers were separately analysed for species which cause taxonomic homogenization and those which cause taxonomic differentiation. This analysis allowed disentangling whether drivers of species introduction differ in their effect on taxonomic similarity change, i.e. either causing homogenization or differentiation. We additionally analyzed whether the body size of species with a homogenization effect differs of those with a differentiation effect.

3.2.3 Threshold of equivalent catchment range

Each introduced (translocated and exotic) species differentiates the newly colonised catchments from all other catchments not having this species, here referred to as a differentiation effect. In contrast, all the newly colonised catchments become more similar, because they now share this newly introduced species. Moreover, in the case of translocated species, the newly colonised catchments become not only more similar to each other, but also to the native range, i.e. donor catchments with which they now share a further species. Both are referred to as homogenization effects.

The rate of change in taxonomic similarity caused by each single introduced species was calculated by adding only this species to the historic species pool and calculating the pairwise taxonomic similarity among catchments as described above separately for all 77 translocated and 26 exotic species (Table S3). To standardise the increment, the change of taxonomic similarity caused by each introduced species was divided by the number of newly colonised catchments. This value was plotted as the "equivalent change of taxonomic similarity" to compare introduced species that differ in the number of newly colonised catchments (Table S3).

At a certain number of colonised catchments each newly occupied catchment is expected to increase taxonomic homogenization. The point at which an introduced species (translocated or exotic) has occupied a sufficient number of catchments that it starts to cause taxonomic homogenization at the continental scale marks the threshold number or range of catchments. Mathematically, it is the number of catchments at which the average change of taxonomic similarity is zero. Therefore, this metric allows testing the influence of the geographic origin of introduced species, i.e. whether translocated or exotic species have higher homogenization effects.

To calculate the threshold number of catchments when the species effect turns from differentiation to homogenization, first the total number of catchment pairs with a homogenization effect was computed:

$$(n \cdot i) + \frac{i \cdot (i-1)}{2}$$

with i = the number of newly colonised catchments (= translocated range of a native species or introduced range of an exotic species) and n = the number of native range catchments, which was zero for all exotic species.

To quantify how many catchment pairs with a homogenization effect became established on average per single, newly colonised catchment, the resulting total number of catchment pairs with a homogenization effect was then divided by the number of newly colonised catchments:

$$\frac{(n \cdot i) + \frac{i \cdot (i-1)}{2}}{i} = n + \frac{(i-1)}{2}$$

The result represents the "equivalent catchment range", which was plotted against the equivalent change of taxonomic similarity. It has to be noted that the *equivalent* catchment range of exotic species is about half of their *actual* catchment range, because they lack a native catchment range (n=0). The resulting plot indicates the shift from a taxonomic differentiation to a taxonomic homogenization effect.

To determine if the regression lines of the equivalent change of taxonomic similarity and equivalent catchment range differ significantly between translocated and exotic species, the mean square errors of the individual regression lines were compared with those calculated over both groups jointly using an F-test. Linear regressions were calculated using PASW Statistics 17 (SPSS Inc., Chicago, Illinois, USA), and the F-test using Excel 2010 (Microsoft Corporation, Redmond, USA).

4 Results

The contemporary freshwater fish fauna within all 251 catchments (Fig. S1) consisted of 468 native and 26 exotic species, corresponding to 87% of the European species pool. Fifteen of the historically native species went extinct, 6 are extinct in the wild; total S = 515 species (Table 1 and Supporting Information).

Table 1: Contemporary native and exotic freshwater fish richness, number of extinct species, and the relative proportion (%) of threatened species in geographic Europe and in the 251 study catchments. See Methods and Table S1 for details.

	Total area [km^2]	Native species	Exotic species	Extinct species	Threatened species [%]
Europe	9.54×10^6	541	28	16	37.7
251 catchments	8.30×10^6	468	26	15	31.2

The number of species per catchment ranged between 7 and 132 (mean ± SD: 39.3 ± 15.8, median = 39). The relative proportion of threatened species per catchment ranged between 0 and 50% (8.8 ± 6%, median = 6.8%), with a particularly high proportion of threatened species in Southern Europe (Fig. 1A, Table S2a). All catchments host exotic species and 76% of the catchments contain translocated species. Up to 26 (6.2 ± 4.6; median = 5) non-native species (exotic and translocated species combined) occur (Fig. 1B) per catchment, contributing up to 51% (15.5 ± 9.6%, median = 13%) of the contemporary richness. Catchments located in SW Europe contain the highest share of non-native species (Table S2a).

A total of 41 native species has undergone a range loss (Table S1). Twelve species, mainly diadromous migratory species, have lost at least 50% of their historic catchment range (Table 2). Per catchment, up to 7 (0.5 ± 1.1) species and up to 11% (1.1 ± 2.2%) of the historic species pool have disappeared (Fig. 1C, Table S2a). However, more than half of the catchments did not experience a species loss.

Table 2: Species that have lost at least 50% of their historic catchment range. Only species that have disappeared in three or more catchments are included. *Migratory species.

Species	Historic range	Current range	Loss [%]
*Acipenser sturio**	28	1	96
*Acipenser naccarii**	10	0	100
*Acipenser gueldenstaedtii**	10	5	50
*Huso huso**	8	3	63
*Acipenser oxyrinchus**	7	0	100
*Rutilus frisii**	7	1	86
*Eudontomyzon sp. migratory**	5	0	100
*Acipenser nudiventris**	5	2	60
Scardinius scardafa	4	1	75
Alburnus mentoides	3	0	100
*Coregonus oxyrinchus**	3	0	100
*Stenodus leucichthys**	3	0	100

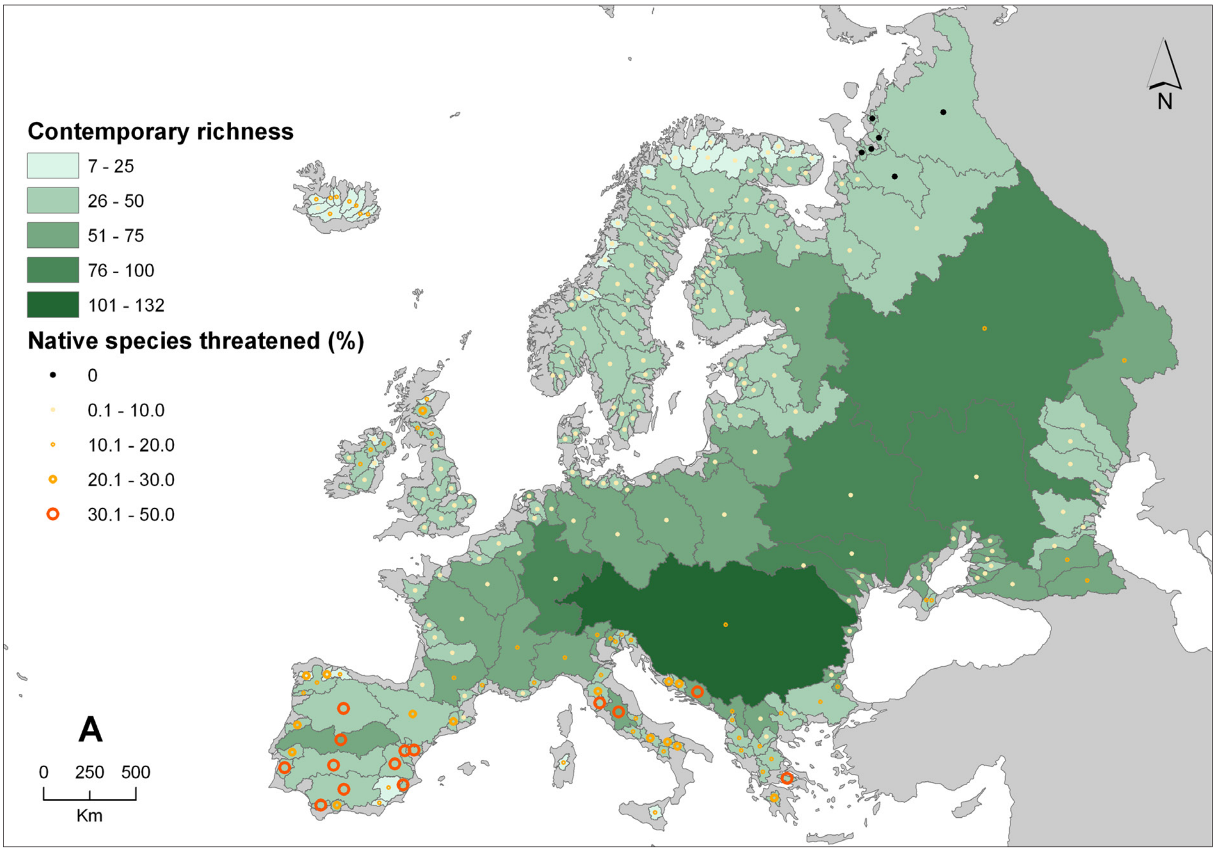

Figure 1A: Map of the contemporary freshwater fish species richness and proportion (%) of threatened species. See Methods and Supporting Information for details.

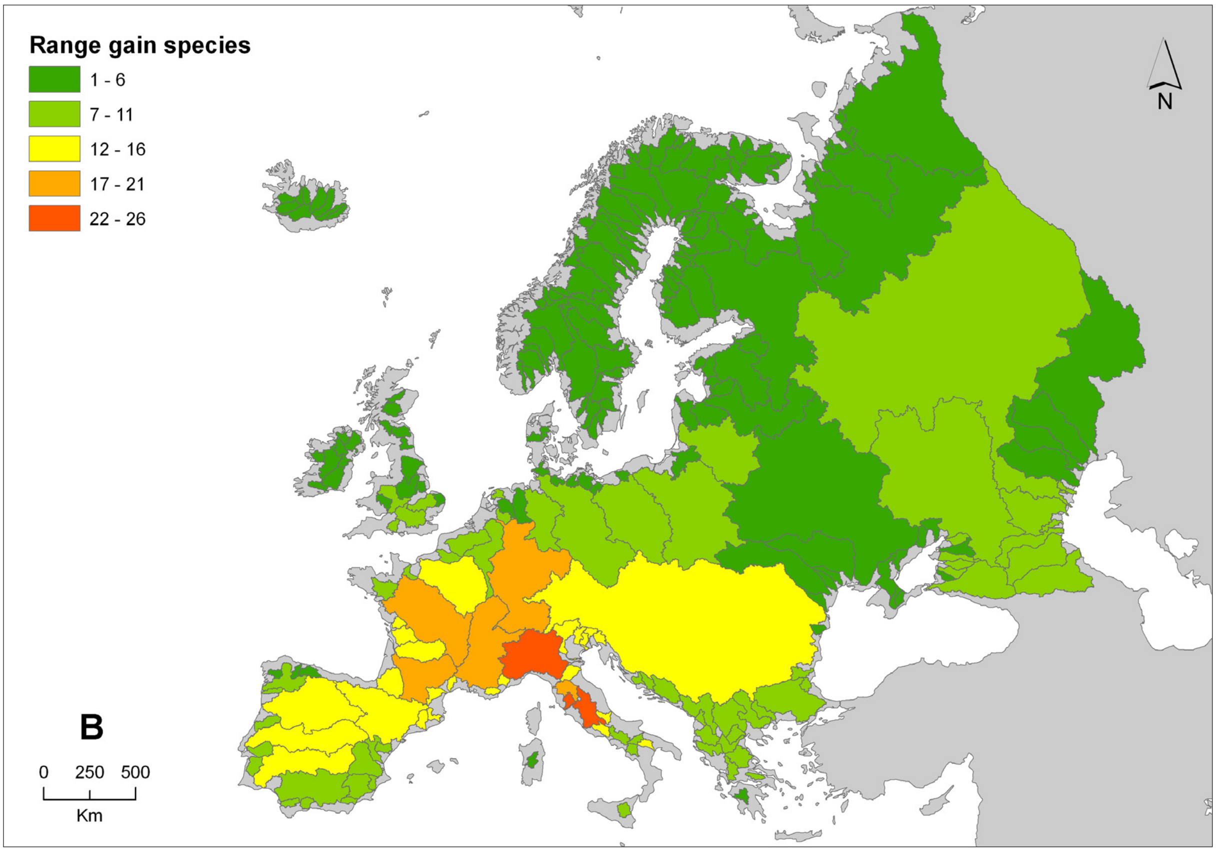

Figure 1B: Map of species with catchment range gain (sum of translocated and exotic species). See Methods and Supporting Information for details.

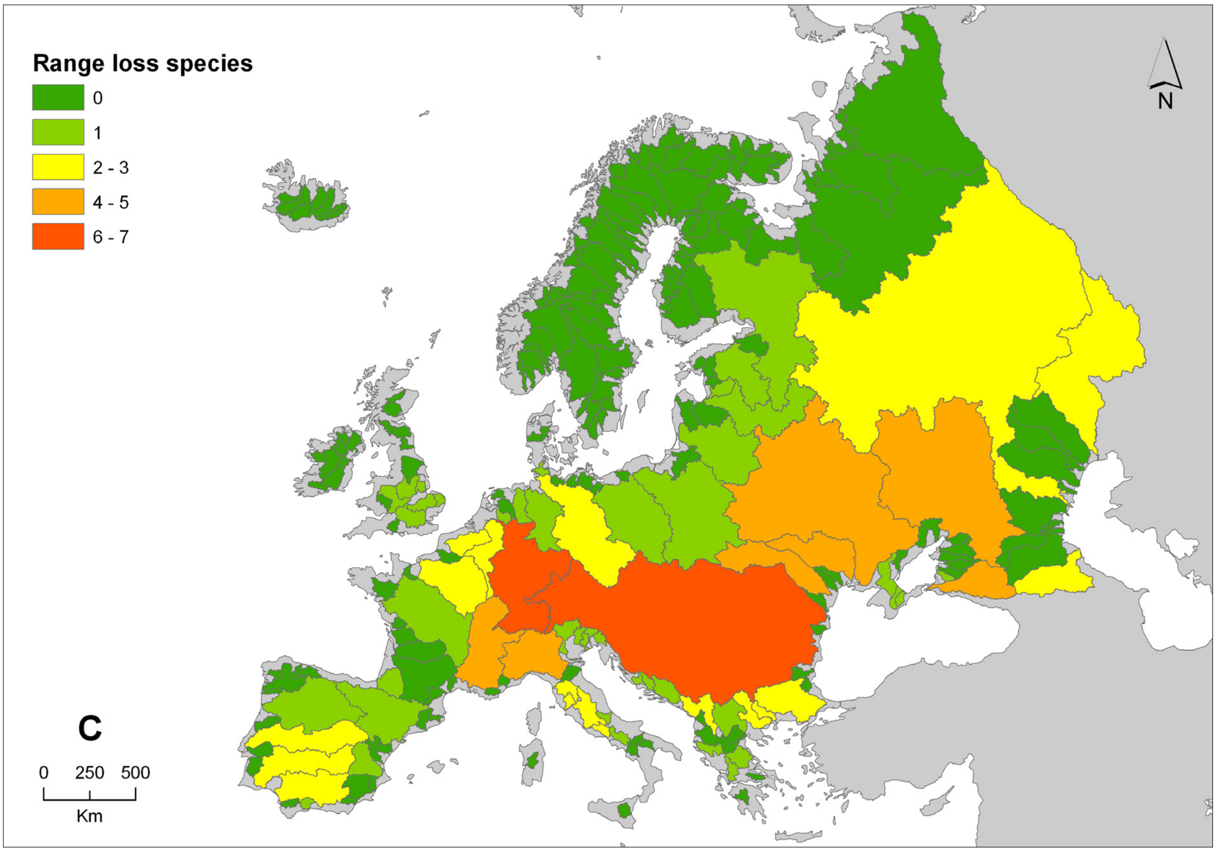

Figure 1C: Map of species with catchment range loss (sum of extinct and extirpated species). See Methods and Supporting Information for details.

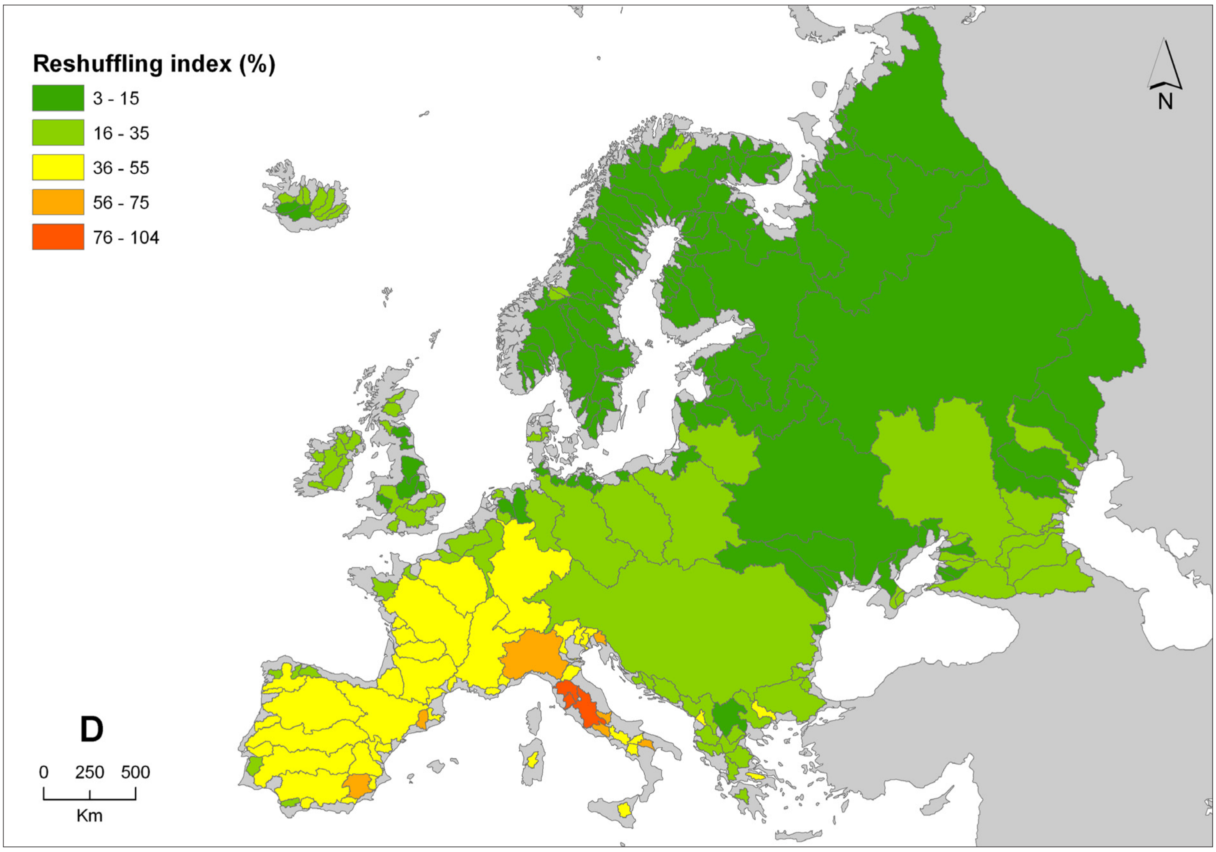

Figure 1D: Reshuffling Index [%]. See Methods and Supporting Information for details.

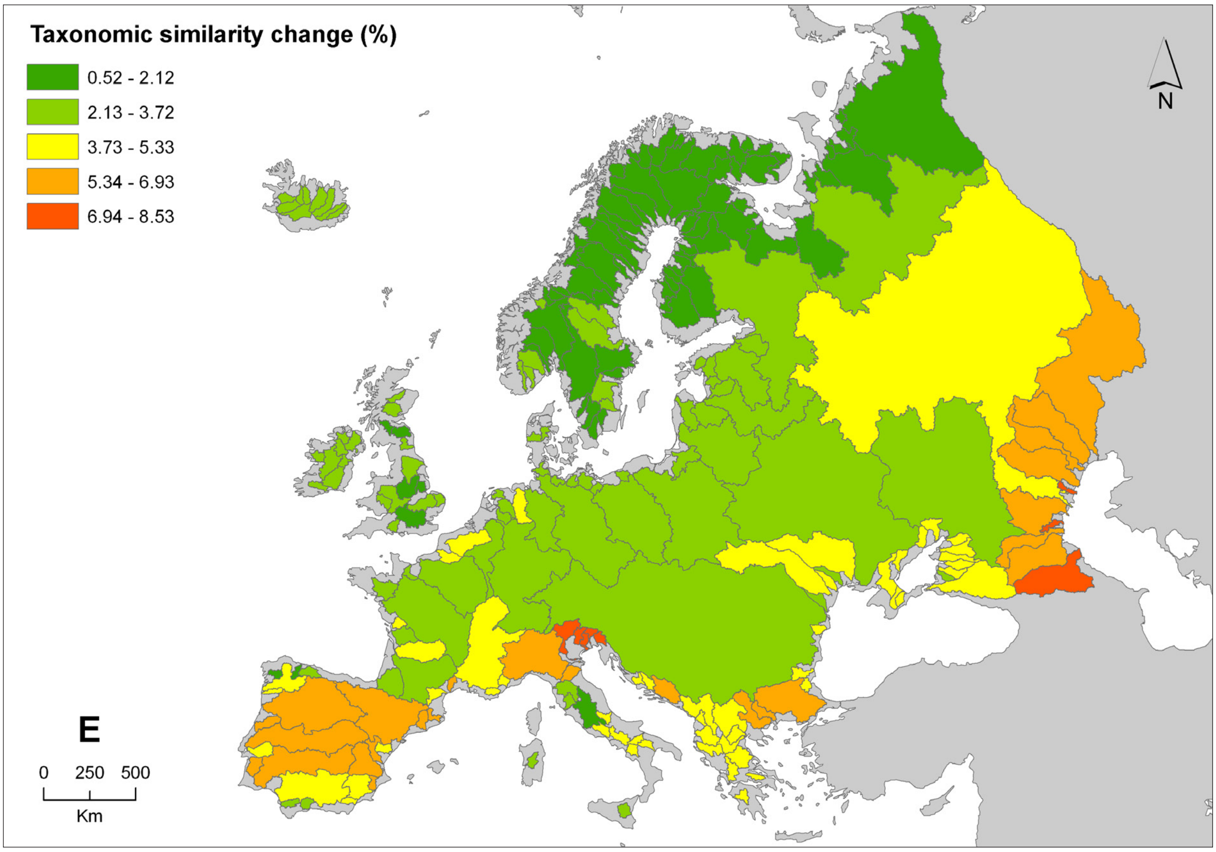

Figure 1E: Map of taxonomic similarity change [%], full set of species (S = 515). See Methods and Supporting Information for details.

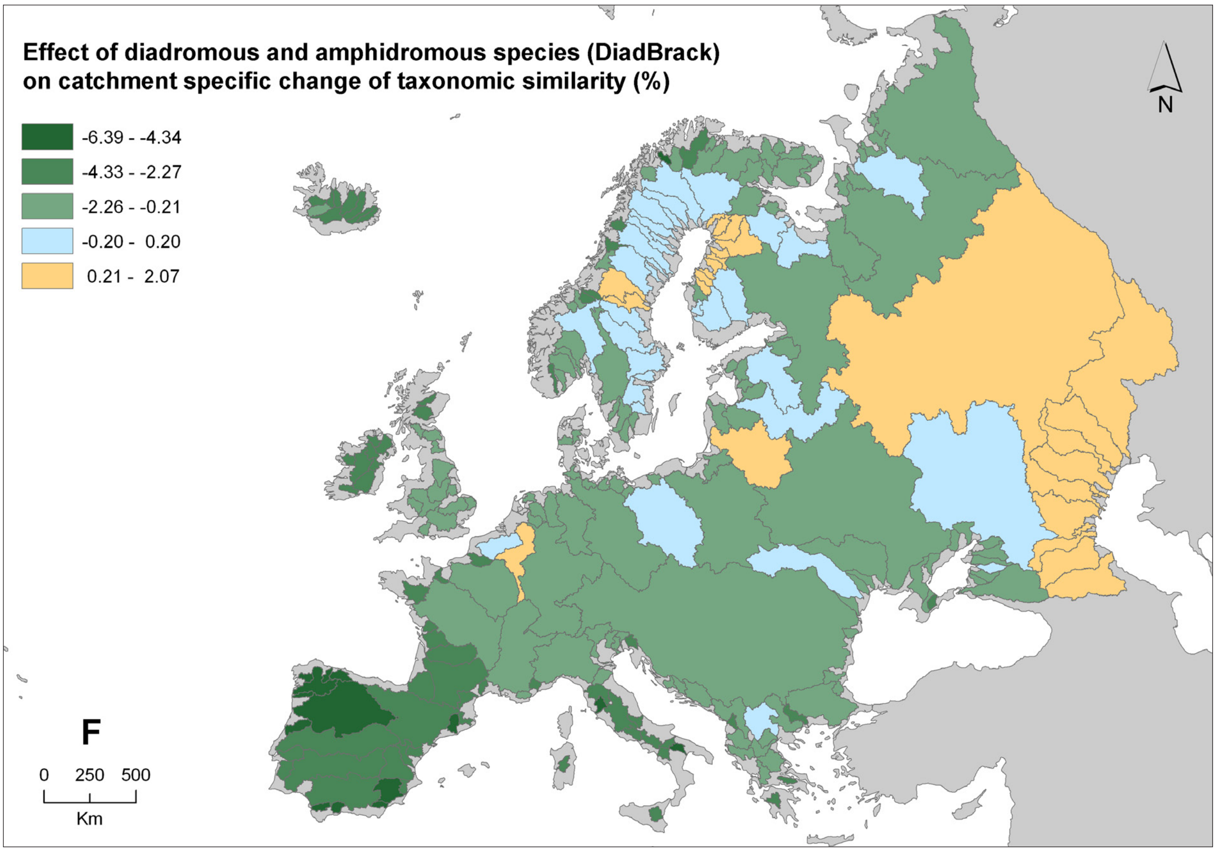

Figure 1F: Map of the effect of diadromous and amphidromous species (DiadBrack) on catchment specific change of taxonomic similarity [%]. See Methods and Supporting Information for details.

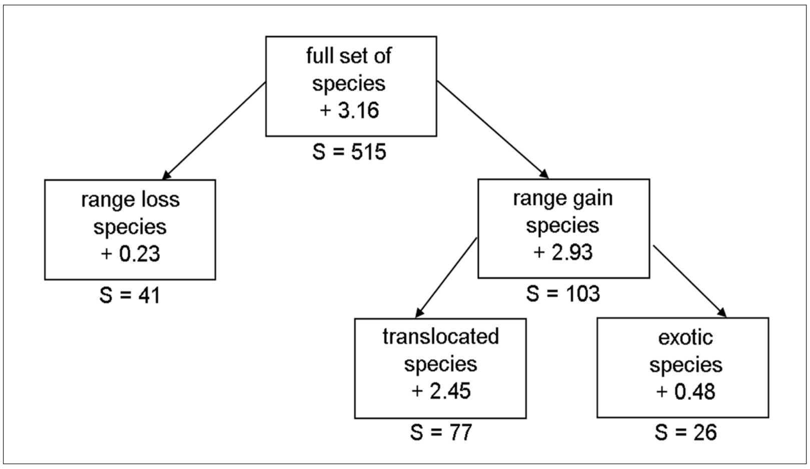

Figure 2: Components of change and their relative contribution to changes in taxonomic similarity (%). S = number of species.

A total of 103 species, including 26 exotic and 77 translocated species, have exhibited a range gain (Table S1). Exotic species have populated on average 30 catchments (29.9 ± 53.5, median = 5.5). Today, translocated species occur, on average, in 57.1 (± 69.1, median = 13) catchments with 47.1 (± 61.1, median = 9) catchments belonging to the native range and 10.1 (± 25.3, median = 2) to the translocated range. As a consequence, all catchments have faced a net species gain since the year 1840. The average gain is 5.7 (± 4.1; median = 5) species per catchment, with a relative increase of up to 88% (Table S2a). Range gain of species was more than twice as high as range loss of species.

The RI, a measure of the relative species turnover between the historic and contemporary species inventory, ranged between 3% and 104% (21 ± 16.6%; median = 15.2%) per catchment (Fig. 1D, Table S2b). RI was inversely, but non-significantly correlated to the historic species richness of a catchment (Spearmans rho = –0.118; ρ (2-tailed) = 0.062). Two Italian catchments, Ombrone and Tevere, exhibited species turnover rates that exceeded the historic species richness (RI >100%, Table S2b). At present, European catchments share on average 3.9 ± 2.7 more species compared to the past. Therefore, all catchments exhibited an increase in taxonomic similarity, particularly catchments located in Southern and South-eastern Europe (Fig. 1E). Since the first half of the 19th century, the faunal similarity has increased on average by 3.1% (from 26.8% to 29.9%), mainly due to the translocation of native species (Fig. 2).

In total, 96 diadromous and amphidromous species (DiadBrack) occur within the 251 catchments. The faunal similarity across Europe has increased by 4.6 ± 2.6% (from 23.0 % to 27.6 %) when DiadBrack are excluded, compared to an increase by 3.1 ± 1.8% when they are included (see above). The most pronounced increase in similarity has been observed in SW Europe. In contrast, 10% of the catchments became more similar when DiadBrack species are included (Fig. 1F).

The shift from taxonomic differentiation to homogenization occurs at an equivalent catchment range threshold of 47.4 ± 4.4 catchments for exotic species and of 46.5 ± 3.2 catchments for translocated species. For exotic species this equals to an actual catchment range threshold of 95 colonised catchments. Accordingly, exotic species started to cause taxonomic homogenization when introduced to at least 95 catchments. In contrast, translocated species started to cause taxonomic homogenization if the sum of their native range and half of the newly colonised catchments reached the threshold. This allows for

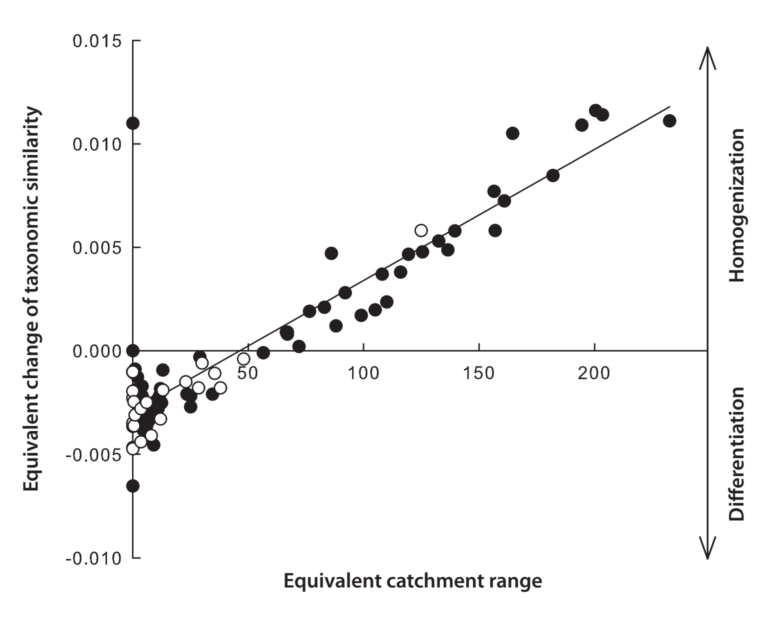

Figure 3: Catchment range thresholds for introduced species from a taxonomic differentiation to a taxonomic homogenization effect. Solid line represents the regression line for both translocated (full circles) and exotic (open circles) species datasets jointly: $y = 6.3 \cdot 10^{-5} \cdot x - 2.9 \cdot 10^{-3}$. See Methods and Table S3 for details.

multiple solutions for the catchment range threshold in form of different combinations between the number catchments natively and newly colonised. For example, a translocated species can be similarly homogenising at either 46 native plus two new ($46 + 0.5 \cdot 1$) catchments or at 15 native catchments and 64 newly colonised ($15 + 0.5 \cdot 63$) catchments. The higher the number of catchments a species occurs in as a native species, the more likely this species causes homogenization when introduced into new catchments. The regression lines of equivalent change of taxonomic similarity related to equivalent catchment ranges were not significantly different for translocated and exotic species (F-test mean square errors, $p = 0.30$, $F = 1.21$). The threshold of the combined datasets was 46.2 catchments at the x-axis with an intercept of ± 2.5 (Fig. 3). At this threshold, the ratio between catchment pairs with a homogenization effect to catchment pairs with a differentiation effect was 1:4 for both translocated and exotic species.

The drivers of species introductions did not differ in their effect on taxonomic similarity change. Improving recreational and commercial fisheries were the primary reasons for species introduction in both those with a homogenization effect (47% and 24%, respectively) and those with a differentiation effect (36% and 20%, respectively) (Table 3; Table S3 for the list of respective species). Range gain of species was clearly positively correlated to fisheries importance, with exotic species having, on average, populated many more new catchments than native species (Table S1 and S3). The taxonomic differentiation effect of exotic species is purely based on the fact that they did not yet reach the actual catchment range threshold of 95 colonised catchments, despite their considerable range gain. In contrast, 18 of the widespread native species have been translocated beyond their native range and cause taxonomic homogenization although their translocation range is surprisingly small: <10, often only one additional catchment (Table S3).

Table 3: Drivers of introduction (%) for species causing taxonomic homogenization (N = 29) and differentiation (N = 72), respectively (multiple drivers per species possible).

Drivers of species introduction	Species with a differentiation effect in %	Species with a homogenization effect in %
Aquaculture	9	0
Commercial fisheries	20	24
Weed	16	21
Recreational fisheries	36	47
Ornamental fish	20	9

Species causing a homogenization effect were larger than those causing a differentiation effect with mean total lengths of 501 mm (± 419 mm, median = 400) and 264 mm (± 194 mm, median = 204), respectively (Table S3).

5 Discussion

Since the first taxonomic revision of the European freshwater fish fauna (Kottelat, 1997), about 160 sub-species have been revised to species and 60 new species have been described (until to the year 2010). Therefore, the actual number of 515 species (Table S1) is much higher than previous inventories of the European freshwater fauna. Accordingly, the present analyses are based on the most comprehensive dataset available (Kottelat & Freyhof, 2007; J. Freyhof, unpubl. data), allowing an in-depth assessment of taxonomic change.

Our study showed that the European freshwater fish fauna has changed profoundly since 1840. At the continental scale, the contemporary fauna holds 14 more species because species introduction exceeds species loss; a common phenomenon observed worldwide (e.g. Rosenzweig, 2001; Sax & Gaines, 2003; Cassey *et al.*, 2007). All 251 river catchments exhibited a net species gain. However, species turnover was much higher than the net gain indicates. On average, one fifth of the historic assemblages became reshuffled (mean RI = 21%). Reshuffling was very pronounced in South-western European rivers; in two catchments species turnover even exceeded the historic species richness. Species gains have led to an overall increase in faunal similarity, both in number of shared species as well as in species composition, across European catchments.

Previous studies showed that the identity of non-native species (exotic or translocated) can have opposite effects on change in taxonomic similarity: while homogenization is commonly attributed to translocated species, the introduction of exotic species was reported to result in faunal differentiation (McKinney, 2004; Leprieur *et al.* 2008; Rahel, 2010), which led to a shift from differentiation to homogenization with time (Rahel, 2010). For Europe, this study clearly identified a differentiation effect of nearly all introduced exotic fish species. Only rainbow trout *Oncorhynchus mykiss* exceeded the homogenization threshold, which had an overriding effect resulting in the observed, albeit small, overall homogenization effect of exotic species (Figs. 2 & 3). Rainbow trout has been introduced to all 251 catchments, which superimposed the taxonomic differentiation effect of all other 25 exotic species.

The threshold that displays how widespread a species must be to cause taxonomic homogenization did not differ between translocated and exotic species (46 and 47 equivalent catchments, respectively); neither did the regressions between their equivalent catchment range and equivalent change of taxonomic similarity. Similar findings were obtained by Guo & Olden (2014) when plotting the foreign exotic fraction (here exotic) against the domestic exotic fraction (here translocated species) in North America. Both were positively correlated and increased with the native species richness (Guo & Olden, 2014). Therefore, it was concluded that the effect of an introduced species on the change of taxonomic similarity is not determined by its geographic origin.

Although the equivalent catchment range of translocated and exotic species was similar; the native range size of a translocated species has about twice the importance for the homogenization effect compared to the newly colonised range size. Thus, the effect of a translocated species is positively related to its native catchment range. In contrast, an exotic species without a native range in European rivers has to colonise in minimum 95 catchments (two times the equivalent catchment range of 47) before it becomes homogenizing.

Interestingly, the majority of translocated species (49 out of 77) and nearly all exotic species do not reach the threshold and have a differentiation effect (Fig. 3). Still, the 28 translocated species above the homogenization threshold (Fig. 3) cause overall a pronounced increase in taxonomic similarity (Fig. 2). Similar large effects of a small set of wide-spread non-native species were reported by Toussant *et al.* (2014) in their study of decline in fish assemblage dissimilarity in 1054 river basins throughout the world.

Taxonomic homogenization is commonly attributed to translocated species (e.g. Leprieur *et al.*, 2008; Matsuzaki *et al.*, 2013), because of their closer geographic proximity, they are more commonly introduced than exotic species (e.g. McKinney, 2005) and they have larger distribution ranges compared to exotic species (La Sorte & McKinney, 2006; Rahel, 2010). The general findings presented here are in full agreement with previous studies (La Sorte & McKinney, 2006; Leprieur *et al.*, 2008; Rahel, 2010; Villéger *et al.*, 2011); however, the proposed causalities mentioned above are only partially confirmed. While close geographic proximity was supported, easier introductions of translocated species were not. The ratio of 77 translocated to 26 exotic species corresponds to the proposed positive effect of geographic proximity. In contrast, the average range gain of 10 and 30 catchments by translocated and exotic species, respectively, does not indicate easier or more common introductions of translocated species. Additionally, the influence of the often large distribution ranges of translocated species was confirmed and further specified. The result of the equivalent catchment range threshold calculation allowed us to quantify the range size (number of catchments) from which a species i) even without gaining new range size, contributes to the general taxonomic similarity of the European catchments and ii) even if it gains only minor additional range size, contributes immediately to the taxonomic homogenization of the catchments. Thus, the predominant taxonomic homogenization effect of translocated species, which was supported by this study, was best explained by the native catchment range of a species: not the most frequently introduced but the species with the widest distribution have the highest potential for homogenization when introduced into new catchments. For example, 35 species already have a native catchment range ≥95 (Table S1), i.e. they contribute to the similarity of the European fish fauna. A single introduction or spread elsewhere immediately makes them "taxonomic homogenisers". This finding corresponds to the study by La Sorte & McKinney (2006): The wider the native range of a species, the more catchments share this species and the greater the homogenization effect when this species reaches or is translocated into a new catchment. The homogenization effect of translocated species might even accelerate, because those species which are currently increasing their range are able to tolerate substantial human alterations (Wolter, 2008); their larger body size as detected in this study (Table S3) may aid their tolerance. Moreover, these species will most likely benefit from predicted changes in climate conditions (e.g. Markovic *et al.*, 2012). However, our study revealed that the majority of translocated species (49 out of 77) still have a differentiation effect.

In consequence, the common statement that species translocation drives taxonomic homogenization appears to be too simplistic and should be treated with caution. While it is undeniable that humans influence ecosystems in various ways and mitigation is needed measures to prevent intentional or accidental species introduction will not slow down the rate of homogenization, per se, since the potential homogenization effect of a species is pre-determined by the extent of its native range size as outlined above. If the native distribution range of a species together with its additional introduced range is still below the catchment range threshold, the species will cause taxonomic differentiation despite its range gain and despite its then wide distribution. Most exotic species have been introduced to much more catchments than translocated species due to their fisheries importance. Thus, while exotic species greatly contribute to taxonomic change which might potentially result in negative effects on native biodiversity related ecosystem services and functions; this change is not reflected in an increase of taxonomic similarity (homogenization) but on the contrary causes a decrease in similarity, i.e. differentiation of species assemblages.

Our second hypothesis that the large-scale disappearance of migratory fish contributes to dissimilarity between catchments was fully confirmed. Historically, 96 diadromous and amphidromous species colonized most European catchments and their wide distribution caused a higher degree of similarity. These species faced the strongest decline of all fish species in the past decades (Table 2; Limburg & Waldman, 2009). Considering these losses in analyses of taxonomic turn-over significantly lowers the increase in overall similarity, as demonstrated by our analyses. This finding should lead to a more differentiated view on taxonomic homogenisation in river management. Successful attempts to re-establish diadromous species will contribute to an increase in similarity.

Interestingly though, the common perception (e.g. Rahel, 2000) and our hypothesis that commercial and recreational fisheries are the main drivers of homogenization was not confirmed. The primary objectives for species introduction did not differ between species with a homogenization or a differentiation effect.

The European freshwater fish fauna has undergone considerable changes since the mid-19th century. Climate-induced changes in temperature, flow, and water quality are predicted to increasingly cause range shifts and even losses of native and non-native species (e.g. Xenopoulos *et al.*, 2005; Hickling *et al.*, 2006; Buisson *et al.*, 2008; Markovic *et al.*, 2012). Thus, new freshwater fish species may establish and previously introduced species will further expand their range (e.g. Rahel, 2004; Clavero & García-Berthou, 2006), while threatened native species, which already account for more than 1/3 of European freshwater fish species (Table 1), might face further range declines (e.g. Rhymer & Simberloff, 1996; Sax *et al.*, 2002; Jelks *et al.*, 2008). Stocking unsorted coarse or feedfish (common practice in recreational fisheries) has the highest potential to translocate already wide-spread species and therefore increase taxonomic homogenization. Education is needed to abandon further stocking of unsorted fish species. Indirectly, further habitat homogenization will favour eurytopic generalist species and their expansion and therefore, contribute to taxonomic homogenization.

In summary, it becomes evident that simply looking at species richness numbers (Sax & Gaines, 2003) or homogenization scores fall short to depict all taxonomic changes. Therefore the reshuffling index was introduced as a metric to better identify and address the specific components of change. Moreover, the drivers of homogenization and the individual effects of species on taxonomic similarity change were analysed and quantified. Component-specific analyses of freshwater fish diversity change in time are pivotal in identifying and implementing appropriate management strategies for species protection and biodiversity management.

6 Acknowledgements

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Supporting Information

A Methods

The distribution data for all fish species are mainly based on Kottelat and Freyhof (2007); however, distribution maps of exotic species have been newly prepared and the data adjusted regarding the catchment accuracy, now discriminating catchments down to 2,500 km². Compared to Kottelat and Freyhof (2007), 17 native species and 2 introduced species (exotics) have been added. The name of 17 species has changed in the meantime, and the catchment range of 14 species has been adapted. Due to the frequent misidentification of the exotic species *Ameiurus melas* and *Ameiurus nebulosus*, they are listed as a single taxon *Ameiurus* spp.

The year 1840 was used as a reliable baseline of the historic faunal situation, referred to as "historic fish fauna", because for a substantial amount of European fish species – except all later described species and some endemics – the distribution had been described and validated in a reliable manner by 1840 (J. Freyhof, unpubl. data). Indeed, the introduction of exotic fish accelerated after 1870, as demonstrated for Germany (Wolter and Röhr, 2010, and references therein).

We focused on primary river catchments that directly drain into the sea and cover an area of more than 2,500 km². Smaller catchments are often located in flat coastal areas where their delineation remains a challenge as demonstrated by the mismatch between HydroBasin and CCM2 catchment layers (J.-F. Cornu, pers. com.). The Pechora catchment (WSO_ID 3), which is not in the CCM2 dataset, has been added based on Tockner et al. (2009). The Drin catchment (WSO_ID 125570) has been enlarged through the inclusion of the Skadar region (WSO_ID 129534).

The classification of species based on their level of threat is based on the IUCN Red List www.iucnredlist.org and Freyhof & Brooks (2011). The classes "critically endangered", "endangered" and "vulnerable" have been included in the "threatened" category.

Subsequent of the exclusion of diadromous species and species that inhabit brackish habitats but regularly enter freshwater (DiadBrack), we reduced the number of species included in the calculations of the Jaccard similarity coefficient. Therefore these calculations are no shares of the overall rate of homogenization when calculated with the full set of species (while the calculated values of a) extinct and extirpated, b) nonnative (tranlsocated + exotics), c) translocated and d) exotic species are true shares), but nevertheless allow an evaluation of the effects and give evidence what to account for when in- or excluding DiadBrack species.

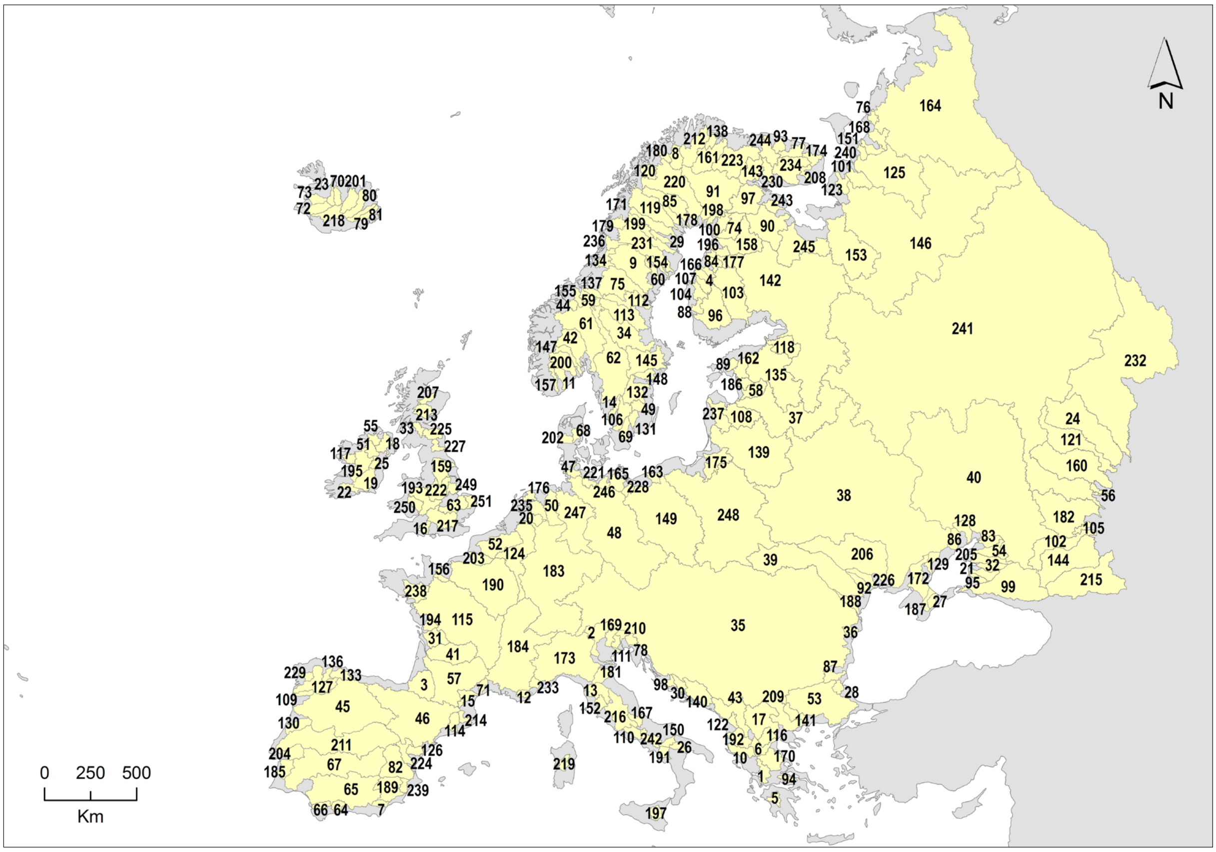

Figure S1: The 251 river catchments >2,500 km² covered in the study; code numbers see Table S2a and S2b.

B References

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C Results

Table S1: List of 515 European freshwater fish species (family, genus, species names) and their category as native (1) with lost (2) or gained (3) catchment range; number of catchments historically and contemporarily colonised is indicated and the number of catchments gained or lost; species listed as threatened in the IUCN Red List (indicated as x); dia- and amphidromous species are indicated as d, extinct species as ex, extinct in the wild species as ex_w and exotic species as e.

Table S1

No.	Family	Genus	Species	Occurence category	Occurence in # of catchments				Threatened species	Dia-, amphi-dromous, extinct and exotic species
					Historic	Contem-porary	Range gain	Range loss		
1	Cyprinidae	Abramis	brama	1, 3	157	158	1	0		
2	Cyprinidae	Achondrostoma	arcasii	1, 3	13	14	1	0	x	
3	Cyprinidae	Achondrostoma	occidentale	1	1	1	0	0	x	
4	Cyprinidae	Achondrostoma	oligolepis	1	4	4	0	0		
5	Cyprinidae	Achondrostoma	salamanticum	1	1	1	0	0	x	
6	Acipenseridae	Acipenser	colchicus	2	1	0	0	1	x	d
7	Acipenseridae	Acipenser	gueldenstaedtii	1, 2	10	5	0	5	x	d
8	Acipenseridae	Acipenser	naccarii	2	10	0	0	10	x	d
9	Acipenseridae	Acipenser	nudiventris	1, 2	5	2	0	3	x	d
10	Acipenseridae	Acipenser	oxyrinchus	2	7	0	0	7		d
11	Acipenseridae	Acipenser	persicus	1	5	5	0	0	x	d
12	Acipenseridae	Acipenser	ruthenus	1, 2	8	7	0	1	x	
13	Acipenseridae	Acipenser	stellatus	1, 2	13	9	0	4	x	d
14	Acipenseridae	Acipenser	sturio	1, 2	28	1	0	27	x	d
15	Cyprinidae	Albunroides	bipunctatus	1	23	23	0	0		
16	Cyprinidae	Alburnoides	gmelini	1	3	3	0	0		
17	Cyprinidae	Alburnoides	ohridanus	1	1	1	0	0	x	
18	Cyprinidae	Alburnoides	rossicus	1	18	18	0	0		
19	Cyprinidae	Alburnoides	thessalicus	1	7	7	0	0		
20	Cyprinidae	Alburnoides	tzanevi	1	2	2	0	0		
21	Cyprinidae	Alburnus	albidus	1	4	4	0	0	x	
22	Cyprinidae	Alburnus	alburnus	1, 3	136	138	2	0		
23	Cyprinidae	Alburnus	arborella	1, 3	11	13	2	0		
24	Cyprinidae	Alburnus	chalcoides	1	11	11	0	0		d
25	Cyprinidae	Alburnus	danubicus	2	1	0	0	1		ex
26	Cyprinidae	Alburnus	hohenackeri	1	4	4	0	0		
27	Cyprinidae	Alburnus	kubanicus	1	1	1	0	0		
28	Cyprinidae	Alburnus	leobergi	1	8	8	0	0		d
29	Cyprinidae	Alburnus	macedonicus	1	1	1	0	0	x	
30	Cyprinidae	Alburnus	maculatus	1	3	3	0	0	x	
31	Cyprinidae	Alburnus	mandrensis	1	1	1	0	0	x	
32	Cyprinidae	Alburnus	mento	1	1	1	0	0		
33	Cyprinidae	Alburnus	mentoides	2	3	0	0	3	x	
34	Cyprinidae	Alburnus	neretvae	1	1	1	0	0		
35	Cyprinidae	Alburnus	sarmaticus	1	3	3	0	0	x	d
36	Cyprinidae	Alburnus	schischkovi	1	2	2	0	0	x	
37	Cyprinidae	Alburnus	scoranza	1	1	1	0	0		
38	Cyprinidae	Alburnus	sp. Volvi	1	1	1	0	0		
39	Cyprinidae	Alburnus	thessalicus	1	8	8	0	0		
40	Clupeidae	Alosa	agone	1, 3	1	2	1	0		
41	Clupeidae	Alosa	algeriensis	1	1	1	0	0		d
42	Clupeidae	Alosa	alosa	1, 2	9	7	0	2		d
43	Clupeidae	Alosa	caspia	1	2	2	0	0		d
44	Clupeidae	Alosa	fallax	1, 3	110	111	1	0		d
45	Clupeidae	Alosa	immaculata	1	5	5	0	0	x	d
46	Clupeidae	Alosa	kessleri	1	2	2	0	0		d
47	Clupeidae	Alosa	maeotica	1	24	24	0	0		d

Table S1

No.	Family	Genus	Species	Occurence category	Occurence in # of catchments				Threatened species	Dia-, amphi-dromous, extinct and exotic species
					Historic	Contem-porary	Range gain	Range loss		
48	Clupeidae	Alosa	sp. Skadar	1	1	1	0	0	x	
49	Clupeidae	Alosa	tanaica	1	10	10	0	0		d
50	Clupeidae	Alosa	volgensis	1, 2	3	2	0	1	x	d
51	Centrarchidae	Ambloplites	rupestris	3	0	1	1	0		e
52	Ictaluridae	Ameiurus	spp.	3	0	58	58	0		e
53	Cyprinidae	Anaecypris	hispanica	1	1	1	0	0	x	
54	Anguillidae	Anguilla	anguilla	1	234	234	0	0	x	d
55	Cyprinodontidae	Aphanius	baeticus	1	3	3	0	0	x	
56	Cyprinodontidae	Aphanius	fasciatus	1, 2, 3	30	30	1	1		d
57	Cyprinodontidae	Aphanius	iberus	1	8	8	0	0	x	d
58	Atherinidae	Atherina	boyeri	1, 2	2	1	0	1		d
59	Cyprinidae	Aulopyge	huegeli	1	3	3	0	0	x	
60	Cichlidae	Australheros	facetus	3	0	1	1	0		e
61	Gobiidae	Babka	gymnotrachelus	1, 3	34	36	2	0		d
62	Cyprinidae	Ballerus	ballerus	1	55	55	0	0		
63	Cyprinidae	Ballerus	sapa	1, 3	24	27	3	0		d
64	Nemacheilidae	Barbatula	barbatula	1	135	135	0	0		
65	Nemacheilidae	Barbatula	quignardi	1, 3	5	6	1	0		
66	Nemacheilidae	Barbatula	sturanyi	1	1	1	0	0		
67	Nemacheilidae	Barbatula	zetensis	1	1	1	0	0		
68	Cyprinidae	Barbus	balcanicus	1	4	4	0	0		
69	Cyprinidae	Barbus	barbus	1	55	55	0	0		
70	Cyprinidae	Barbus	bergi	1	2	2	0	0		
71	Cyprinidae	Barbus	caninus	1, 3	5	8	3	0	x	
72	Cyprinidae	Barbus	carpathicus	1	3	3	0	0		
73	Cyprinidae	Barbus	ciscaucasicus	1, 3	3	4	1	0		
74	Cyprinidae	Barbus	cyclolepis	1	1	1	0	0		
75	Cyprinidae	Barbus	haasi	1	3	3	0	0	x	
76	Cyprinidae	Barbus	kubanicus	1, 2	2	1	0	1		
77	Cyprinidae	Barbus	macedonicus	1	4	4	0	0		
78	Cyprinidae	Barbus	meridionalis	1, 3	6	7	1	0		
79	Cyprinidae	Barbus	peloponnesius	1	3	3	0	0		
80	Cyprinidae	Barbus	petenyi	1	1	1	0	0		
81	Cyprinidae	Barbus	plebejus	1, 3	10	13	3	0		
82	Cyprinidae	Barbus	prespensis	1	2	2	0	0	x	
83	Cyprinidae	Barbus	rebeli	1	1	1	0	0		
84	Cyprinidae	Barbus	sp. Drin	1	1	1	0	0		
85	Cyprinidae	Barbus	sperchiensis	1	2	2	0	0		
86	Cyprinidae	Barbus	strumicae	1	4	4	0	0		
87	Cyprinidae	Barbus	tauricus	1	2	2	0	0	x	
88	Cyprinidae	Barbus	tyberinus	1, 3	7	8	1	0	x	
89	Cyprinidae	Barbus	waleckii	1	2	2	0	0		
90	Gobiidae	Benthophiloides	brauneri	1	7	7	0	0		d
91	Gobiidae	Benthophilus	durrelli	1, 3	2	3	1	0		
92	Gobiidae	Benthophilus	granulosus	1	2	2	0	0		d
93	Gobiidae	Benthophilus	leobergius	1	1	1	0	0		d
94	Gobiidae	Benthophilus	macrocephalus	1	1	1	0	0		d
95	Gobiidae	Benthophilus	magistri	1	8	8	0	0		d
96	Gobiidae	Benthophilus	mahmudbejovi	1	1	1	0	0		d
97	Gobiidae	Benthophilus	nudus	1	9	9	0	0		
98	Gobiidae	Benthophilus	stellatus	1	1	1	0	0		d
99	Cyprinidae	Blicca	bjoerkna	1	116	116	0	0		
100	Cyprinidae	Carassius	carassius	1, 3	129	151	22	0		
101	Cyprinidae	Carassius	gibelio	1, 3	12	155	143	0		
102	Petromyzontidae	Caspiomyzon	wagneri	1, 2	3	2	0	1		d

Table S1

No.	Family	Genus	Species	Occurence category	Occurence in # of catchments				Threatened species	Dia-, amphi-dromous, extinct and exotic species
					Historic	Contem-porary	Range gain	Range loss		
103	Petromyzontidae	Caspiomyzon	hellenicus	1	1	1	0	0	x	
104	Gobiidae	Caspiosoma	caspium	1	27	27	0	0		d
105	Mugilidae	Chelon	labrosus	1	143	143	0	0		d
106	Mugilidae	Chelon	auratus	1	143	143	0	0		d
107	Mugilidae	Chelon	haematocheilus	3	0	27	27	0		d, e
108	Mugilidae	Chelon	ramada	1	143	143	0	0		d
109	Mugilidae	Chelon	saliens	1, 3	87	98	11	0		d
110	Cyprinidae	Chondrostoma	knerii	1	1	1	0	0	x	
111	Cyprinidae	Chondrostoma	kubanicum	1	2	2	0	0		
112	Cyprinidae	Chondrostoma	nasus	1, 3	22	29	7	0		
113	Cyprinidae	Chondrostoma	oxyrhynchum	1	4	4	0	0		
114	Cyprinidae	Chondrostoma	phoxinus	1	3	3	0	0	x	
115	Cyprinidae	Chondrostoma	scodrense	2	1	0	0	1		ex
116	Cyprinidae	Chondrostoma	soetta	1, 3	8	9	1	0	x	
117	Cyprinidae	Chondrostoma	vardarense	1	11	11	0	0		
118	Cyprinidae	Chondrostoma	variabile	1	8	8	0	0		
119	Clupeidae	Clupeonella	caspia	1	3	3	0	0		d
120	Clupeidae	Clupeonella	cultriventris	1	23	23	0	0		d
121	Clupeidae	Clupeonella	tscharchalensis	1, 3	2	3	1	0		
122	Cobitidae	Cobitis	bilineata	1, 3	7	19	12	0		
123	Cobitidae	Cobitis	calderoni	1	4	4	0	0	x	
124	Cobitidae	Cobitis	dalmatina	1	1	1	0	0	x	
125	Cobitidae	Cobitis	elongata	1	1	1	0	0		
126	Cobitidae	Cobitis	elongatoides	1	3	3	0	0		
127	Cobitidae	Cobitis	illyrica	1	1	1	0	0	x	
128	Cobitidae	Cobitis	melanoleuca	1	8	8	0	0		
129	Cobitidae	Cobitis	narentana	1	1	1	0	0	x	
130	Cobitidae	Cobitis	ohridana	1	4	4	0	0		
131	Cobitidae	Cobitis	paludica	1	16	16	0	0	x	
132	Cobitidae	Cobitis	punctilineata	1	1	1	0	0	x	
133	Cobitidae	Cobitis	punctilineata	1	1	1	0	0	x	
134	Cobitidae	Cobitis	stephanidisi	1	1	1	0	0	x	
135	Cobitidae	Cobitis	strumicae	1	6	6	0	0		
136	Cobitidae	Cobitis	taenia	1	73	73	0	0		
137	Cobitidae	Cobitis	tanaitica	1	18	18	0	0		
138	Cobitidae	Cobitis	trichonica	1	1	1	0	0	x	
139	Cobitidae	Cobitis	vardarensis	1	7	7	0	0		
140	Cobitidae	Cobitis	vettonica	1	1	1	0	0	x	
141	Cobitidae	Cobitis	zanandreai	1	1	1	0	0	x	
142	Coregonidae	Coregonus	albellus	1	1	1	0	0		
143	Coregonidae	Coregonus	albula	1, 2, 3	89	87	1	3		
144	Coregonidae	Coregonus	alpinus	1	1	1	0	0		
145	Coregonidae	Coregonus	arenicolus	1	1	1	0	0	x	
146	Coregonidae	Coregonus	atterensis	1	1	1	0	0	x	
147	Coregonidae	Coregonus	austriacus	1	1	1	0	0	x	
148	Coregonidae	Coregonus	autumnalis	1	6	6	0	0		d
149	Coregonidae	Coregonus	baerii	1, 2	2	1	0	1		
150	Coregonidae	Coregonus	bavaricus	1	1	1	0	0	x	
151	Coregonidae	Coregonus	bezola	2	1	0	0	1		ex
152	Coregonidae	Coregonus	candidus	1, 3	1	2	1	0	x	
153	Coregonidae	Coregonus	confusus	1	1	1	0	0	x	
154	Coregonidae	Coregonus	danneri	1	1	1	0	0	x	
155	Coregonidae	Coregonus	duplex	1	1	1	0	0		
156	Coregonidae	Coregonus	fatioi	1	1	1	0	0		
157	Coregonidae	Coregonus	fera	2	1	0	0	1		ex

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158	Coregonidae	Coregonus	fontanae	1	1	1	0	0		
159	Coregonidae	Coregonus	gutturosus	2	1	0	0	1		ex
160	Coregonidae	Coregonus	heglingus	1	1	1	0	0		
161	Coregonidae	Coregonus	hiemalis	2	1	0	0	1		ex
162	Coregonidae	Coregonus	hoferi	1	1	1	0	0	x	
163	Coregonidae	Coregonus	holsatus	2, 3	1	1	1	1		ex_w
164	Coregonidae	Coregonus	kiletz	1	1	1	0	0		
165	Coregonidae	Coregonus	ladogae	1	1	1	0	0		
166	Coregonidae	Coregonus	lavaretus	1	1	1	0	0	x	
167	Coregonidae	Coregonus	lucinensis	1	1	1	0	0	x	
168	Coregonidae	Coregonus	lutokka	1	1	1	0	0		
169	Coregonidae	Coregonus	macrophthalmus	1, 3	1	2	1	0		
170	Coregonidae	Coregonus	maraena	1, 3	65	69	4	0	x	d
171	Coregonidae	Coregonus	maraenoides	1, 2	2	1	0	1	x	
172	Coregonidae	Coregonus	maxillaris	1	6	6	0	0		
173	Coregonidae	Coregonus	megalops	1	11	11	0	0		
174	Coregonidae	Coregonus	muksun	1	1	1	0	0		d
175	Coregonidae	Coregonus	nasus	1	1	1	0	0		d
176	Coregonidae	Coregonus	nilssoni	1	20	20	0	0		
177	Coregonidae	Coregonus	nobilis	1	1	1	0	0		
178	Coregonidae	Coregonus	oxyrinchus	2	3	0	0	3		d, ex
179	Coregonidae	Coregonus	palaea	1, 3	1	2	1	0		
180	Coregonidae	Coregonus	pallasii	1	9	9	0	0		
181	Coregonidae	Coregonus	peled	1	6	6	0	0		
182	Coregonidae	Coregonus	pidschian	1	27	27	0	0		d
183	Coregonidae	Coregonus	pollan	1	3	3	0	0	x	
184	Coregonidae	Coregonus	renke	1	1	1	0	0		
185	Coregonidae	Coregonus	restrictus	2	1	0	0	1		ex
186	Coregonidae	Coregonus	sardinella	1	5	5	0	0		d
187	Coregonidae	Coregonus	sp. winter spawning	1	1	1	0	0		
188	Coregonidae	Coregonus	suidteri	1, 3	1	2	1	0		
189	Coregonidae	Coregonus	trybomi	1	4	4	0	0	x	
190	Coregonidae	Coregonus	vandesius	3	0	1	1	0	x	
191	Coregonidae	Coregonus	vessicus	1	1	1	0	0		
192	Coregonidae	Coregonus	wartmanni	1	1	1	0	0		
193	Coregonidae	Coregonus	widegreni	1	6	6	0	0		d
194	Coregonidae	Coregonus	zuerichensis	1	1	1	0	0		
195	Coregonidae	Coregonus	zugensis	1	1	1	0	0		
196	Cottidae	Cottus	aturi	1	1	1	0	0		
197	Cottidae	Cottus	duranii	1	2	2	0	0		
198	Cottidae	Cottus	gobio	1	45	45	0	0		
199	Cottidae	Cottus	haemusi	1	1	1	0	0		
200	Cottidae	Cottus	hispaniolensis	1	1	1	0	0		
201	Cottidae	Cottus	koshewnikowi	1	43	43	0	0		
202	Cottidae	Cottus	metae	1	1	1	0	0		
203	Cottidae	Cottus	microstomus	1	5	5	0	0		
204	Cottidae	Cottus	perifretum	1	26	26	0	0		
205	Cottidae	Cottus	poecilopus	1	52	52	0	0		
206	Cottidae	Cottus	rhenanus	1	4	4	0	0		
207	Cottidae	Cottus	rondeleti	1	1	1	0	0	x	
208	Cottidae	Cottus	transsilvaniae	1	1	1	0	0		
209	Gasterosteidae	Cualea	inconstans	3	0	1	1	0		e
210	Cyprinidae	Cyprinus	carpio	1, 3	33	184	151	0	x	
211	Cyprinidae	Delminichthys	adspersus	1	1	1	0	0	x	
212	Cyprinidae	Delminichthys	ghetaldii	1	1	1	0	0	x	

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213	Cyprinidae	Delminichthys	krbavensis	1	1	1	0	0	x	
214	Moronidae	Dicentrarchus	labrax	1	148	148	0	0		d
215	Gobiidae	Economidichthys	pygmaeus	1	1	1	0	0		
216	Gobiidae	Economidichthys	trichonis	1	1	1	0	0	x	
217	Esocidae	Esox	lucius	1, 3	191	211	20	0		
218	Petromyzontidae	Eudontomyzon	danfordi	1	1	1	0	0		
219	Petromyzontidae	Eudontomyzon	mariae	1	8	8	0	0		
220	Petromyzontidae	Eudontomyzon	sp. migratory	2	5	0	0	5		ex
221	Petromyzontidae	Eudontomyzon	stankokaramani	1	1	1	0	0		
222	Petromyzontidae	Eudontomyzon	vladykovi	1	1	1	0	0		
223	Fundilidae	Fundulus	heteroclitus	3	0	2	2	0		
224	Poeciliidae	Gambusia	holbrooki	3	0	61	61	0		e
225	Gasterosteidae	Gasterosteus	aculeatus	1, 3	159	164	5	0		d, e
226	Gasterosteidae	Gasterosteus	gymnurus	1, 3	99	100	1	0		
227	Gasterosteidae	Gasterosteus	islandicus	1	9	9	0	0		
228	Cyprinidae	Gobio	alverniae	1	2	2	0	0		
229	Cyprinidae	Gobio	brevicirris	1	1	1	0	0		
230	Cyprinidae	Gobio	bulgaricus	1	6	6	0	0		
231	Cyprinidae	Gobio	carpathicus	1	1	1	0	0		
232	Cyprinidae	Gobio	feraeensis	1	2	2	0	0	x	
233	Cyprinidae	Gobio	gobio	1, 3	68	86	18	0		
234	Cyprinidae	Gobio	holurus	1	3	3	0	0		
235	Cyprinidae	Gobio	kovatschevi	1	1	1	0	0	x	
236	Cyprinidae	Gobio	krymensis	1	3	3	0	0	x	
237	Cyprinidae	Gobio	kubanicus	1	1	1	0	0		
238	Cyprinidae	Gobio	lozanoi	1, 3	2	22	20	0		
239	Cyprinidae	Gobio	obtusirostris	1	1	1	0	0		
240	Cyprinidae	Gobio	occitaniae	1	4	4	0	0		
241	Cyprinidae	Gobio	ohridanus	1	1	1	0	0	x	
242	Cyprinidae	Gobio	sarmaticus	1	5	5	0	0		
243	Cyprinidae	Gobio	skadarensis	1	1	1	0	0	x	
244	Cyprinidae	Gobio	volgensis	1	12	12	0	0		
245	Percidae	Gymnocephalus	acerina	1	7	7	0	0		
246	Percidae	Gymnocephalus	ambriaelacus	1	1	1	0	0	x	
247	Percidae	Gymnocephalus	baloni	1	3	3	0	0		
248	Percidae	Gymnocephalus	cernua	1, 3	148	166	18	0		
249	Percidae	Gymnocephalus	schraetser	1	1	1	0	0		
250	Cichlidae	Hemichromis	fasciatus	3	0	1	1	0		e
251	Cichlidae	Hemichromis	guttatus	3	0	1	1	0		e
252	Cichlidae	Herotilapia	multispinosa	3	0	1	1	0		e
253	Salmonidae	Hucho	hucho	1	1	1	0	0	x	
254	Salmonidae	Hucho	taimen	1	4	4	0	0		
255	Acipenseridae	Huso	huso	1, 2	8	3	0	5	x	d
256	Cyprinidae	Iberochondrostoma	almacai	1	2	2	0	0	x	
257	Cyprinidae	Iberochondrostoma	lemmingii	1	6	6	0	0	x	
258	Cyprinidae	Iberochondrostoma	lusitanicum	1	4	4	0	0	x	
259	Cyprinidae	Iberochondrostoma	oretanum	1	1	1	0	0	x	
260	Cyprinidae	Iberocypris	alburnoides	1	10	10	0	0	x	
261	Cyprinidae	Iberocypris	palaciosi	1	1	1	0	0	x	
262	Ictaluridae	Ictalurus	punctatus	3	0	8	8	0		e
263	Gobiidae	Knipowitschia	bergi	1	11	11	0	0		d
264	Gobiidae	Knipowitschia	caucasica	1	42	42	0	0		d
265	Gobiidae	Knipowitschia	croatica	1	1	1	0	0	x	
266	Gobiidae	Knipowitschia	longecaudata	1	30	30	0	0		d
267	Gobiidae	Knipowitschia	montenegrina	1	1	1	0	0		

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					Historic	Contem-porary	Range gain	Range loss		
268	Gobiidae	Knipowitschia	mrakovici	1	1	1	0	0	x	
269	Gobiidae	Knipowitschia	panizzae	1	10	10	0	0		d
270	Gobiidae	Knipowitschia	punctatissima	1	3	3	0	0		
271	Gobiidae	Knipowitschia	radovici	1	1	1	0	0	x	
272	Gobiidae	Knipowitschia	thessala	1	1	1	0	0	x	
273	Petromyzontidae	Lampetra	fluviatilis	1, 2	96	89	0	7		d
274	Petromyzontidae	Lampetra	planeri	1	125	125	0	0		
275	Gobiidae	Lampetra	zanandreai	1	11	11	0	0		
276	Centrarchidae	Lepomis	gibbosus	3	0	72	72	0		
277	Petromyzontidae	Lethenteron	camtschaticum	1	23	23	0	0		d, e
278	Petromyzontidae	Lethenteron	reissneri	1	9	9	0	0		
279	Cyprinidae	Leucaspius	delineatus	1, 3	63	82	19	0		
280	Cyprinidae	Leuciscus	aspius	1, 3	67	68	1	0		d
281	Cyprinidae	Leuciscus	bearnensis	1	1	1	0	0		
282	Cyprinidae	Leuciscus	burdigalensis	1	6	6	0	0		
283	Cyprinidae	Leuciscus	danilewskii	1	1	1	0	0		
284	Cyprinidae	Leuciscus	idus	1, 3	128	138	10	0		
285	Cyprinidae	Leuciscus	leuciscus	1	132	132	0	0		
286	Cyprinidae	Leuciscus	oxyrrhis	1	2	2	0	0		
287	Pleuronectidae	Liopsetta	glacialis	1	29	29	0	0		d
288	Lotidae	Lota	lota	1, 2	139	134	0	5		
289	Cyprinidae	Luciobarbus	albanicus	1	2	2	0	0		
290	Cyprinidae	Luciobarbus	bocagei	1	8	8	0	0		
291	Cyprinidae	Luciobarbus	brachycephalus	1	11	11	0	0	x	d
292	Cyprinidae	Luciobarbus	capito	1	8	8	0	0	x	d
293	Cyprinidae	Luciobarbus	comizo	1, 2	8	6	0	2	x	
294	Cyprinidae	Luciobarbus	graecus	1	1	1	0	0	x	
295	Cyprinidae	Luciobarbus	graellsii	1, 3	4	5	1	0		
296	Cyprinidae	Luciobarbus	guiraonis	1	6	6	0	0	x	
297	Cyprinidae	Luciobarbus	microcephalus	1	3	3	0	0	x	
298	Cyprinidae	Luciobarbus	sclateri	1	10	10	0	0		
299	Cyprinidae	Luciobarbus	steindachneri	1	4	4	0	0	x	
300	Gobiidae	Mesogobius	batrachocephalus	1	1	1	0	0		d
301	Centrarchidae	Micropterus	salmoides	3	0	47	47	0		e
302	Cobitidae	Misgurnus	anguillicaudatus	3	0	3	3	0		e
303	Cobitidae	Misgurnus	fossilis	1	49	49	0	0		
304	Mugilidae	Mugil	cephalus	1	86	86	0	0		d
305	Gobiidae	Neogobius	fluviatilis	1, 3	23	25	2	0		d
306	Gobiidae	Neogobius	melanostomus	1, 3	5	11	6	0		d
307	Gobiidae	Neogobius	pallasi	1	1	1	0	0		d
308	Atherinopsidae	Odontestes	bonariensis	3	0	1	1	0		e
309	Salmonidae	Oncorhynchus	gorbuscha	3	0	25	25	0		d, e
310	Salmonidae	Oncorhynchus	mykiss	3	0	251	251	0		e
311	Adrianichthydae	Oryzias	sinensis	3	0	1	1	0		d, e
312	Osmeridae	Osmerus	eperlanus	1	116	116	0	0		d
313	Osmeridae	Osmerus	dentex	1	18	18	0	0		d
314	Nemacheilidae	Oxynoemacheilus	bureschi	1	6	6	0	0		
315	Nemacheilidae	Oxynoemacheilus	merga	1	2	2	0	0		
316	Nemacheilidae	Oxynoemacheilus	pindus	1	2	2	0	0	x	
317	Cyprinidae	Pachychilon	macedonicum	1	6	6	0	0		
318	Cyprinidae	Pachychilon	pictum	1, 3	4	6	2	0		
319	Gobiidae	Padogobius	bonelli	1, 3	8	10	2	0		
320	Gobiidae	Padogobius	nigricans	1	3	3	0	0	x	
321	Cyprinidae	Parachondrostoma	arrigonis	1, 2	2	1	0	1	x	
322	Cyprinidae	Parachondrostoma	miegii	1	4	4	0	0		

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					Historic	Contem-porary	Range gain	Range loss		
323	Cyprinidae	Parachondrostoma	toxostoma	1, 3	9	10	1	0	x	
324	Cyprinidae	Parachondrostoma	turiense	1	2	2	0	0	x	
325	Cobitidae	Paramisgurnus	dabryanus	3	0	1	1	0		e
326	Cyprinidae	Pelasgus	laconicus	1	1	1	0	0	x	
327	Cyprinidae	Pelasgus	marathonicus	1	1	1	0	0		
328	Cyprinidae	Pelasgus	minutus	1	1	1	0	0		
329	Cyprinidae	Pelasgus	stymphalicus	1	2	2	0	0		
330	Cyprinidae	Pelasgus	thesproticus	1	2	2	0	0		
331	Cyprinidae	Pelecus	cultratus	1	16	16	0	0		d
332	Percidae	Perca	fluviatilis	1, 3	190	200	10	0		
333	Percidae	Percarina	demidoffii	1	7	7	0	0		d
334	Percidae	Percarina	maeotica	1	12	12	0	0		d
335	Odontobutidae	Perccottus	glenii	3	0	13	13	0		e
336	Cyprinidae	Petroleuciscus	borysthenicus	1	19	19	0	0		
337	Petromyzontidae	Petromyzon	marinus	1	19	19	0	0		d
338	Cyprinidae	Phoxinellus	alepidotus	1	2	2	0	0	x	
339	Cyprinidae	Phoxinellus	dalmaticus	1	1	1	0	0	x	
340	Cyprinidae	Phoxinellus	pseudalepidotus	1	1	1	0	0	x	
341	Cyprinidae	Phoxinus	bigerri	1, 3	3	4	1	0		
342	Cyprinidae	Phoxinus	colchicus	1	1	1	0	0		
343	Cyprinidae	Phoxinus	lumaireul	1	11	11	0	0		
344	Cyprinidae	Phoxinus	phoxinus	1	141	141	0	0		
345	Cyprinidae	Phoxinus	septimaniae	1	4	4	0	0		
346	Cyprinidae	Phoxinus	strandjae	1	2	2	0	0	x	
347	Cyprinidae	Phoxinus	strymonicus	1	1	1	0	0	x	
348	Cyprinidae	Pimephales	promelas	3	0	1	1	0		e
349	Pleuronectidae	Platichthys	flesus	1, 3	228	238	10	0		d
350	Pleuronectidae	Pleuronectes	platessa	1	128	128	0	0		d
351	Poeciliidae	Poecilia	reticulata	3	0	2	2	0		e
352	Gobiidae	Pomatoschistus	canestrinii	1	5	5	0	0		d
353	Gobiidae	Pomatoschistus	microps	1	93	93	0	0		d
354	Gobiidae	Pomatoschistus	montenegrensis	1	1	1	0	0		
355	Gobiidae	Ponticola	constructor	1	1	1	0	0		
356	Gobiidae	Ponticola	eurycephalus	1	1	1	0	0		d
357	Gobiidae	Ponticola	gorlap	1, 3	1	2	1	0		
358	Gobiidae	Ponticola	kessleri	1, 3	4	5	1	0		
359	Gobiidae	Ponticola	syrman	1	30	30	0	0		d
360	Gobiidae	Proterorhinus	nasalis	1	24	24	0	0		
361	Gobiidae	Proterorhinus	semilunaris	1, 3	12	13	1	0		
362	Cyprinidae	Protochondrostoma	genei	1, 2, 3	7	9	3	1		
363	Cyprinidae	Pseudochondrostoma	duriense	1	6	6	0	0	x	
364	Cyprinidae	Pseudochondrostoma	polylepis	1, 3	6	8	2	0		
365	Cyprinidae	Pseudochondrostoma	willkommii	1	7	7	0	0	x	
366	Cyprinidae	Pseudorasbora	parva	3	0	97	97	0		e
367	Gasterosteidae	Pungitius	laevis	1	31	31	0	0		
368	Gasterosteidae	Pungitius	platygaster	1	38	38	0	0		
369	Gasterosteidae	Pungitius	pungitius	1, 3	105	106	1	0		d
370	Cyprinidae	Rhodeus	amarus	1, 3	40	74	34	0		
371	Cyprinidae	Rhodeus	meridionalis	1	4	4	0	0		
372	Cyprinidae	Rhynchocypris	czekanowskii	1	1	1	0	0		
373	Cyprinidae	Rhynchocypris	percnurus	1	17	17	0	0		
374	Percidae	Romanichthys	valsanicola	1	1	1	0	0	x	
375	Cyprinidae	Romanogobio	albipinnatus	1	2	2	0	0		
376	Cyprinidae	Romanogobio	antipai	2	1	0	0	1		ex
377	Cyprinidae	Romanogobio	belingi	1	7	7	0	0		

Table S1

No.	Family	Genus	Species	Occurence category	Occurence in # of catchments				Threatened species	Dia-, amphi-dromous, extinct and exotic species
					Historic	Contem-porary	Range gain	Range loss		
378	Cyprinidae	Romanogobio	benacensis	1, 3	7	10	3	0	x	
379	Cyprinidae	Romanogobio	ciscaucasicus	1	2	2	0	0		
380	Cyprinidae	Romanogobio	elimeius	1	4	4	0	0		
381	Cyprinidae	Romanogobio	kesslerii	1	3	3	0	0		
382	Cyprinidae	Romanogobio	parvus	1	5	5	0	0		
383	Cyprinidae	Romanogobio	pentatrichus	1	4	5	1	0		
384	Cyprinidae	Romanogobio	tanaiticus	1	1	1	0	0		
385	Cyprinidae	Romanogobio	uranoscopus	1	1	1	0	0		
386	Cyprinidae	Romanogobio	vladykovi	1	1	1	0	0		
387	Cyprinidae	Rutilus	aula	1, 3	7	12	5	0		
388	Cyprinidae	Rutilus	basak	1	1	1	0	0		
389	Cyprinidae	Rutilus	caspicus	1	3	3	0	0		d
390	Cyprinidae	Rutilus	frisii	1	7	1	0	6		d
391	Cyprinidae	Rutilus	heckelii	1	16	16	0	0		d
392	Cyprinidae	Rutilus	karamani	1	1	1	0	0		
393	Cyprinidae	Rutilus	meidingeri	1	1	1	0	0	x	
394	Cyprinidae	Rutilus	ohridanus	1	1	1	0	0		
395	Cyprinidae	Rutilus	panosi	1	1	1	0	0	x	
396	Cyprinidae	Rutilus	pigus	1, 3	5	8	3	0		
397	Cyprinidae	Rutilus	rubilio	1, 3	8	10	2	0		
398	Cyprinidae	Rutilus	rutilus	1, 3	180	185	5	0		
399	Cyprinidae	Rutilus	virgo	1	1	1	0	0		
400	Cyprinidae	Rutilus	ylikiensis	1	1	1	0	0	x	
401	Cobitidae	Sabanejewia	balcanica	1	16	16	0	0		
402	Cobitidae	Sabanejewia	baltica	1	5	5	0	0		
403	Cyprinidae	Sabanejewia	bulgarica	1	1	1	0	0		
404	Cobitidae	Sabanejewia	caucasica	1	3	3	0	0		
405	Cobitidae	Sabanejewia	kubanica	1	1	1	0	0		
406	Cobitidae	Sabanejewia	larvata	1, 3	3	5	2	0		
407	Cobitidae	Sabanejewia	romanica	1	1	1	0	0		
408	Cobitidae	Sabanejewia	vallachica	1	1	1	0	0		
409	Blenniidae	Salaria	economidisi	1	1	1	0	0	x	
410	Blenniidae	Salaria	fluviatilis	1	47	47	0	0		
411	Salmonidae	Salmo	aphelios	1	1	1	0	0		
412	Salmonidae	Salmo	balcanicus	1	1	1	0	0		
413	Salmonidae	Salmo	carpio	1	1	1	0	0	x	
414	Salmonidae	Salmo	cenerinus	1	7	7	0	0		
415	Salmonidae	Salmo	cettii	1	8	8	0	0		
416	Salmonidae	Salmo	ciscaucasicus	1	11	11	0	0		d
417	Salmonidae	Salmo	dentex	1	7	7	0	0		
418	Salmonidae	Salmo	ezenami	1	1	1	0	0	x	
419	Salmonidae	Salmo	farioides	1	9	9	0	0		
420	Salmonidae	Salmo	ferox	1	2	2	0	0		
421	Salmonidae	Salmo	fibreni	1	1	1	0	0	x	
422	Salmonidae	Salmo	labrax	1	25	25	0	0		d
423	Salmonidae	Salmo	letnica	1	1	1	0	0		
424	Salmonidae	Salmo	lumi	1	1	1	0	0		
425	Salmonidae	Salmo	macedonicus	1	2	2	0	0		
426	Salmonidae	Salmo	marmoratus	1, 3	5	6	1	0		
427	Salmonidae	Salmo	montenigrinus	1	2	2	0	0		
428	Salmonidae	Salmo	obtusirostris	1	4	4	0	0	x	
429	Salmonidae	Salmo	ohridanus	1	1	1	0	0	x	
430	Salmonidae	Salmo	pelagonicus	1	3	3	0	0	x	
431	Salmonidae	Salmo	peristericus	1	2	2	0	0	x	
432	Salmonidae	Salmo	rhodanensis	1	4	4	0	0		

Table S1

No.	Family	Genus	Species	Occurence category	Occurence in # of catchments				Threatened species	Dia-, amphi-dromous, extinct and exotic species
					Historic	Contem-porary	Range gain	Range loss		
433	Salmonidae	Salmo	salar	1	159	159	0	0		
434	Salmonidae	Salmo	schiefermuelleri	2	1	0	0	1		d, ex
435	Salmonidae	Salmo	taleri	1	1	1	0	0		
436	Salmonidae	Salmo	trutta	1, 3	163	245	82	0		d
437	Salmonidae	Salvelinus	alpinus	1	61	61	0	0		d
438	Salmonidae	Salvelinus	colii	1	2	2	0	0		
439	Salmonidae	Salvelinus	evasus	1	1	1	0	0	x	
440	Salmonidae	Salvelinus	fontinalis	3	0	77	77	0		e
441	Salmonidae	Salvelinus	lepechini	1	28	28	0	0		
442	Salmonidae	Salvelinus	murta	1	1	1	0	0		
443	Salmonidae	Salvelinus	namaycush	3	0	17	17	0		e
444	Salmonidae	Salvelinus	neocomensis	2	1	0	0	1		ex
445	Salmonidae	Salvelinus	profundus	2	1	0	0	1		ex
446	Salmonidae	Salvelinus	sp. Fjellfrøsvatn	1	1	1	0	0	x	
447	Salmonidae	Salvelinus	sp. Rannoch benthivorous	1	1	1	0	0	x	
448	Salmonidae	Salvelinus	sp. Rannoch piscivorous	1	1	1	0	0	x	
449	Salmonidae	Salvelinus	sp. Thingvalla large benthivorous	1	1	1	0	0		
450	Salmonidae	Salvelinus	struanensis	1	1	1	0	0	x	
451	Salmonidae	Salvelinus	thingvallensis	1	1	1	0	0		
452	Salmonidae	Salvelinus	umbla	1, 3	3	4	1	0		
453	Salmonidae	Salvelinus	youngeri	1, 3	1	2	1	0	x	
454	Percidae	Sander	lucioperca	1, 3	96	137	41	0		
455	Percidae	Sander	volgensis	1, 3	8	13	5	0		
456	Cyprinidae	Scardinius	acarnanicus	1	1	1	0	0		
457	Cyprinidae	Scardinius	dergle	1	2	2	0	0		
458	Cyprinidae	Scardinius	erythrophthalmus	1, 3	122	130	8	0		
459	Cyprinidae	Scardinius	graecus	1	1	1	0	0	x	
460	Cyprinidae	Scardinius	hesperidicus	1, 3	7	15	8	0		
461	Cyprinidae	Scardinius	knezevici	1	1	1	0	0	x	
462	Cyprinidae	Scardinius	plotizza	1	1	1	0	0		
463	Cyprinidae	Scardinius	racovitzai	1	1	1	0	0	x	
464	Cyprinidae	Scardinius	scardafa	2, 3	4	1	1	4	x	
465	Siluridae	Silurus	aristotelis	1	1	1	0	0		
466	Siluridae	Silurus	glanis	1, 3	80	97	17	0		
467	Cyprinidae	Squalius	aphipsi	1	1	1	0	0		
468	Cyprinidae	Squalius	aradensis	1	1	1	0	0	x	
469	Cyprinidae	Squalius	carolitertii	1	1	1	0	0		
470	Cyprinidae	Squalius	castellanus	1	1	1	0	0	x	
471	Cyprinidae	Squalius	cephalus	1	111	111	0	0		
472	Cyprinidae	Squalius	illyricus	1	2	2	0	0		
473	Cyprinidae	Squalius	laietanus	1	1	1	0	0		
474	Cyprinidae	Squalius	lucumonis	1	3	3	0	0	x	
475	Cyprinidae	Squalius	microlepis	1	1	1	0	0	x	
476	Cyprinidae	Squalius	moreoticus	1	1	1	0	0	x	
477	Cyprinidae	Squalius	orpheus	1	4	4	0	0		
478	Cyprinidae	Squalius	peloponnensis	1	1	1	0	0		
479	Cyprinidae	Squalius	platyceps	1	1	1	0	0		
480	Cyprinidae	Squalius	pyrenaicus	1	14	14	0	0		
481	Cyprinidae	Squalius	sp. Aoos	1	1	1	0	0		
482	Cyprinidae	Squalius	sp. Evinos	1	2	2	0	0		
483	Cyprinidae	Squalius	squalus	1	21	21	0	0		
484	Cyprinidae	Squalius	svallize	1	1	1	0	0	x	
485	Cyprinidae	Squalius	tenellus	1	1	1	0	0	x	
486	Cyprinidae	Squalius	torgalensis	1	2	2	0	0	x	
487	Cyprinidae	Squalius	valentinus	1	3	3	0	0	x	

Table S1

No.	Family	Genus	Species	Occurence category	Occurence in # of catchments				Threatened species	Dia-, amphi-dromous, extinct and exotic species
					Historic	Contem-porary	Range gain	Range loss		
488	Cyprinidae	Squalius	vardarensis	1	9	9	0	0		
489	Cyprinidae	Squalius	zrmanjae	1	1	1	0	0		
490	Coregonidae	Stenodus	leucichthys	2	3	0	0	3		d, ex_w
491	Coregonidae	Stenodus	nelma	1	19	19	0	0		d
492	Syngnathidae	Syngnathus	abaster	1	97	97	0	0		d
493	Cyprinidae	Telestes	beoticus	1	1	1	0	0	x	
494	Cyprinidae	Telestes	montenigrinus	1	1	1	0	0		
495	Cyprinidae	Telestes	muticellus	1	8	8	0	0		
496	Cyprinidae	Telestes	pleurobipunctatus	1	4	4	0	0		
497	Cyprinidae	Telestes	polylepis	1	1	1	0	0	x	
498	Cyprinidae	Telestes	souffia	1	8	8	0	0		
499	Cyprinidae	Telestes	turskyi	1	1	1	0	0	x	
500	Cyprinidae	Telestes	ukliva	1	1	1	0	0	x	
501	Thymallidae	Thymallus	arcticus	1	1	1	0	0		
502	Thymallidae	Thymallus	thymallus	1, 3	117	123	6	0		
503	Cyprinidae	Tinca	tinca	1, 3	161	169	8	0		
504	Cottidae	Triglopsis	quadricornis	1	91	91	0	0		d
505	Cyprinidae	Tropidophoxinellus	hellenicus	1	1	1	0	0		
506	Umbridae	Umbra	krameri	1	3	3	0	0	x	
507	Umbridae	Umbra	pygmaea	3	0	8	8	0		e
508	Valenciidae	Valencia	hispanica	1	3	3	0	0	x	
509	Valenciidae	Valencia	letourneuxi	1	2	2	0	0	x	
510	Cyprinidae	Vimba	melanops	1	7	7	0	0		
511	Cyprinidae	Vimba	vimba	1, 3	67	68	1	0		d
512	Percidae	Zingel	asper	1	1	1	0	0	x	
513	Percidae	Zingel	balcanicus	1	1	1	0	0		
514	Percidae	Zingel	streber	1	3	3	0	0		
515	Percidae	Zingel	zingel	1	2	2	0	0		

Table S2a: List of 251 European river catchments, with number of contemporarily present, net gain, historically occurring native, contemporary native, lost and gained catchment range, reshuffled, dia- and amphidromous, and threatened freshwater fish species.

Table S2a

No.	Name	Number of species												
		Contemporary (total)	Net gain	Historic	Contemporary native	Range loss (extinct+extirpated)	Extinct	Extirpated	Range gain (exotic + translocated)	Translocated	Exotic	Reshuffled	Dia- and amphidromous	Threatened
1	Acheloos	49	6	43	42	1	0	1	7	3	4	8	14	8
2	Adige	52	15	37	36	1	0	1	16	8	8	17	15	5
3	Adour	45	11	34	33	1	0	1	12	5	7	13	15	3
4	Ähtävänjoki / Purmonjoki	30	1	29	29	0	0	0	1	0	1	1	10	2
5	Alfeios	27	5	22	22	0	0	0	5	3	2	5	13	5
6	Aliakmon	39	7	32	32	0	0	0	7	3	4	7	13	4
7	Almanzora	25	8	17	17	0	0	0	8	5	3	8	13	3
8	Altaelva	16	1	15	15	0	0	0	1	0	1	1	11	1
9	Ångermanälven	30	2	28	28	0	0	0	2	0	2	2	9	2
10	Aoös / Vjosa	36	7	29	28	1	0	1	8	3	5	9	13	4
11	Arendalsvassdraget	32	3	29	29	0	0	0	3	2	1	3	15	2
12	Argens	46	14	32	32	0	0	0	14	9	5	14	12	3
13	Arno	46	18	28	26	2	0	2	20	14	6	22	14	7
14	Ätran	48	3	45	45	0	0	0	3	1	2	3	17	4
15	Aude	47	14	33	33	0	0	0	14	7	7	14	14	3
16	Avon	40	7	33	33	0	0	0	7	5	2	7	13	2
17	Axios / Vardar	60	6	54	53	1	0	1	7	3	4	8	16	5
18	Bann	26	4	22	22	0	0	0	4	3	1	4	12	3
19	Barrow	26	4	22	22	0	0	0	4	3	1	4	13	2
20	Berkel	49	7	42	41	1	0	1	8	4	4	9	12	3
21	Beysug	54	7	47	47	0	0	0	7	4	3	7	26	2
22	Blackwater	27	4	23	23	0	0	0	4	3	1	4	13	2
23	Blanda	7	1	6	6	0	0	0	1	0	1	1	5	1
24	Bolshoy Uzen' and swamps	39	5	34	34	0	0	0	5	3	2	5	11	2
25	Boyne	25	4	21	21	0	0	0	4	3	1	4	12	2
26	Bradano	28	12	16	16	0	0	0	12	8	4	12	12	4
27	Bulhanak-Mokryj Indol	40	5	35	34	1	0	1	6	3	3	7	23	5
28	Burgas Lakes and Wetland	52	7	45	45	0	0	0	7	3	4	7	21	5
29	Byskeälven	29	2	27	27	0	0	0	2	0	2	2	10	2
30	Cetina	46	8	38	37	1	0	1	9	3	6	10	13	9
31	Charente	47	13	34	34	0	0	0	13	8	5	13	14	2
32	Chelbas	40	7	33	33	0	0	0	7	4	3	7	13	2
33	Clyde	29	4	25	25	0	0	0	4	3	1	4	12	3
34	Dalälven	42	3	39	39	0	0	0	3	1	2	3	11	3
35	Danube	131	10	121	115	6	3	3	16	3	13	22	49	21
36	Danube Delta channels and lakes	63	6	57	57	0	0	0	6	2	4	6	26	3
37	Daugava	47	4	43	42	1	0	1	5	2	3	6	14	3
38	Dnieper	84	2	82	78	4	1	3	6	1	5	10	45	6
39	Dnister / Nistru	77	1	76	71	5	1	4	6	1	5	11	29	5
40	Don	85	7	78	74	4	1	3	11	6	5	15	44	5
41	Dordogne	49	14	35	35	0	0	0	14	8	6	14	14	3
42	Drammensvassdraget	36	4	32	32	0	0	0	4	1	3	4	14	2
43	Drin	64	6	58	55	3	1	2	9	3	6	12	14	9
44	Driva	28	3	25	25	0	0	0	3	2	1	3	13	2
45	Duero	42	11	31	30	1	0	1	12	7	5	13	17	10
46	Ebro	39	12	27	26	1	0	1	13	6	7	14	16	7
47	Eider	48	4	44	43	1	0	1	5	1	4	6	19	3
48	Elbe	65	6	59	56	3	0	3	9	3	6	12	21	3
49	Emän	44	3	41	41	0	0	0	3	1	2	3	13	3
50	Ems	53	5	48	47	1	0	1	6	2	4	7	19	3

Table S2a

No.	Name	Number of species												
		Contemporary (total)	Net gain	Historic	Contemporary native	Range loss (extinct+extirpated)	Extinct	Extirpated	Range gain (exotic + translocated)	Translocated	Exotic	Reshuffled	Dia- and amphidromous	Threatened
51	Erne	27	4	23	23	0	0	0	4	3	1	4	12	3
52	Escaut / Schelde	47	9	38	36	2	1	1	11	6	5	13	12	2
53	Evros / Maritsa	50	5	45	42	3	0	3	8	3	5	11	21	5
54	Eya	52	6	46	46	0	0	0	6	3	3	6	26	2
55	Foyle	25	4	21	21	0	0	0	4	3	1	4	12	2
56	Ganyushkino salt marshs	45	7	38	38	0	0	0	7	5	2	7	16	3
57	Garonne	55	17	38	38	0	0	0	17	10	7	17	16	4
58	Gauja	44	4	40	39	1	0	1	5	3	2	6	13	3
59	Gaula	17	3	14	14	0	0	0	3	1	2	3	11	1
60	Gideälven	29	2	27	27	0	0	0	2	0	2	2	10	2
61	Glomma	40	5	35	35	0	0	0	5	1	4	5	16	3
62	Göta älv	48	3	45	45	0	0	0	3	1	2	3	17	3
63	Great Ouse	43	7	36	35	1	0	1	8	5	3	9	14	2
64	Guadalhorce	26	6	20	19	1	0	1	7	4	3	8	11	5
65	Guadalquivir	35	8	27	25	2	0	2	10	5	5	12	15	9
66	Guadelete	29	7	22	22	0	0	0	7	4	3	7	12	7
67	Guadiana	50	12	38	36	2	0	2	14	9	5	16	15	18
68	Gudenå	44	6	38	38	0	0	0	6	3	3	6	13	3
69	Helgeån	47	3	44	44	0	0	0	3	1	2	3	15	3
70	Héraðsvötn (Austari-Jökulsá and Vestari-Jökulsá)	7	1	6	6	0	0	0	1	0	1	1	5	1
71	Hérault	49	16	33	33	0	0	0	16	10	6	16	14	4
72	Hvítá (Árnessýsla)	11	1	10	10	0	0	0	1	0	1	1	6	1
73	Hvítá (Borgarfjarðarsýsla)	7	1	6	6	0	0	0	1	0	1	1	5	1
74	Iijoki	31	1	30	30	0	0	0	1	0	1	1	9	3
75	Indalsälven	31	3	28	28	0	0	0	3	0	3	3	10	2
76	Indiga	26	2	24	24	0	0	0	2	0	2	2	16	0
77	Iokanga / Lylyok	23	2	21	21	0	0	0	2	0	2	2	15	1
78	Isonzo / Soca	40	13	27	26	1	0	1	14	7	7	15	12	4
79	Jökulsá á Dal (á Bru)	7	1	6	6	0	0	0	1	0	1	1	5	1
80	Jökulsá á Fjöllum	7	1	6	6	0	0	0	1	0	1	1	5	1
81	Jökulsá í Fljótsdal	7	1	6	6	0	0	0	1	0	1	1	5	1
82	Júcar	38	10	28	27	1	0	1	11	7	4	12	14	13
83	Kagal'nik	53	7	46	46	0	0	0	7	3	4	7	26	2
84	Kalajoki	31	1	30	30	0	0	0	1	0	1	1	11	2
85	Kalixälven	29	2	27	27	0	0	0	2	0	2	2	9	2
86	Kalmius	55	5	50	50	0	0	0	5	2	3	5	26	2
87	Kamchiya	52	8	44	44	0	0	0	8	3	5	8	22	3
88	Karvianjoki	35	2	33	33	0	0	0	2	1	1	2	11	3
89	Kasari	43	5	38	38	0	0	0	5	3	2	5	12	3
90	Kem	35	2	33	33	0	0	0	2	0	2	2	15	1
91	Kemijoki	30	2	28	28	0	0	0	2	0	2	2	10	2
92	Khadzhybeiśkyi and Kuyal'nytśkyi liman	61	6	55	55	0	0	0	6	2	4	6	25	2
93	Kharlovka	21	2	19	19	0	0	0	2	0	2	2	14	1
94	Kifisos	26	7	19	19	0	0	0	7	3	4	7	13	6
95	Kirpili-Kochety	56	5	51	50	1	0	1	6	3	3	7	27	2
96	Kokemäenjoki	37	2	35	35	0	0	0	2	1	1	2	12	3
97	Kovda / Koutajoki	35	3	32	32	0	0	0	3	0	3	3	16	1
98	Krka	40	8	32	31	1	0	1	9	3	6	10	14	9
99	Kuban	72	5	67	63	4	1	3	9	4	5	13	37	4
100	Kuivajoki	30	1	29	29	0	0	0	1	0	1	1	9	2
101	Kulay	31	2	29	29	0	0	0	2	0	2	2	16	1
102	Kuma	49	7	42	42	0	0	0	7	5	2	7	18	3

Table S2a

No.	Name	Number of species: Contemporary (total)	Net gain	Historic	Contemporary native	Range loss (extinct+extirpated)	Extinct	Extirpated	Range gain (exotic + translocated)	Translocated	Exotic	Reshuffled	Dia- and amphidromous	Threatened
103	Kymijoki	37	2	35	35	0	0	0	2	1	1	2	12	3
104	Kyrönjoki	32	2	30	30	0	0	0	2	1	1	2	11	3
105	Lagan wetlands	40	7	33	33	0	0	0	7	5	2	7	17	3
106	Lagan / Nissan	49	3	46	46	0	0	0	3	1	2	3	17	3
107	Lapuanjoki	31	1	30	30	0	0	0	1	0	1	1	11	2
108	Lielupe	47	6	41	41	0	0	0	6	3	3	6	13	3
109	Lima	28	8	20	20	0	0	0	8	4	4	8	14	4
110	Liri	36	11	25	23	2	0	2	13	9	4	15	14	4
111	Livenza	48	13	35	34	1	0	1	14	8	6	15	15	5
112	Ljungan	30	2	28	28	0	0	0	2	0	2	2	11	2
113	Ljusnan	37	3	34	34	0	0	0	3	1	2	3	11	3
114	Llobregat	31	12	19	19	0	0	0	12	6	6	12	13	5
115	Loire	59	17	42	41	1	0	1	18	8	10	19	16	3
116	Loudias	41	7	34	34	0	0	0	7	3	4	7	13	2
117	Lough Corrib	26	4	22	22	0	0	0	4	3	1	4	14	2
118	Luga	43	3	40	40	0	0	0	3	2	1	3	13	3
119	Luleälven	35	2	33	33	0	0	0	2	0	2	2	14	2
120	Målselva	25	1	24	24	0	0	0	1	0	1	1	11	2
121	Malyy uzen' / Ashshiözek and swamps	44	6	38	38	0	0	0	6	4	2	6	15	2
122	Mat	27	9	18	18	0	0	0	9	3	6	9	12	2
123	Megra	26	3	23	23	0	0	0	3	1	2	3	16	1
124	Meuse / Maas	51	8	43	40	3	1	2	11	4	7	14	12	2
125	Mezen	37	2	35	35	0	0	0	2	0	2	2	16	0
126	Mijares	31	9	22	22	0	0	0	9	5	4	9	13	9
127	Miño	28	8	20	20	0	0	0	8	4	4	8	14	4
128	Mius	56	6	50	50	0	0	0	6	3	3	6	27	2
129	Molochnaya	55	5	50	50	0	0	0	5	2	3	5	26	2
130	Mondego	30	9	21	21	0	0	0	9	5	4	9	14	6
131	Mörrumsån	46	3	43	43	0	0	0	3	1	2	3	14	3
132	Motala ström	46	3	43	43	0	0	0	3	1	2	3	14	3
133	Nalón	24	6	18	18	0	0	0	6	3	3	6	14	3
134	Namsen	20	1	19	19	0	0	0	1	0	1	1	8	1
135	Narva	45	3	42	41	1	0	1	4	3	1	5	14	4
136	Navia	23	4	19	19	0	0	0	4	3	1	4	15	5
137	Nea-Nidelvvassdraget	18	3	15	15	0	0	0	3	1	2	3	11	1
138	Neiden / Näätämöjoki	19	3	16	16	0	0	0	3	0	3	3	13	1
139	Nemunas	51	7	44	43	1	0	1	8	3	5	9	14	3
140	Neretva	60	10	50	49	1	0	1	11	5	6	12	15	16
141	Nestos	38	7	31	29	2	0	2	9	4	5	11	18	2
142	Neva	52	5	47	46	1	0	1	6	4	2	7	15	4
143	Niva / Imandara	30	3	27	27	0	0	0	3	0	3	3	16	1
144	Nogayskaya step swamps	53	7	46	46	0	0	0	7	5	2	7	21	6
145	Norrström	44	3	41	41	0	0	0	3	1	2	3	13	3
146	Northern Dvina	41	5	36	36	0	0	0	5	2	3	5	15	2
147	Numedalslagen	32	2	30	30	0	0	0	2	1	1	2	14	2
148	Nyköpingsän	43	3	40	40	0	0	0	3	1	2	3	13	3
149	Oder	56	6	50	49	1	0	1	7	1	6	8	12	3
150	Ofanto	28	9	19	19	0	0	0	9	6	3	9	12	4
151	Oma	27	2	25	25	0	0	0	2	0	2	2	16	0
152	Ombrone	47	22	25	23	2	0	2	24	18	6	26	13	7
153	Onega	39	3	36	36	0	0	0	3	1	2	3	16	1
154	Oreälven	29	2	27	27	0	0	0	2	0	2	2	10	2

Table S2a

No.	Name	Number of species												
		Contemporary (total)	Net gain	Historic	Contemporary native	Range loss (extinct+extirpated)	Extinct	Extirpated	Range gain (exotic + translocated)	Translocated	Exotic	Reshuffled	Dia- and amphidromous	Threatened
155	Orkla	26	3	23	23	0	0	0	3	1	2	3	11	1
156	Orne	42	8	34	34	0	0	0	8	6	2	8	15	2
157	Otra	29	3	26	26	0	0	0	3	2	1	3	16	2
158	Oulujoki	35	1	34	34	0	0	0	1	0	1	1	11	3
159	Ouse / Trent / Humber	38	4	34	34	0	0	0	4	3	1	4	14	2
160	oz. El'ton and swamps	46	6	40	40	0	0	0	6	4	2	6	17	3
161	Paatsjoki / Pasvikelva	23	5	18	18	0	0	0	5	1	4	5	13	1
162	Parnu	44	5	39	39	0	0	0	5	3	2	5	12	3
163	Parsęta	52	6	46	46	0	0	0	6	1	5	6	14	3
164	Pechora	41	2	39	39	0	0	0	2	0	2	2	18	0
165	Peene	48	3	45	45	0	0	0	3	1	2	3	16	3
166	Perhonjoki	30	1	29	29	0	0	0	1	0	1	1	11	2
167	Pescara	33	11	22	21	1	0	1	12	9	3	13	12	3
168	Pesha	27	2	25	25	0	0	0	2	0	2	2	16	0
169	Piave	51	14	37	36	1	0	1	15	9	6	16	16	5
170	Pinios	42	6	36	35	1	0	1	7	3	4	8	14	5
171	Piteälven	29	2	27	27	0	0	0	2	0	2	2	10	2
172	Pivnično Krymśkij Kanal - Krasnohvardijśke	64	4	60	59	1	0	1	5	2	3	6	27	4
173	Po	62	18	44	40	4	0	4	22	12	10	26	19	7
174	Ponoy	24	2	22	22	0	0	0	2	0	2	2	15	1
175	Pregolja	53	6	47	47	0	0	0	6	1	5	6	15	3
176	Prinses Margrietkanaal channels	51	7	44	44	0	0	0	7	4	3	7	17	3
177	Pyhäjoki	32	1	31	31	0	0	0	1	0	1	1	11	2
178	Råneälven	28	2	26	26	0	0	0	2	0	2	2	10	2
179	Ranelva	14	1	13	13	0	0	0	1	0	1	1	11	1
180	Reisaelva	12	1	11	11	0	0	0	1	0	1	1	11	1
181	Reno	50	13	37	37	0	0	0	13	6	7	13	14	5
182	Rep. Kalmykiya wetlands	49	7	42	42	0	0	0	7	5	2	7	19	4
183	Rhine	81	13	68	61	7	5	2	20	13	7	27	23	6
184	Rhone	63	12	51	46	5	3	2	17	9	8	22	16	5
185	Sado	40	10	30	30	0	0	0	10	6	4	10	13	12
186	Salaca	43	5	38	38	0	0	0	5	3	2	5	12	3
187	Salgir	44	5	39	38	1	0	1	6	3	3	7	23	5
188	Sarata-Cogalnic	63	6	57	57	0	0	0	6	2	4	6	26	2
189	Segura	25	9	16	16	0	0	0	9	6	3	9	12	3
190	Seine	55	14	41	39	2	0	2	16	9	7	18	17	3
191	Sele	29	9	20	20	0	0	0	9	6	3	9	12	4
192	Seman	39	8	31	31	0	0	0	8	3	5	8	12	5
193	Severn	43	7	36	35	1	0	1	8	4	4	9	15	2
194	Sevre Nantaise	46	12	34	34	0	0	0	12	8	4	12	14	2
195	Shannon	29	4	25	25	0	0	0	4	3	1	4	14	3
196	Siikajoki	32	1	31	31	0	0	0	1	0	1	1	11	2
197	Simeto	21	7	14	14	0	0	0	7	3	4	7	11	2
198	Simojoki	29	1	28	28	0	0	0	1	0	1	1	9	2
199	Skellefteälven	30	2	28	28	0	0	0	2	0	2	2	10	2
200	Skiensvassdraget	33	3	30	30	0	0	0	3	2	1	3	15	2
201	Skjálfandafljót	7	1	6	6	0	0	0	1	0	1	1	5	1
202	Skjern Å	45	6	39	39	0	0	0	6	3	3	6	16	3
203	Somme	50	11	39	39	0	0	0	11	8	3	11	15	2
204	Sorraia	33	9	24	24	0	0	0	9	5	4	9	14	6
205	Sosyka-Yasemi	53	7	46	46	0	0	0	7	4	3	7	25	2
206	Southern Bug	79	2	77	73	4	1	3	6	1	5	10	40	6

Table S2a

No.	Name	Number of species												
		Contemporary (total)	Net gain	Historic	Contemporary native	Range loss (extinct+extirpated)	Extinct	Extirpated	Range gain (exotic + translocated)	Translocated	Exotic	Reshuffled	Dia- and amphidromous	Threatened
207	Spey	22	4	18	18	0	0	0	4	3	1	4	11	2
208	Strelna	26	2	24	24	0	0	0	2	0	2	2	16	1
209	Strymon	49	7	42	40	2	0	2	9	4	5	11	18	5
210	Tagliamento	46	13	33	32	1	0	1	14	8	6	15	15	4
211	Tajo	51	12	39	37	2	0	2	14	8	6	16	17	17
212	Tana	16	1	15	15	0	0	0	1	0	1	1	12	1
213	Tay	30	4	26	26	0	0	0	4	3	1	4	14	6
214	Ter	37	12	25	25	0	0	0	12	7	5	12	12	2
215	Terek	52	4	48	45	3	0	3	7	5	2	10	23	6
216	Tevere	51	23	28	25	3	0	3	26	20	6	29	14	8
217	Thames	44	8	36	35	1	0	1	9	5	4	10	14	2
218	Þjórsá	8	1	7	7	0	0	0	1	0	1	1	6	1
219	Tirso	21	6	15	15	0	0	0	6	3	3	6	12	2
220	Törneälven	30	2	28	28	0	0	0	2	0	2	2	10	2
221	Trave	50	3	47	47	0	0	0	3	1	2	3	16	3
222	Trent	38	3	35	34	1	0	1	4	3	1	5	14	2
223	Tuloma	25	3	22	22	0	0	0	3	0	3	3	9	1
224	Turia	30	9	21	21	0	0	0	9	6	3	9	12	8
225	Tweed	32	4	28	28	0	0	0	4	3	1	4	14	3
226	Tylihul'skyi liman	64	6	58	58	0	0	0	6	2	4	6	28	2
227	Tyne	34	4	30	30	0	0	0	4	3	1	4	14	2
228	Uecker	53	6	47	47	0	0	0	6	1	5	6	13	4
229	Ulla	22	4	18	18	0	0	0	4	3	1	4	14	4
230	Umba	28	3	25	25	0	0	0	3	0	3	3	16	1
231	Umeälven	32	2	30	30	0	0	0	2	0	2	2	11	2
232	Ural	61	4	57	55	2	0	2	6	4	2	8	32	9
233	Var	44	15	29	29	0	0	0	15	8	7	15	12	4
234	Varzuga	26	2	24	24	0	0	0	2	0	2	2	16	1
235	Vecht	46	6	40	40	0	0	0	6	4	2	6	12	3
236	Vefsna	14	1	13	13	0	0	0	1	0	1	1	11	1
237	Venta	47	6	41	41	0	0	0	6	3	3	6	14	3
238	Vilaine	40	10	30	30	0	0	0	10	6	4	10	14	2
239	Vinalopó	29	8	21	21	0	0	0	8	6	2	8	13	7
240	Vizhas	28	2	26	26	0	0	0	2	0	2	2	17	0
241	Volga	85	5	80	77	3	0	3	8	5	3	11	51	10
242	Volturno	32	8	24	23	1	0	1	9	6	3	10	14	5
243	Von'ga	29	2	27	27	0	0	0	2	0	2	2	16	1
244	Voronya	25	2	23	23	0	0	0	2	0	2	2	15	1
245	Vyg / Belomorsko-Baltiyskiy kanal	36	2	34	34	0	0	0	2	0	2	2	15	1
246	Warnow	49	4	45	45	0	0	0	4	1	3	4	16	3
247	Weser	59	8	51	50	1	0	1	9	2	7	10	20	3
248	Wisla	67	9	58	57	1	0	1	10	5	5	11	22	3
249	Witham	39	3	36	35	1	0	1	4	3	1	5	14	2
250	Wye	38	4	34	34	0	0	0	4	3	1	4	14	2
251	Yare	40	4	36	35	1	0	1	5	4	1	6	14	2

Table S2b: The 251 river catchments considered in this study, with catchment area and catchment specific scores of change in taxonomic similarity (%) (all species, DiadBrack excluded, and difference between both), and results of the reshuffling index (%).

Table S2b

No.	Name	Area [km^2]	All species (n=515)		DiadBrack excluded (n=419)	Difference in change of taxonomic similarity [%]. All species *minus* DiadBrack excluded
			Change of taxonomic similarity [%]	Reshuffling Index [%]	Change of taxonomic similarity [%]	
1	Acheloos	5686	4.36	18.6	5.35	-0.99
2	Adige	12417	7.2	45.95	8.69	-1.49
3	Adour	16861	3.69	38.24	6.17	-2.48
4	Ähtävänjoki / Purmonjoki	4318	0.87	3.45	0.58	0.29
5	Alfeios	3501	4.22	22.73	6.84	-2.62
6	Aliakmon	6581	4.59	21.88	6.14	-1.55
7	Almanzora	2604	5.09	47.06	10.23	-5.14
8	Altaelva	7332	1.17	6.67	3.33	-2.16
9	Ångermanälven	31815	1.44	7.14	1.31	0.13
10	Aoös / Vjosa	6640	5.08	31.03	7.17	-2.09
11	Arendalsvassdraget	4062	2.38	10.34	4.35	-1.97
12	Argens	2762	4.66	43.75	5.66	-1
13	Arno	8544	3.51	78.57	7.82	-4.31
14	Ätran	3320	1.82	6.67	2.27	-0.45
15	Aude	5226	5.08	42.42	7.42	-2.34
16	Avon	2994	3.17	21.21	5.07	-1.9
17	Axios / Vardar	24397	3.89	14.81	4.04	-0.15
18	Bann	5811	2.74	18.18	5.62	-2.88
19	Barrow	9224	2.53	18.18	5.64	-3.11
20	Berkel	4336	2.88	21.43	3.23	-0.35
21	Beysug	5439	4.04	14.89	4.9	-0.86
22	Blackwater	3239	2.44	17.39	5.25	-2.81
23	Blanda	2565	2.54	16.67	4.88	-2.34
24	Bolshoy Uzen' and swamps	63888	5.59	14.71	4.71	0.88
25	Boyne	2713	2.69	19.05	5.64	-2.95
26	Bradano	2910	4.3	75	9.04	-4.74
27	Bulhanak-Mokryj Indol	2820	4.74	20	7.04	-2.3
28	Burgas Lakes and Wetland	3113	4.39	15.56	5.38	-0.99
29	Byskeälven	3677	1.16	7.41	1.1	0.06
30	Cetina	3869	4.68	26.32	5.38	-0.7
31	Charente	9526	3.54	38.24	5.95	-2.41
32	Chelbas	5855	4.86	21.21	4.93	-0.07
33	Clyde	2972	0.79	16	2	-1.21
34	Dalälven	28638	2.15	7.69	2.23	-0.08
35	Danube	802032	3.03	18.18	3.31	-0.28
36	Danube Delta channels and lakes	3282	4.1	10.53	4.78	-0.68
37	Daugava	84608	3.58	13.95	3.5	0.08
38	Dnieper	512379	3.62	12.2	4.27	-0.65
39	Dnister / Nistru	72531	4.01	14.47	4.13	-0.12
40	Don	429400	2.29	19.23	2.39	-0.1
41	Dordogne	23902	4.33	40	7.54	-3.21
42	Drammensvassdraget	17063	0.86	12.5	1.41	-0.55
43	Drin	19124	4.37	20.69	4.75	-0.38
44	Driva	2508	2.71	12	4.52	-1.81
45	Duero	97419	5.65	41.94	11.03	-5.38
46	Ebro	85612	6.7	51.85	10.89	-4.19
47	Eider	3405	3.44	13.64	4.05	-0.61
48	Elbe	143656	3.17	20.34	3.72	-0.55
49	Emän	4427	2.18	7.32	2.32	-0.14
50	Ems	12185	4.2	14.58	5.41	-1.21
51	Erne	4339	2.79	17.39	5.6	-2.81
52	Escaut / Schelde	18949	4.93	34.21	4.93	0

Table S2b

No.	Name	Area [km^2]	All species (n=515)		DiadBrack excluded (n=419)	Difference in change of taxonomic similarity [%]. All species *minus* DiadBrack excluded
			Change of taxonomic similarity [%]	Reshuffling Index [%]	Change of taxonomic similarity [%]	
53	Evros / Maritsa	53026	5.35	24.44	6.16	-0.81
54	Eya	9192	4.38	13.04	5.52	-1.14
55	Foyle	2919	2.69	19.05	5.64	-2.95
56	Ganyushkino salt marshs	2760	7	18.42	5.01	1.99
57	Garonne	55703	3.3	44.74	6.03	-2.73
58	Gauja	8951	3.38	15	4.3	-0.92
59	Gaula	3668	1.66	21.43	5.21	-3.55
60	Gideälven	3437	1.16	7.41	1.1	0.06
61	Glomma	41911	0.63	14.29	0.74	-0.11
62	Göta älv	51464	1.93	6.67	2.44	-0.51
63	Great Ouse	8443	2.23	25	3.34	-1.11
64	Guadalhorce	3330	3.51	40	9.19	-5.68
65	Guadalquivir	57052	5.24	44.44	8.49	-3.25
66	Guadelete	3397	2.45	31.82	7.85	-5.4
67	Guadiana	67063	6.23	42.11	9.1	-2.87
68	Gudenå	2718	2.49	15.79	3.12	-0.63
69	Helgeån	4677	2.05	6.82	2.32	-0.27
70	Héraðsvötn (Austari-Jökulsá and Vestari-Jökulsá)	3361	2.54	16.67	4.88	-2.34
71	Hérault	2625	5.5	48.48	8.26	-2.76
72	Hvítá (Árnessýsla)	5794	2.26	10	4.44	-2.18
73	Hvítá (Borgarfjarðarsýsla)	3766	2.54	16.67	4.88	-2.34
74	Iijoki	11698	1.02	3.33	0.67	0.35
75	Indalsälven	25839	0.77	10.71	0.46	0.31
76	Indiga	2739	0.98	8.33	2.41	-1.43
77	Iokanga / Lylyok	6427	1.04	9.52	2.47	-1.43
78	Isonzo / Soca	3334	7.58	55.56	10.95	-3.37
79	Jökulsá á Dal (á Bru)	4048	2.54	16.67	4.88	-2.34
80	Jökulsá á Fjöllum	7399	2.54	16.67	4.88	-2.34
81	Jökulsá í Fljótsdal	3345	2.54	16.67	4.88	-2.34
82	Júcar	21555	5.53	42.86	8.75	-3.22
83	Kagal'nik	4997	3.98	15.22	4.7	-0.72
84	Kalajoki	4457	0.86	3.33	0.58	0.28
85	Kalixälven	17696	1.34	7.41	1.2	0.14
86	Kalmius	5024	4.28	10	5.28	-1
87	Kamchiya	5359	4.5	18.18	5.64	-1.14
88	Karvianjoki	3245	1.75	6.06	1.85	-0.1
89	Kasari	3236	2.65	13.16	3.14	-0.49
90	Kem	30903	0.52	6.06	0.55	-0.03
91	Kemijoki	52513	1.29	7.14	1.17	0.12
92	Khadzhybeiśkyi and Kuyal'nytśkyi liman	5073	3.73	10.91	4.19	-0.46
93	Kharlovka	3865	0.98	10.53	2.61	-1.63
94	Kifisos	2550	4.92	36.84	8.78	-3.86
95	Kirpili-Kochety	3001	3.56	13.73	5.62	-2.06
96	Kokemäenjoki	27124	1.66	5.71	1.65	0.01
97	Kovda / Koutajoki	22406	1.06	9.38	1.45	-0.39
98	Krka	2549	5.17	31.25	7.14	-1.97
99	Kuban	52689	4.09	19.4	5.01	-0.92
100	Kuivajoki	6339	1.07	3.45	0.79	0.28
101	Kulay	9584	0.8	6.9	1.28	-0.48
102	Kuma	23510	6.66	16.67	5.15	1.51
103	Kymijoki	35709	1.4	5.71	1.33	0.07
104	Kyrönjoki	4936	1.81	6.67	2.05	-0.24
105	Lagan wetlands	3466	7.4	21.21	5.66	1.74
106	Lagan / Nissan	8356	1.94	6.52	2.38	-0.44

Table S2b

No.	Name	Area [km²]	All species (n=515)		DiadBrack excluded (n=419)	Difference in change of taxonomic similarity [%]. All species *minus* DiadBrack excluded
			Change of taxonomic similarity [%]	Reshuffling Index [%]	Change of taxonomic similarity [%]	
107	Lapuanjoki	4060	0.86	3.33	0.58	0.28
108	Lielupe	17814	2.49	14.63	2.85	-0.36
109	Lima	2520	4.02	40	10.35	-6.33
110	Liri	4104	5.11	60	9.32	-4.21
111	Livenza	2503	8.25	42.86	10.13	-1.88
112	Ljungan	12605	1.32	7.14	1.1	0.22
113	Ljusnan	20024	2.15	8.82	2.31	-0.16
114	Llobregat	4938	6.68	63.16	12.34	-5.66
115	Loire	116981	3.21	45.24	4.76	-1.55
116	Loudias	5680	4.45	20.59	5.76	-1.31
117	Lough Corrib	3167	2.87	18.18	6.98	-4.11
118	Luga	13700	2.38	7.5	2.79	-0.41
119	Luleälven	24554	1.17	6.06	1.31	-0.14
120	Målselva	5722	1.05	4.17	1.51	-0.46
121	Malyy uzen' / Ashshiözek and swamps	36444	6.72	15.79	4.65	2.07
122	Mat	2596	5.13	50	9.4	-4.27
123	Megra	5847	1.68	13.04	3.55	-1.87
124	Meuse / Maas	32047	2.8	32.56	2.4	0.4
125	Mezen	74052	1.06	5.71	1.11	-0.05
126	Mijares	4043	4.63	40.91	8.28	-3.65
127	Miño	16985	3.96	40	10.35	-6.39
128	Mius	7064	4.15	12	5.02	-0.87
129	Molochnaya	4548	4.28	10	5.23	-0.95
130	Mondego	6663	5.37	42.86	10.02	-4.65
131	Mörrumsån	3376	2.09	6.98	2.32	-0.23
132	Motala ström	12934	2.18	6.98	2.32	-0.14
133	Nalón	4887	2.15	33.33	7.93	-5.78
134	Namsen	6163	1.18	5.26	1.5	-0.32
135	Narva	58126	3.2	11.9	3	0.2
136	Navia	2542	2	21.05	7	-5
137	Nea-Nidelvvassdraget	3101	1.56	20	4.51	-2.95
138	Neiden / Näätämöjoki	3055	0.6	18.75	2.67	-2.07
139	Nemunas	95925	3.4	20.45	2.8	0.6
140	Neretva	13122	5.48	24	6.59	-1.11
141	Nestos	6218	5.82	35.48	8.35	-2.53
142	Neva	279586	2.53	14.89	2.76	-0.23
143	Niva / Imandara	12275	1.16	11.11	2.19	-1.03
144	Nogayskaya step swamps	48029	6.41	15.22	5.34	1.07
145	Norrström	23076	2.05	7.32	2.17	-0.12
146	Northern Dvina	379061	2.47	13.89	3.75	-1.28
147	Numedalslagen	5494	1.73	6.67	2.84	-1.11
148	Nyköpingsän	4440	2.06	7.5	2.17	-0.11
149	Oder	118938	3.42	16	3.48	-0.06
150	Ofanto	2777	4.74	47.37	8.32	-3.58
151	Oma	4877	0.99	8	2.37	-1.38
152	Ombrone	3562	2.31	104	6.79	-4.48
153	Onega	56037	1.27	8.33	1.66	-0.39
154	Öreälven	3046	1.16	7.41	1.1	0.06
155	Orkla	3182	1.09	13.04	1.81	-0.72
156	Orne	2948	3.14	23.53	5.51	-2.37
157	Otra	3557	2.31	11.54	5.21	-2.9
158	Oulujoki	24242	1.09	2.94	0.79	0.3
159	Ouse / Trent / Humber	10611	2.47	11.76	4	-1.53
160	oz. El'ton and swamps	55447	6.55	15	4.65	1.9

Table S2b

No.	Name	Area [km²]	All species (n=515)		DiadBrack excluded (n=419)	Difference in change of taxonomic similarity [%]. All species *minus* DiadBrack excluded
			Change of taxonomic similarity [%]	Reshuffling Index [%]	Change of taxonomic similarity [%]	
161	Paatsjoki / Pasvikelva	18045	1.22	27.78	3.46	-2.24
162	Parnu	6600	2.66	12.82	3.19	-0.53
163	Parsęta	3265	3.39	13.04	4.26	-0.87
164	Pechora	330871	0.72	5.13	1.16	-0.44
165	Peene	5497	3.5	6.67	4.7	-1.2
166	Perhonjoki	2519	0.86	3.45	0.57	0.29
167	Pescara	3153	4.82	59.09	8.76	-3.94
168	Pesha	6911	0.99	8	2.37	-1.38
169	Piave	4433	8.53	43.24	10.58	-2.05
170	Pinios	10701	4.6	22.22	6	-1.4
171	Piteälven	11152	1.27	7.41	1.1	0.17
172	Pivnično Krymśkij Kanal - Krasnohvardijśke	13863	4.32	10	5.36	-1.04
173	Po	71327	5.37	59.09	6.96	-1.59
174	Ponoy	4373	0.85	9.09	1.98	-1.13
175	Pregolja	13419	2.87	12.77	3.65	-0.78
176	Prinses Margrietkanaal channels	2561	2.89	15.91	3.97	-1.08
177	Pyhäjoki	3727	0.84	3.23	0.57	0.27
178	Råneälven	4175	1.16	7.69	1.08	0.08
179	Ranelva	3966	1.5	7.69	4.86	-3.36
180	Reisaelva	2691	1.52	9.09	6.66	-5.14
181	Reno	5912	5.97	35.14	8.15	-2.18
182	Rep. Kalmykiya wetlands	53747	6.6	16.67	4.84	1.76
183	Rhine	160221	3.4	39.71	4.19	-0.79
184	Rhone	96619	4.83	43.14	6.26	-1.43
185	Sado	6531	5.49	33.33	8.43	-2.94
186	Salaca	3508	2.69	13.16	3.21	-0.52
187	Salgir	3465	4.78	17.95	6.64	-1.86
188	Sarata-Cogalnic	5327	3.63	10.53	3.89	-0.26
189	Segura	14985	4.78	56.25	9.77	-4.99
190	Seine	75990	3.7	43.9	4.57	-0.87
191	Sele	3227	4.45	45	8.08	-3.63
192	Seman	8411	4.72	25.81	6.33	-1.61
193	Severn	11382	3.6	25	4.69	-1.09
194	Sevre Nantaise	3398	3.99	35.29	6.69	-2.7
195	Shannon	11619	2.53	16	5.6	-3.07
196	Siikajoki	4109	0.84	3.23	0.57	0.27
197	Simeto	4220	3.58	50	6.76	-3.18
198	Simojoki	3141	1.05	3.57	0.73	0.32
199	Skellefteälven	11613	1.31	7.14	1.21	0.1
200	Skiensvassdraget	11171	2.35	10	4.19	-1.84
201	Skjálfandafljót	7305	2.54	16.67	4.88	-2.34
202	Skjern Å	3031	2.29	15.38	3.26	-0.97
203	Somme	6223	3.97	28.21	6.44	-2.47
204	Sorraia	7697	4.81	37.5	8.64	-3.83
205	Sosyka-Yasemi	7048	4.09	15.22	4.9	-0.81
206	Southern Bug	64146	3.88	12.99	4.5	-0.62
207	Spey	3061	3.09	22.22	6.64	-3.55
208	Strelna	3323	0.89	8.33	1.93	-1.04
209	Strymon	16827	5.33	26.19	6.77	-1.44
210	Tagliamento	2610	8.35	45.45	10.43	-2.08
211	Tajo	71202	6.08	41.03	8.93	-2.85
212	Tana	15868	1.27	6.67	3.97	-2.7
213	Tay	5902	2.74	15.38	5.98	-3.24
214	Ter	2955	6.62	48	10.11	-3.49

Table S2b

No.	Name	Area [km²]	All species (n=515)		DiadBrack excluded (n=419)	Difference in change of taxonomic similarity [%]. All species *minus* DiadBrack excluded
			Change of taxonomic similarity [%]	Reshuffling Index [%]	Change of taxonomic similarity [%]	
215	Terek	56525	7.04	20.83	5.44	1.6
216	Tevere	17861	1.77	103.57	5.75	-3.98
217	Thames	13514	1.78	27.78	2.76	-0.98
218	Þjórsá	7978	2.26	14.29	4.88	-2.62
219	Tirso	3353	3.05	40	5.35	-2.3
220	Törneälven	40112	1.27	7.14	1.12	0.15
221	Trave	2826	3.49	6.38	4.66	-1.17
222	Trent	10393	1.69	14.29	2.52	-0.83
223	Tuloma	26771	1.3	13.64	1.8	-0.5
224	Turia	6345	5.7	42.86	9.76	-4.06
225	Tweed	5074	1.26	14.29	2.95	-1.69
226	Tylihul'skyi liman	5390	3.68	10.34	4.19	-0.51
227	Tyne	2886	2.38	13.33	4.32	-1.94
228	Uecker	2740	3.56	12.77	4.39	-0.83
229	Ulla	2773	1.94	22.22	7	-5.06
230	Umba	5342	1.07	12	2.2	-1.13
231	Umeälven	26939	1.4	6.67	1.31	0.09
232	Ural	253147	5.86	14.04	4.25	1.61
233	Var	2819	5.01	51.72	7.58	-2.57
234	Varzuga	19731	0.89	8.33	1.93	-1.04
235	Vecht	6056	3.72	15	4.57	-0.85
236	Vefsna	4218	1.26	7.69	4.86	-3.6
237	Venta	11692	2.47	14.63	3.04	-0.57
238	Vilaine	10490	2.88	33.33	5.34	-2.46
239	Vinalopó	2775	5.55	38.1	9.62	-4.07
240	Vizhas	2973	1.39	7.69	2.37	-0.98
241	Volga	1392007	4.1	13.75	3.71	0.39
242	Volturno	5622	4.01	41.67	7.83	-3.82
243	Von'ga	4764	0.75	7.41	1.24	-0.49
244	Voronya	9495	0.87	8.7	1.93	-1.06
245	Vyg / Belomorsko-Baltiyskiy kanal	33646	0.67	5.88	0.72	-0.05
246	Warnow	3051	3.38	8.89	4.5	-1.12
247	Weser	45211	2.91	19.61	3.58	-0.67
248	Wisla	193894	2.21	18.97	3.95	-1.74
249	Witham	2915	1.76	13.89	2.49	-0.73
250	Wye	4145	2.42	11.76	3.92	-1.5
251	Yare	3017	2.37	16.67	3.52	-1.15

Table S3: List of all translocated (n = 77, Table S3a) and exotic (n = 26, Table S3b) species considered in this study with their equivalent catchment range and catchment range as a native and translocated species (Table S3a) or exotic species (Table S3b); change of taxonomic similarity and equivalent change of taxonomic similarity per species; average body size per species in mm.

Table S3a

species TRANSLOCATED	equivalent catchment range	catchment range		change of taxonomic similarity [%]	equivalent change of taxonomic similarity	body size [mm]
		native	translocated			
Coregonus holsatus	0	0	1	0	0	470
Coregonus vandesius	0	0	1	-0.0065	-0.0065	200
Scardinius scardafa	0	0	1	0.0109	0.0109	350
Alosa agone	1	1	1	-0.0035	-0.0035	340
Coregonus candidus	1	1	1	-0.0022	-0.0022	320
Coregonus macrophthalmus	1	1	1	-0.0022	-0.0022	300
Coregonus palaea	1	1	1	-0.0034	-0.0034	450
Coregonus suidteri	1	1	1	-0.0022	-0.0022	380
Ponticola gorlap	1	1	1	-0.0019	-0.0019	200
Salvelinus youngeri	1	1	1	-0.0008	-0.0008	250
Benthophilus durrelli	2	2	1	-0.0012	-0.0012	66
Clupeonella tscharchalensis	2	2	1	-0.0018	-0.0018	100
Barbus ciscaucasicus	3	3	1	-0.0018	-0.0018	500
Phoxinus bigerri	3	3	1	-0.0019	-0.0019	66
Salvelinus umbla	3	3	1	-0.0021	-0.0021	400
Sabanejewia larvata	3.5	3	2	-0.0071	-0.0035	80
Luciobarbus graellsii	4	4	1	-0.0035	-0.0035	650
Ponticola kessleri	4	4	1	-0.0021	-0.0021	200
Romanogobio pentatrichus	4	4	1	-0.0017	-0.0017	130
Pachychilon pictum	4.5	4	2	-0.0076	-0.0038	180
Barbatula quignardi	5	5	1	-0.0024	-0.0024	70
Salmo marmoratus	5	5	1	-0.0032	-0.0032	200
Barbus caninus	6	5	3	-0.0095	-0.0031	250
Rutilus pigus	6	5	3	-0.0095	-0.0031	450
Barbus meridionalis	6	6	1	-0.0036	-0.0036	270
Pseudochondrostoma polylepis	6.5	6	2	-0.0062	-0.0031	400
Protochondrostoma genei	7	6	3	-0.009	-0.003	200
Barbus tyberinus	7	7	1	-0.0033	-0.0033	400
Neogobius melanostomus	7.5	5	6	-0.016	-0.0026	220
Romanogobio benacensis	8	7	3	-0.009	-0.003	100
Chondrostoma soetta	8	8	1	-0.0029	-0.0029	350
Padogobius bonelli	8.5	8	2	-0.0061	-0.003	76
Rutilus rubilio	8.5	8	2	-0.0053	-0.0026	180
Rutilus aula	9	7	5	-0.0146	-0.0029	180
Parachondrostoma toxostoma	9	9	1	-0.0045	-0.0045	300
Sander volgensis	10	8	5	-0.0121	-0.0024	400
Scardinius hesperidicus	10.5	7	8	-0.0218	-0.0027	400
Barbus plebejus	11	10	3	-0.0083	-0.0028	600
Gobio lozanoi	11.5	2	20	-0.0446	-0.0022	120
Alburnus arborella	11.5	11	2	-0.0051	-0.0025	100
Proterorhinus semilunaris	12	12	1	-0.0018	-0.0018	90
Cobitis bilineata	12.5	7	12	-0.0301	-0.0025	80
Achondrostoma arcasii	13	13	1	-0.0009	-0.0009	104
Neogobius fluviatilis	23.5	23	2	-0.0039	-0.0021	200
Chondrostoma nasus	25	22	7	-0.0189	-0.0027	460
Ballerus sapa	25	24	3	-0.0066	-0.0022	250
Aphanius fasciatus	29	29	1	-0.0003	-0.0003	60
Babka gymnotrachelus	34.5	34	2	-0.0042	-0.0021	160
Rhodeus amarus	56.5	40	34	-0.0039	-0.0001	95
Coregonus maraena	66.5	65	4	0.0036	0.0009	600
Leuciscus aspius	67	67	1	0.0008	0.0008	800
Vimba vimba	67	67	1	0.0009	0.0009	350
Leucaspius delineatus	72	63	19	0.0039	0.0002	90
Gobio gobio	76.5	68	18	0.0336	0.0019	130

Table S3a

species TRANSLOCATED	equivalent catchment range	catchment range		change of taxonomic similarity [%]	equivalent change of taxonomic similarity	body size [mm]
		native	translocated			
Carassius gibelio	83	12	143	0.3054	0.0021	350
Coregonus albula	86	86	1	0.0047	0.0047	230
Silurus glanis	88	80	17	0.0198	0.0012	2000
Liza saliens	92	87	11	0.0306	0.0028	350
Gasterosteus gymnurus	99	99	1	0.0017	0.0017	70
Pungitius pungitius	105	105	1	0.0019	0.0019	64
Cyprinus carpio	108	33	151	0.5518	0.0037	400
Alosa fallax	110	110	1	0.0023	0.0023	500
Sander lucioperca	116	96	41	0.1559	0.0038	1000
Thymallus thymallus	119.5	117	6	0.0279	0.0046	500
Scardinius erythrophthalmus	125.5	122	8	0.0381	0.0047	350
Leuciscus idus	132.5	128	10	0.0529	0.0052	375
Alburnus alburnus	136.5	136	2	0.0097	0.0048	160
Carassius carassius	139.5	129	22	0.1273	0.0057	550
Gymnocephalus cernua	156.5	148	18	0.1392	0.0077	200
Abramis brama	157	157	1	0.0058	0.0058	700
Gasterosteus aculeatus	161	159	5	0.0361	0.0072	65
Tinca tinca	164.5	161	8	0.0839	0.0104	600
Rutilus rutilus	182	180	5	0.0423	0.0084	500
Perca fluviatilis	194.5	190	10	0.1089	0.0108	200
Esox lucius	200.5	191	20	0.2321	0.0116	1300
Salmo trutta	203.5	163	82	0.9315	0.0114	600
Platichthys flesus	232.5	228	10	0.1102	0.0111	500

Table S3b

species EXOTIC	equivalent catchment range	catchment range		change of taxonomic similarity [%]	equivalent change of taxonomic similarity	body size [mm]
		native	exotic			
Ambloplites rupestris	0	0	1	-0.0046	-0.0046	270
Australheros facetus	0	0	1	-0.0022	-0.0022	250
Cualea inconstans	0	0	1	-0.001	-0.001	80
Hemichromis fasciatus	0	0	1	-0.001	-0.001	204
Hemichromis guttatus	0	0	1	-0.001	-0.001	120
Herotilapia multispinosa	0	0	1	-0.001	-0.001	100
Odontestes bonariensis	0	0	1	-0.0036	-0.0036	520
Oryzias sinensis	0	0	1	-0.0019	-0.0019	31
Paramisgurnus dabryanus	0	0	1	-0.0034	-0.0034	no data
Pimephales promelas	0	0	1	-0.0047	-0.0047	50
Fundulus heteroclitus	0.5	0	2	-0.0072	-0.0036	100
Poecilia reticulata	0.5	0	2	-0.0049	-0.0024	35
Misgurnus anguillicaudatus	1	0	3	-0.0094	-0.0031	280
Ictalurus punctatus	3.5	0	8	-0.0222	-0.0028	1000
Umbra pygmaea	3.5	0	8	-0.0352	-0.0044	120
Perccottus glenii	6	0	13	-0.0329	-0.0025	250
Salvelinus namaycush	8	0	17	-0.0699	-0.0041	400
Oncorhynchus gorbuscha	12	0	25	-0.0815	-0.0033	760
Liza haematocheilus	13	0	27	-0.0516	-0.0019	530
Micropterus salmoides	23	0	47	-0.0682	-0.0015	650
Ameiurus spp.	28.5	0	58	-0.1065	-0.0018	462
Gambusia holbrooki	30	0	61	-0.0362	-0.0006	40
Lepomis gibbosus	35.5	0	72	-0.0821	-0.0011	320
Salvelinus fontinalis	38	0	77	-0.1365	-0.0018	500
Pseudorasbora parva	48	0	97	-0.0351	-0.0004	95
Oncorhynchus mykiss	125	0	251	1.4663	0.0058	1000

Chapter II
Responses of the European freshwater biodiversity to anthropogenic stressors & geo-climatic drivers

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In preparation

NS compiled and analysed the data, conceived the content of and wrote the paper. DE wrote the R-scripts for BRT and GLM. The co-authors contributed to the text.

1 Abstract

Aim Human population density, land use change, and gross domestic product (GDP) are integrators of multiple human activities that cause adverse effects on freshwater ecosystems and their biodiversity. So far, few studies have addressed the potential effects of multiple anthropogenic stressors on large-scale contemporary freshwater biodiversity patterns. Moreover, the effects of anthropogenic stressors were rarely tested in combination with the effects of natural drivers, although these factors are known to covary. This study aims to quantify the consequences of anthropogenic stressors and geo-climatic drivers, single and in combination, on contemporary biodiversity patterns, and to analyze how different freshwater faunal groups respond to these factors.

Location Geographic Europe, 251 river basins >2,500 km² (total area: 8.3×10^6 km²).

Methods We used a variance partitioning scheme based on boosted regression tree analysis (BRT) and generalized linear modelling (GLM) to quantify the proportion of variance in response patterns of species richness, taxonomic distinctness, and endemicity of five faunal groups of freshwater species (fish, odonates, amphibians, birds, molluscs) explained by (i) anthropogenic stressors (land use and socio-economic factors) and (ii) eight geo-climatic drivers (precipitation, temperature, actual and potential evapotranspiration, catchment area and elevational range, longitude, latitude) as well as (iii) their shared/interacting influence.

Results Land use was a weak predictor of the variation of freshwater biodoversity (mean: 0.3%) across all faunal groups and biodiversity metrics. In contrast, geo-climatic drivers uniquely and the joint effects of geo-climatic, socio-economic and land use factors explained, on average, 9.9 and 30.9% of the variation in biodiversity, respectively. Geo-climatic conditions were the most important drivers for rare species with a restricted range of occurrence, independent of the faunal group. "Taxonomic distinctness" increased, independent of the faunal group, with increasing socio-economic activity in the catchments, and it responded most coherently among all tested biodiversity metrics.

Main conclusions Our results emphasize that the effects of anthropogenic stressors on (freshwater) biodiversity must be considered in the context of its natural, geo-climatic setting. Taxonomic distinctness has been identified as a very useful response indicator, in addition to species richness and endemicity, as it responded coherently to anthropogenic stressors, and across several faunal groups.

2 Introduction

Globally, agriculture and deforestation are the dominant land use changes (MEA 2005). Land use alteration is an integrator of multiple human activities that may impede freshwater ecosystems through increased sedimentation, nutrient enrichment, contaminant pollution, and hydrological alteration (Bunn et al. 1999, Allan 2004, Schindler 2006). In particular, urban land areas exhibit strong adverse effects on aquatic ecosystems, despite their relatively small extent (Paul and Meyer 2001). Therefore, land use change, economic activity (expressed as the gross domestic product, GDP), and human population density are indicators of human stressor effects (Leprieur et al. 2008 and references therein, Feld et al. 2013). They are proxies of the overall environmental state of freshwater ecosystems (Bunn et al. 1999; Peterson et al. 2011).

So far, few studies have assessed the potential effects of multiple anthropogenic stressors on large-scale (global or continental) contemporary freshwater biodiversity patterns (Stendera et al. 2012). This is mainly due to the fact that freshwater research has traditionally focused on small-scale patterns and processes (Heino et al. 2002 and references therein). Furthermore, previous studies rarely tested for the combined impacts of natural, geo-climatic drivers and anthropogenic stressors (e.g. Irz et al. 2008). The natural, geo-climatic setting however provides the context within which anthropogenic stressors act (Allen 2004, Evans et al. 2005, Brucet et al. 2013).

The increasing availability of large-scale spatial data on freshwater biodiversity facilitates a better understanding of global freshwater diversity patterns and trends, and of their underlying mechanisms, and allows assessing the generality of contemporary distribution patterns among different groups of freshwater species (Lawton 1999, Tisseuil et al. 2012). Large-scale distribution patterns of different groups of organisms are often correlated geographically, referred to as cross-taxon congruence (Pearson and Carroll 1999) or concordance (Lamoreux et al. 2006). Cross-taxon congruence is relevant to conservation planning: if a single organism group can be used as a surrogate of other groups, it would (i) support for a more effective delineation of protected areas and (ii) also aid cost-effective monitoring; both are crucial considering the limited resources available for conservation. In general, concordant spatial patterns in species richness among different taxa may result from: (i) random draw of species; (ii) biotic interactions among different taxa; (iii) common environmental determinants; or (iv) spatial covariance in different environmental factors that independently account for diversity variation in different taxa (see Heino et al. 2002, 2010 and references therein). Cross-taxon congruence is scale dependent (e.g. Heino et al. 2010, Chase and Knight 2013, Chase 2014). Studies spanning large-scale grids (e.g. 2,500–10,000 km^2) and large spatial extents (e.g. countries to continents) have typically reported strongest cross-taxon congruence in species richness patterns; but most studies have been done at small spatial scales and report weak cross-taxon congruence in the species richness patterns of aquatic organisms (see Heino et al. 2010 for a review; Tisseuil et al. 2012). Moreover, the metric "species richness" (i.e. the total number of species in a certain area) has limitations, as it considers all species as equivalent. At the same time, little is known about other components of biodiversity. Therefore, we used taxonomic distinctness and endemicity as additional metrics. The metric "taxonomic distinctness" attributes different weights to species according to their taxonomic relationship with other species in the community, while "endemicity" refers to the proportion of rare species in a given area. Rare species include habitat specialists and species that are highly sensitive to anthropogenic stressors (Feld et al. 2014). Taxonomic distinctness and endemicity are known to add unique aspects of biodiversity aspects which are not covered by species richness (Pienkowski et al. 1998, Gallardo et al. 2011, Tisseuil et al. 2012, Feld et al. 2014).

In a recent publication, Feld et al. (2016) addressed the impact of land use effects on four biodiversity metrics of eleven faunal groups in five freshwater ecosystem types across Europe. Their results suggested that variation in biodiversity due to effects of land use was consistently low for all ecosystem types and organism groups, compared to the variance explained by geo-climatic conditions (unique and also shared effects with land use). Moreover, they revealed significant interactions between geo-climatic conditions and land use, concluding that anthropogenic and geo-climatic factors should be analyzed in combination. Their study set-up and analytical approach is likely to prove seminal, nevertheless, the authors acknowledged the constraint of their species data stemming mostly from national water quality monitoring programs, which were not designed to record biodiversity exhaustively. The lack of data at equivalent spatial resolution and extent of the different taxonomic groups strongly constrained their abilities to develop a cross-taxon congruence approach limiting the generalization of biodiversity responses. Feld et al. (2016) included urban and agricultural land use as indicators of anthropogenic effects; however, gross domestic product (GDP) and human population density are recognized as additional quantitative surrogates of the intensity of anthropogenic activity and resulting pressures (e.g. Leprieur et al. 2008 and references therein). Both socio-economic factors represent structural conditions of human societies such as the extent of economic production and consumption (see Clausen and York 2008 for an overview). In general, the level of environmental degradation increases with the increase in economic activity, at least up to a certain extent (Schnaiberg 1980, but also see Kuznets 1973 and Vörösmarty et al. 2010).

To quantify the effects of various anthropogenic stressors and natural, geo-climatic drivers, individually and in combination, we used the most comprehensive dataset of European freshwater biodiversity including freshwater fish, freshwater molluscs, amphibians, odonates and wetland birds (Kottelat and Freyhof 2007, unpublished update 2010; European Red List 2013, see Methods section). The study covers geographic Europe with the river catchment as study grain. In addition to land use (proportions of agricultural and urban land) and geo-climatic conditions (precipitation, temperature, actual and potential evapotranspiration, catchment area and elevational range, longitude, latitude), we included GDP and human population density as surrogates of habitat disturbance and fragmentation.

We employed a variance partitioning approach, which allowed us to determine the proportion of the variance in patterns of freshwater biodiversity of the five faunal groups that can be attributed to i) anthropogenic stressors, ii) geo-climatic drivers and iii) shared/overlapping influence. Moreover, we analyzed the interactions between geo-climatic drivers and anthropogenic stressors. Additionally, we compared the strength of relationships found among the five faunal groups in order to know whether the detected mechanisms act similarly among these taxa. We hypothesized that rather limited dispersal characteristics of faunal groups such as amphibians or molluscs might be reflected in a higher amount of variance explained by geo-climatic drivers when compared to faunal groups with moderate motility such as fish or high dispersal capacities such as birds (Klvaňova et al. 2009, Tisseuil et al. 2012). Finally, we accounted for different components of diversity, i.e. species richness, taxonomic distinctness (Pienkowski et al. 1998) and endemicity (Crisp et al. 2001) and tested whether these components differed in their response to anthropogenic impact.

3 Methods

3.1 Biological data

Presence/absence data of contemporary native European freshwater fish species were obtained from a GIS referenced species inventory (Kottelat and Freyhof 2007, J. Freyhof, unpubl. data). For native amphibians, wetland birds, odonates and freshwater molluscs, GIS referenced presence/absence data stem from the IUCN Freshwater Biodiversity Unit (European Red List, 2013; http://www.iucnredlist.org/initiatives/europe) and have been catchment corrected. In total, 468 native freshwater fish species, 126 native Odonata species, 232 native wetland bird species, 108 native Amphibia species and 584 native freshwater mollusc species were considered in the analyses.

3.2 River catchments

The river catchment was the spatial unit in our analyses. All river catchments in geographic Europe larger than 2,500 km² that directly drain into the sea were selected from the CCM2 River Network (Vogt et al. 2007); in total 251 catchments (Figure 1). Each of these catchments represents a study site. In total, the 251 catchments combined covered 8.30 × 10⁶ km².

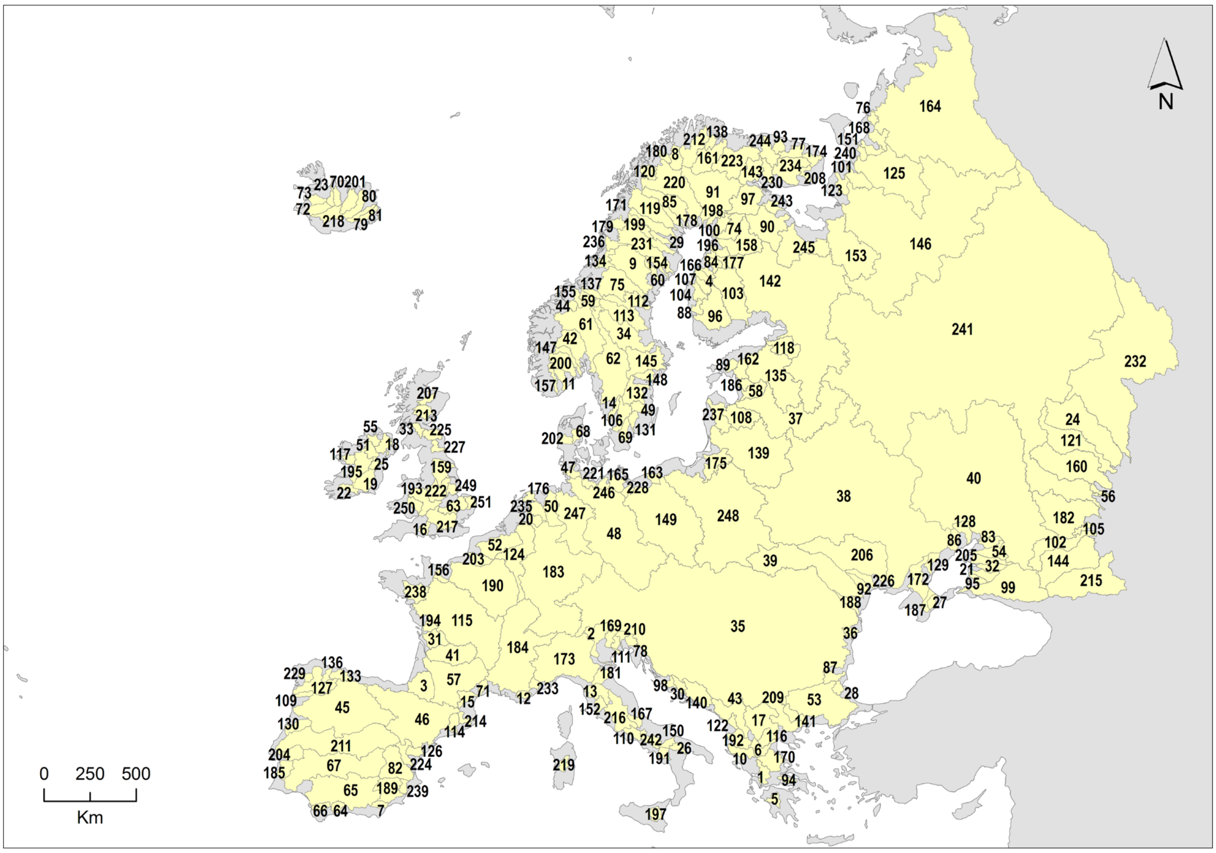

Figure 1: The 251 river catchments >2,500 km² covered in the study; code numbers see Table S3 (Supporting Information).

3.3 Anthropogenic and natural, geo-climatic descriptors

3.3.1 Land use descriptors

The GlobCover land cover map (2010, v2.3; http://due.esrin.esa.int/page_globcover.php) was used to quantify the proportion of agricultural and urban land per catchment. It is a global land cover map at a 10 arc seconds resolution (300m at the equator). We used the class "urban land", based on GlobCover type "Artificial surfaces and associated areas" and the class "agricultural land" for which we aggregated GlobCover types "Post-flooding or irrigated croplands", "Rainfed croplands" and "Mosaic cropland/vegetation". We used the spatial analyst tool of ArcGIS (ESRI ArcGIS 9, Redlands, CA) to obtain the proportions of different land use types for each catchment.

3.3.2 Socio-economic descriptors

We used an ESRI Data and Maps (2013; http://www.arcgis.com/home/item.html?id=cf3c8303e85748b5bc097cdbb5d39c31) layer to obtain human population and GDP (gross domestic product) data per square kilometre and catchment and also GDP per person and catchment. The layer maps the population and GDP for various NUTS (Nomenclature of Territorial Units for Statistics) level 3 geographical units for geographic Europe. We calculated the coverage of each catchment by NUTS level 3 cells and used the sums of the weighted cell values. While the information on the population and GDP per square kilometres are used as quantitative surrogates of habitat disturbance since they reflect the total scale of economic production and consumption, the data on GDP per person serves the purpose to indicate the wealth of the population per catchment and as such as a measure of the standard of living (e.g. Clausen and York, 2008).

3.3.3 Geo-climatic descriptors

Eight natural environmental descriptors were used to account for natural patterns in biodiversity distribution. Catchment area and altitudinal range (highest difference in elevation in each catchment) were derived from the CCM2 River Network (Vogt et al. 2007), latitude and longitude were calculated for each catchment centroid. Mean annual air temperature and mean annual precipitation were derived from the WorldClim database (version 1.4, release 3, 30 arc seconds). Actual and potential evapotranspiration (AET, PET) were derived from the CGIAR-CSI Global PET database (www.cgiar-csi.org and Zomer et al. 2008).

Actual and potential evapotranspiration, precipitation and temperature were used as surrogates of energy entering the individual catchments; latitude and longitude to reflect for the expansion and shrinkage of Pleistocene glaciers and the attempt to explain differences in gradients of present day biodiversity by the potential for re-colonisation since then; altitudinal range and catchment area are recognized as important factors shaping biodiversity through increased habitat diversity and availability (see Tisseuil et al. 2012 and Eme et al. 2015 for detailed descriptions of the proposed mechanisms).

3.4 Biodiversity metrics

We used species richness, endemicity and taxonomic distinctness. Species richness quantifies the number of native species in a catchment. Endemicity is based on Crisp et al. (2001) and Linder (2001) and shows the proportion of endemics in a catchment. It is calculated as a sum of species present in a catchment weighted by the inverse of the number of catchments where the species occurred divided by species richness of the catchment to ensure independence with species richness. Taxonomic distinctness measures the average relatedness of species occurring in a catchment, i.e. the average distance between any pair of species along the Linnaean tree (species, genus, family, order, class) following Warwick and Clarke (1995), Pienkowski et al. (1998) and Clarke and Warwick (2001). Taxonomic distinctness and endemicity are known to correct for species richness effects (Gaston et al. 1998) and thus add a unique, additional dimension of information on biodiversity response to natural and anthropogenic conditions (Gallardo et al. 2011, Tisseuil et al. 2012, Feld et al. 2014).

3.5 Data analysis

For each faunal group and biodiversity metric boosted regression tree analyses (BRTs) were applied to determine the total variance in the biological data explained by geo-climatic and anthropogenic (land use and socio-economic) factors. We moreover identified pairwise interactions between descriptor variables following Elith et al. (2008). In BRTs, the bag fraction was set to 0.5, meaning that 50% of the data were used to build a model and the remaining 50% to validate the model. Model complexity was set individually for each response variable so that the final model was based on between 1100 and 1400 trees, in order to maximise comparability among different models. Environmental descriptors were not checked for collinearity and normality, since BRTs do not require such procedures prior to analysis.

The results of the BRTs were used to define the entry order of each variable and interaction terms into the generalized linear modelling (GLM, description below). The entry order was based on the individual explanatory strength of each descriptor variable, i.e. sorted in descending order of explanatory strength, and interaction term in the full BRT models.

In addition to the determination of the total variance in the biological data, we partitioned the variance following an additive scheme presented by Legendre and Legendre (1998). In order to rule out the differences in area of the catchments, we first ran all BRTs only with the descriptor "catchment area" and determined the fraction of variance explained by this descriptor. We then used the residual deviance and partitioned it into the following fractions: i) influence of pure effects of geo-climatic, land use and socio-economic descriptors, ii) influence of shared effects of pairs of descriptors (geo-climatic and land use, geo-climatic and socio-economic, socio-economic and land use) as well as iii) shared effects of all three descriptor variables together. We tested whether the fraction of explained variance derived from the BRT partitioning scheme attributable to pure geo-climatic, pure socio-economic and pure land use effects significantly differed. This was tested separately for each biodiversity metric (endemicity, taxonomic distinctness and species richness) using a Friedman`s rank sum test for paired samples followed by a Wilcoxon signed rank test for paired samples. The values were paired by faunal groups. The post hoc significance level was Bonferroni corrected.

In a next step, GLM allowed us to identify the best trade-offs between the model fit on the one and its complexity on the other hand, i.e. the most parsimonious model between anthropogenic and geo-climatic descriptors and their pairwise interactions. Individual GLM models were run for each faunal group and biodiversity metric in combination with the geo-climatic and anthropogenic descriptors. Collinear variables with a variance inflation factor exceeding 8 (Zuur et al. 2008) were excluded from the analysis to remove excessive covariance among explanatory variables.

For species richness data we used a Poisson distribution of the error terms and Negative binomial distribution in case of overdispersion in the data. For endemicity and taxonomic distinctness data we used Gaussian regression and logit transformed the data prior to the analyses in order to reach a better fit to the Gaussian distribution (Warton and Hui 2011). The Akaike Information Criterion (AIC) and the adjusted goodness fit (R^2) were used to assess the quality of the individual GLM models; models with the lowest AIC, highest R^2 values and least structure in the scatterplot of residuals were chosen as final models.

We analysed cross-taxon congruence by calculating, for each biodiversity metric (species richness, endemicity, taxonomic distinctness), pairwise Spearman rank correlation coefficients (ρ) between the five faunal groups. We interpreted the correlation coefficients following the procedure proposed by Lamoreux et al. (2006): correlation values of around 0.50 and higher were considered to be good, around 0.30 as moderate and 0.10 and below as weak (see Tisseuil et al. 2012 for a recent application). The same procedure was applied for calculating cross-taxon congruence for each faunal group between the biodiversity metrics.

All analyses were run in R 2.15.3 (R Development Core Team 2013). For BRT, we used the packages 'gbm' (Ridgeway 2013) and 'dismo' (Hijmans et al. 2013). GLM were run with the package 'MASS' (Venables and Ripley 2002).

4 Results

4.1 Boosted Regression Tree Analysis (BRT) and additive effects

In total, we created 15 models testing the relationships between geo-climatic/anthropogenic factors and three biodiversity metrics across five faunal groups. The catchment area accounted for 18.5% (SD: 9.3%) of the total variance explained over all faunal groups and biodiversity metrics combined; Table S1 in Supporting Information.

After correction for catchment size, geo-climatic and anthropogenic factors together explained about three quarters of the total variance in the full BRT models (Figure 2; mean: 77.1%; range 54.1 to 95.2%). Total variance explained was highest for the biodiversity metric taxonomic distinctness, when averaged over all faunal groups (odonates, fish, amphibians, birds, molluscs) (Table S1: mean: 89.5%, SD: 3.7%).

Regardless of the faunal group and the biodiversity metric (i.e., endemicity, taxonomic distinctness and species richness) considered, the proportion of the variance explained exclusively by land use and socio-economic factors was low (mean: 0.2% and 0.3%, respectively; Table S1). The variance attributable to pure geo-climatic effects was much higher (mean 9.9%, SD: 6.9%; significant after Bonferroni correction only for socio-economic vs. geo-climatic factors for the metrics species richness and endemicity; Table S1).

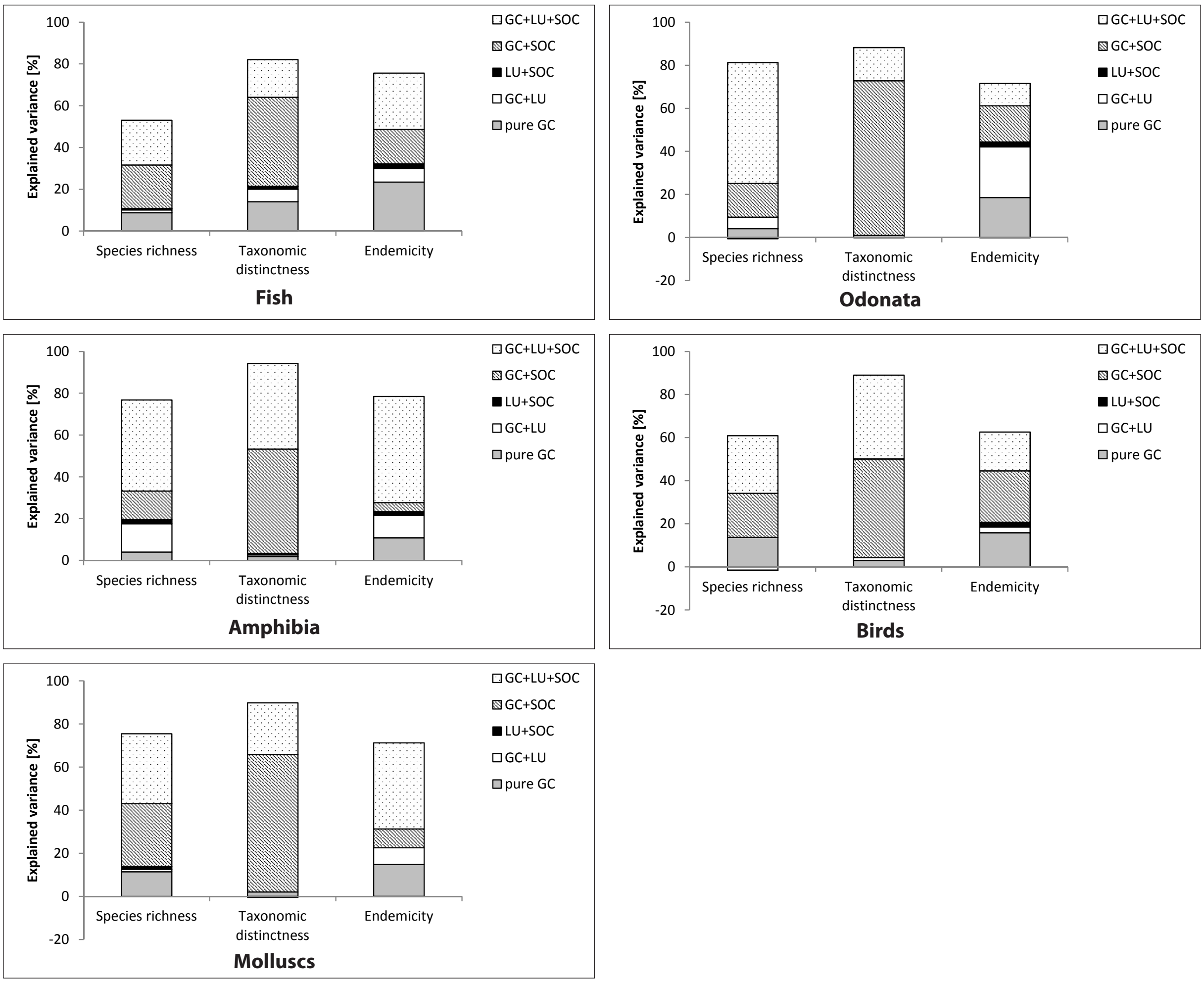

Figure 2: Variance partitioning scheme using three biodiversity metrics and five faunal groups. Each bar plot displays the proportions of variance explained (%) by pure geo-climatic drivers (GC) and shared proportions explained by geo-climatic and land use effects (GC+LU), geo-climatic and socio-economic effects (GC+SOC), socio-economic and land use effects (SOC+LU) as well as geo-climatic, land use and socio-economic effects (GC+LU+SOC) jointly in the Boosted Regression Tree analyses. Pure land use and socio-economic effects are not shown as mostly explained less than 0.5% variance (see Table S1 and Methods).

Among the five faunal groups, averaged over all three biodiversity metrics, the effect of geo-climatic drivers was highest for fish and bird species (median: 14.2%, SD: 7.4% and 13.7%, SD: 6.8%, respectively; Table S1), followed by molluscs, odonates and amphibians (median: 11.4%, SD: 6.6%; 4.2%, SD: 9.4% and 4.0%, SD: 4.7%, respectively).

Among the biodiversity metrics, averaged over all faunal groups, pure geo-climatic effects were highest on endemicity (16.7%, SD: 4.7%; Table S1 and lowest on taxonomic distinctness (mean: 4.5%, SD: 5.5%).

The shared effects of geo-climatic and socio-economic factors together explained 29.6% (SD: 20.4%) of the variance (averaged over all faunal groups and biodiversity metrics) compared to the shared effects of geo-climatic and land use (mean 5.3%, SD: 6.6) and land use and socio-economic factors (mean 0.9%, SD: 1.1%; Figure 2, Table S1). The shared effects of geo-climatic and socio-economic factors were highest for the biodiversity metric taxonomic distinctness, averaged over all faunal groups (mean: 54.8%, SD: 12.5%; Figure 2, Table S1).

Few pairs of anthropogenic and geo-climatic factors exhibited showed negative effect values (Table S1, Figure 2), indicating antithetic effects, or these values were artefacts due to the stochastic nature of BRTs (Real et al. 2003).

4.2 Generalized Linear Modelling (GLM) and interactive effects

In line with the BRT results (described above), all final GLM models showed a high percentage of explained variance. When averaged over all faunal groups and biodiversity metrics, the mean variance in the biological data explained was 66.9% (SD: 10.8%; Table S2).

Urban land use alone explained a low proportion of the variance in the GLM models (<3% for most faunal groups and biodiversity metrics). Agricultural land use accounted for >10% of variance in species richness and endemicity for most faunal groups, but explained a lower proportion of the variance of taxonomic distinctness (mean over all faunal groups: 5.0%, SD: 3.4%; Table 1 and S2). Surprisingly though, species richness and endemicity of almost all faunal groups showed a strong increase in response to increasing area of agricultural land, while for taxonomic distinctness there was no or even a slight negative relationship (Table 1). The percentage of agricultural land use per catchment was relatively low (median 7.3%, SD: 17.5%).

Table 1: Matrix of strength and direction of biodiversity metrics in response to anthropogenic stressors (urban area, agricultural land and socio-economic activity) and geo-climatic drivers across all faunal groups. Precipitation = mean annual precipitation, Temperature = mean annual air temperature, Altitudinal range = altitudinal range of the catchment, Area = catchment area; Response strength and direction („+": positive, „–": negative relationship) are according to the highest explained variance in percent by anthropogenic stressors and geo-climatic drivers in the final GLM models: > [10%] = + + +/– – – ; > [5%] = ++ / – – ; > [3%] = + / – ; ≤ [3%] = 0. „/" indicates that the respective anthropogenic stressor or geo-climatic driver was not included in the final model.

		Fish	Odonata	Amphibia	Birds	Molluscs
Species richness	Urban	/	○	○	○	○
	Agricultural	+	+++	+++	+++	/
	Socio-economic	−−	++	○	○	+++
	Actual evapotranspiration	++	+	+++	++	+++
	Precipitation	○	−−	−	○	−−
	Temperature	/	+++	++	++	○
	Longitude	+++	++	○	++	/
	Altitudinal range	−	○	/	○	−
	Area	+++	+++	++	+++	+
Taxonomic distinctness	Urban	○	○	○	○	○
	Agricultural	−−−	++	−	○	−
	Socio-economic	+++	+++	++	++	+++
	Actual evapotranspiration	○	+++	+++	+++	+++
	Precipitation	−−	−−−	○	○	−−−
	Temperature	○	○	++	+++	○
	Longitude	○	+++	○	++	+
	Altitudinal range	−−−	○	+	○	○
	Area	○	○	○	○	○
Endemicity	Urban	/	−	○	○	/
	Agricultural	+++	○	+++	○	+++
	Socio-economic	−−−	/	○	−−−	/
	Actual evapotranspiration	/	○	○	−−−	+++
	Precipitation	/	−−−	○	−	/
	Temperature	+	+++	+++	○	○
	Longitude	++	+	++	+	○
	Altitudinal range	+++	+++	++	++	+++
	Area	○	/	○	+++	+

Table 2: For species richness, endemicity and taxonomic distinctness we conducted separate Spearman rank correlation tests; pairwise for the five faunal groups of freshwater species. Correlation values (ρ) are calculated using raw data of the 251 river catchments. The significance of (ρ) is indicated as follows: ***p< 0.01, **p<0.05, ns (p>0.1).

		Amphibia	Fish	Odonata	Birds	Molluscs
Species richness	Amphibia		0.45 ***	0.86 ***	0.60 ***	0.70 ***
	Fish			0.64 ***	0.76 ***	0.52 ***
	Odonata				0.75 ***	0.68 ***
	Birds					0.46 ***
	Molluscs					
Endemicity	Amphibia		0.72 ***	0.62 ***	0.53 ***	0.67 ***
	Fish			0.62 ***	0.74 ***	0.56 ***
	Odonata				0.53 ***	0.52 ***
	Birds					0.24 ***
	Molluscs					
Taxonomic distinctness	Amphibia		0.15 **	0.25 ***	0.21 ***	0.24 ***
	Fish			-0.18 ***	-0.51 ***	-0.03 ns
	Odonata				0.51 ***	0.36 ***
	Birds					0.34 ***
	Molluscs					

Socio-economic effects explained >5 and even >10% of the variance in many GLM models. Taxonomic distinctness of all faunal groups increased consistently with increased socio-economic intensity, while the relationship with endemicity, and to a lesser extent also with species richness, was generally negative, regardless of the faunal group considered (Table 1).

We found a negative relationship between precipitation and many faunal groups and the three biodiversity metrics, while other geo-climatic conditions exhibited a positive relationship in many cases (Table 1).

Nine out of 45 of the final GLM models showed significant interactions (Table S4), although the proportion of the explained variance was low for most interactions (mean 2.6%, SD: 2.7).

Analysis of cross-taxon congruence showed that in most cases the biodiversity metrics were significantly correlated across the five faunal groups. The mean correlation strength was higher for species richness (ρ = 0.64, SD = 0.14) and endemicity (ρ = 0.58, SD = 0.14) than for taxonomic distinctness (ρ = 0.13, SD = 0.30) (Table 2).

Within each of the faunal groups the diversity metric taxonomic distinctness showed lower mean correlation values with the other two diversity metrics endemicity and species richness (taxonomic distinctness vs. species richness: ρ = 0.39, SD = 0.45; taxonomic distinctness vs. endemicity: ρ = 0.21, SD = 0.51) than endemicity vs. species richness (ρ = 0.61, SD = 0.14) (Table S5).

5 Discussion

5.1 Single anthropogenic and geo-climatic effects

Our results confirmed the low proportion of variation in biodiversity that can be assigned purely to land use effects across all faunal groups and biodiversity metrics. Similarly, socio-economic effects alone had low influence. In contrast, the geo-climatic conditions explain current biodiversity patterns much better. This is in line with other studies (Brucet et al. 2013, Feld et al. 2016), and suggests that natural gradients inherent in our data are stronger than purely anthropogenic (land use and socio-economic) gradients. The strength of this result was somewhat surprising, since the river catchments we used represented ecologically more meaningful, and in most cases, finer study units (spatial resolution/grain) compared to the large units or grid boundary based cells addressed by previous studies. Therefore, we expected the purely anthropogenic gradients to show a stronger signal. However, apparently, even at this catchment grain resolution, considerable geo-climatic gradients are in place which masked the anthropogenic signals. Thus, our results emphasize the spatial heterogeneity of Europe, where regions such as Scandinavia which were glaciated during the Pleistocene even now host less biodiversity than non-glaciated regions such as the Mediterranean Peninsula (Reyjol et al. 2007; Araújo et al. 2008; Baselga et al. 2012). Moreover, our study catchments covered climatically heterogeneous areas; but climatic effects might still dominate anthropogenic effects even at regional scales (Field et al. 2009).

In contrast to our hypothesis, geo-climatic effects alone explained most of the variation in biodiversity patterns of faunal groups with the highest (e.g., birds) and moderate (e.g., fish) dispersal characteristics. Most likely, the species assemblages of each taxonomic group found in a catchment is comprised of species with heterogeneous dispersal capacities. For instance, about one-fifth of the fish species are migratory (Kottelat and Freyhof 2007), for molluscs, attachment to or ingestion by birds and fish species might allow for long distance dispersal, considerably enhancing the otherwise intrinsically low longitudinal and lateral dispersal capacities of this group (Kappes and Haase 2012). The assumption of heterogeneous dispersal capacities of species of the same faunal group is supported by the fact that for all five faunal groups considered in this study the endemicity metric, which provides a measure of the proportion of endemic species per catchment, showed the highest proportion of variance explained by pure geo-climatic effects. This suggests that for species with a restricted range of occurrence, small-scale geo-climatic effects gain in importance, while geo-climatic effects lose importance for species with high dispersal capacities (Klvaňova et al. 2009).

5.2 Additive anthropogenic and geo-climatic effects

The strong shared effects, especially between geo-climatic and socio-economic factors, suggest that socio-economic effects are strongly linked and interact with natural gradients, i.e. geo-climatic conditions in Europe. Shared effects were especially important in shaping freshwater biodiversity across the five different faunal groups and three biodiversity metrics. In line with Brucet et al. (2013), the results suggest that the single effects of anthropogenic stressors together with the shared effects of geo-climatic and socio-economic factors should be considered if the aim is to quantify the impact of anthropogenic stressors on biodiversity. Otherwise there is the risk of attributing natural effects to those actually caused by humans and vice versa.

5.3 Interaction between anthropogenic and geo-climatic effects

The high fraction of explained variance derived from the BRT partitioning scheme attributable to the shared effects of geo-climatic and socio-economic and also of geo-climatic, socio-economic and land use factors jointly suggested that these factors covary. We therefore investigated and quantified the significant interaction terms resulting from the BRTs in our GLM models, but found that less than one third of the final GLM models showed significant interactions. Considering the strong shared effects detected in the BRTs, it was surprising to have such a low number of final GLM models showing significant interactions. Additionally, the percentage of explained variance of most interaction terms was low. In line with the study by Feld et al. (2016) were we not able to "translate" the strong additive effects identified in the BRTs to the multiplicative interactions identified in the GLM models. Furthermore, did we not find a concordant decline in biodiversity response with increasing anthropogenic stress. Biodiversity metrics of several faunal groups showed a positive relationship, i.e. an increase with increased proportion of agricultural land use (species richness and endemicity) or socio-economic activity (taxonomic distinctness) in the catchments. Other studies have shown that in response to environmental stress, species assemblages have the tendency to phylogenetically deplete, i.e. the taxonomic relatedness of the community members increase, and that rare taxa are among the first to disappear because of being sensitive to impacts such as habitat deterioration (e.g. Pienkowski et al. 1998, Feld et al. 2014). In most of the catchments in our study, agricultural land use took place at low to moderate levels, probably causing only intermediate disturbance with regard to the overall intensity and spatial extent, which allowed for stable overall species richness and also for many species with restricted range of occurrence to exist (Townsend et al. 1997). Species richness and endemicity, however, decreased in response to increased socio-economic activity; obviously, in such settings, species losses were no longer balanced by species gains in the catchments. Species richness of hololimnic species such as fish decreased. Richness of wetland birds was weakly affected, most likely this faunal group was able to compensate the severe loss of floodplains across Europe (see Tockner et al. 2009) through their dispersal capacities.

In contrast, socio-economic activities led to an increase of the taxonomic diversity of community members of all five faunal groups in the study catchments. Apparently, taxonomic distinctness shows a more coherent picture if applied to data at large spatial scales. Among the three biodiversity metrics applied, total variance explained was highest for the metric taxonomic distinctness when averaged over all faunal groups (mean: 89.5%), it responded well to socio-economic factors, and was only weakly correlated to the other two metrics, underpinning its unique contribution to the observed patterns of biodiversity response to anthropogenic impact.

5.4 Conclusions

We used river catchments as spatial units, aiming to overcome the dominance of the supposedly long gradients over which geo-climatic conditions form. Nevertheless, pure geo-climatic drivers were most important in explaining freshwater biodiversity patterns across Europe, therefore, the effects of anthropogenic stressors can only be understood when considering the environmental setting and context. Our results suggest that a finer spatial grain, i.e. (geo-)climatically more homogenous units than entire river catchments, probably need to be used to better disentangle the effects of anthropogenic stressors from those of natural drivers.

Taxonomic distinctness (of all faunal groups), in particular, has been identified as a robust metric responding consistently to habitat disturbance and habitat fragmentation at the catchment level. Taxonomic distinctness is an easy-to-apply indicator, using species presence/ absence data, and it is independent of species richness.

Using different, and complementary, community-based biodiversity metrics supports disentangling the cause-relation chains between anthropogenic stressors, geo-climatic drivers, and their shared effects, single and in combination, on large scale patterns of freshwater biodiversity.

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Supporting Information

A Results

Table S1: Variance partitioning scheme using three biodiversity metrics and five faunal groups. The proportions of variance explained (%) by pure geo-climatic drivers (GC) and shared proportions explained by geo-climatic and land use effects (GC+LU), geo-climatic and socio-economic effects (GC+SOC), socio-economic and land use effects (SOC+LU) as well as geo-climatic, land use and socio-economic effects (GC+LU+SOC) jointly in the Boosted Regression Tree analyses. Sr: Species richness; TaDi: Taxonomic distinctness ; Endm: Endemicity; Area: catchment area.

	Fish			Odonata			Amphibia			Birds			Molluscs		
	Sr	TaDi	Endm	Sr	TaDi	Endm	Sr	TaDi	Endm	Sr	TaDi	Endm	Sr	TaDi	Endm
GC	8.8	14.2	23.5	4.2	1	18.6	4	1.9	10.8	13.7	3.1	15.9	11.4	2.1	14.9
LU	0.9	0	0.6	0.1	0	0	0	0.8	0	0.2	0	0.4	0	0.4	0
SOC	0	2.6	0	0.5	0	0	0	0	1	0	0.6	0	0	0	0
GC+LU	1.3	5.9	6.5	5.4	0	23.5	13.5	0.8	10.8	-1.5	1.3	2.7	1.2	0	7.8
LU+SOC	0.7	1.5	2.2	-0.5	0	2.3	2	0.7	1.8	-0.1	-0.1	2.2	1.3	-0.4	-0.1
GC+SOC	20.9	42.6	16.6	15.6	71.8	16.8	13.7	49.9	4.3	20.5	45.8	23.9	29.2	63.8	8.7
GC+LU+SOC	21.5	18	26.8	56.2	15.4	10.4	43.6	41	50.9	26.8	38.9	18	32.4	23.8	39.9
Unexplained	11.5	2.6	1.1	0.4	0.1	7.7	2.9	0.9	5	3.3	0.5	7.9	9.4	0.6	12
Area	34.4	12.6	22.7	18.1	11.5	20.7	20.2	3.9	15.4	37.1	10	29.1	15.1	9.7	16.9

Table S2: Proportion of variance explained (%) by anthropogenic stressors and geo-climatic drivers in the biological data in the final GLM models. „/" indicates that the respective anthropogenic stressor or geo-climatic driver was not included in the final model. Precipitation = mean annual precipitation, Temperature = mean annual air temperature, Altitudinal range = altitudinal range of the catchment, Area = catchment area.

		Fish	Odonata	Amphibia	Birds	Molluscs
Species richness	Urban	/	0.6	0.1	0.7	0.5
	Agricultural	4.3	26.1	26.1	16.6	/
	Socio-economic	8.5	5.4	0.2	0.3	11.4
	Actual evapotranspiration	8.7	3.5	27.9	5.6	21.8
	Precipitation	2.1	4.8	3.1	1.2	5.8
	Temperature	/	11.3	5.3	6.9	0.3
	Longitude	11.6	5.1	1.4	5.8	/
	Altitudinal range	3.4	1.4	/	1.1	4.5
	Area	23	12	8.7	29.2	3.9
	TOTAL	**62**	**70.2**	**72.8**	**67.4**	**48.2**
Taxonomic distinctness	Urban	0.9	0.2	0	0.2	0.5
	Agricultural	10.6	5.9	3.1	2.3	3.3
	Socio-economic	14.2	11.1	9.1	6.6	12.1
	Actual evapotranspiration	2.8	22.1	26.9	40.8	22.9
	Precipitation	5.5	12.8	1.7	2.9	20.1
	Temperature	0.4	0.3	5	13.3	0.8
	Longitude	0.6	15	0.3	9.7	3.1
	Altitudinal range	14.3	1.2	4.8	0.6	2.7
	Area	0.2	0.1	1.2	1.3	0
	TOTAL	**49.5**	**68.7**	**52.1**	**77.7**	**65.4**
Endemicity	Urban	/	4	0.5	0.5	/
	Agricultural	30.2	2.1	52	1.7	28.3
	Socio-economic	19.7	/	0	33.1	/
	Actual evapotranspiration	/	1.7	0	10.3	13.2
	Precipitation	/	11.3	1.1	3	/
	Temperature	3.7	16.1	19.5	0.4	1.3
	Longitude	6	3.9	5	3.8	0.6
	Altitudinal range	13.4	12.9	5.2	7.9	14.6
	Area	0.7	/	0.5	11.8	3.3
	TOTAL	**73.7**	**52.1**	**83.8**	**72.5**	**61.3**

Table S3: List of catchment code numbers (see Figure 1) and catchment names.

No.	Catchment name	No.	Catchment name	No.	Catchment name	No.	Catchment name
1	Acheloos	64	Guadalhorce	127	Miño	190	Seine
2	Adige	65	Guadalquivir	128	Mius	191	Sele
3	Adour	66	Guadelete	129	Molochnaya	192	Seman
4	Ähtävänjoki / Purmonjoki	67	Guadiana	130	Mondego	193	Severn
5	Alfeios	68	Gudenå	131	Mörrumsån	194	Sevre Nantaise
6	Aliakmon	69	Helgeån	132	Motala ström	195	Shannon
7	Almanzora	70	Héraðsvötn (Austari-Jökulsá and Vestari-Jökulsá)	133	Nalón	196	Siikajoki
8	Altaelva	71	Hérault	134	Namsen	197	Simeto
9	Ångermanälven	72	Hvítá (Árnessýsla)	135	Narva	198	Simojoki
10	Aoös / Vjosa	73	Hvítá (Borgarfjarðarsýsla)	136	Navia	199	Skellefteälven
11	Arendalsvassdraget	74	Iijoki	137	Nea-Nidelvvassdraget	200	Skiensvassdraget
12	Argens	75	Indalsälven	138	Neiden / Näätämöjoki	201	Skjálfandafljót
13	Arno	76	Indiga	139	Nemunas	202	Skjern Å
14	Ätran	77	Iokanga / Lylyok	140	Neretva	203	Somme
15	Aude	78	Isonzo / Soca	141	Nestos	204	Sorraia
16	Avon	79	Jökulsá á Dal (á Bru)	142	Neva	205	Sosyka-Yasemi
17	Axios / Vardar	80	Jökulsá á Fjöllum	143	Niva / Imandara	206	Southern Bug
18	Bann	81	Jökulsá í Fljótsdal	144	Nogayskaya step swamps	207	Spey
19	Barrow	82	Júcar	145	Norrström	208	Strelna
20	Berkel	83	Kagal'nik	146	Northern Dvina	209	Strymon
21	Beysug	84	Kalajoki	147	Numedalslagen	210	Tagliamento
22	Blackwater	85	Kalixälven	148	Nyköpingsän	211	Tajo
23	Blanda	86	Kalmius	149	Oder	212	Tana
24	Bolshoy Uzen' and swamps	87	Kamchiya	150	Ofanto	213	Tay
25	Boyne	88	Karvianjoki	151	Oma	214	Ter
26	Bradano	89	Kasari	152	Ombrone	215	Terek
27	Bulhanak-Mokryj Indol	90	Kem	153	Onega	216	Tevere
28	Burgas Lakes and Wetland	91	Kemijoki	154	Öreälven	217	Thames
29	Byskeälven	92	Khadzhybeiśkyi and Kuyal'nytśkyi liman	155	Orkla	218	Þjórsá
30	Cetina	93	Kharlovka	156	Orne	219	Tirso
31	Charente	94	Kifisos	157	Otra	220	Törneälven
32	Chelbas	95	Kirpili-Kochety	158	Oulujoki	221	Trave
33	Clyde	96	Kokemäenjoki	159	Ouse / Trent / Humber	222	Trent
34	Dalälven	97	Kovda / Koutajoki	160	oz. El'ton and swamps	223	Tuloma
35	Danube	98	Krka	161	Paatsjoki / Pasvikelva	224	Turia
36	Danube Delta channels and lakes	99	Kuban	162	Parnu	225	Tweed
37	Daugava	100	Kuivajoki	163	Parsęta	226	Tylihul'skyi liman
38	Dnieper	101	Kulay	164	Pechora	227	Tyne
39	Dnister / Nistru	102	Kuma	165	Peene	228	Uecker
40	Don	103	Kymijoki	166	Perhonjoki	229	Ulla
41	Dordogne	104	Kyrönjoki	167	Pescara	230	Umba
42	Drammensvassdraget	105	Lagan wetlands	168	Pesha	231	Umeälven
43	Drin	106	Lagan / Nissan	169	Piave	232	Ural
44	Driva	107	Lapuanjoki	170	Pinios	233	Var
45	Duero	108	Lielupe	171	Piteälven	234	Varzuga
46	Ebro	109	Lima	172	Pivnično Krymśkij Kanal - Krasnohvardijśke	235	Vecht
47	Eider	110	Liri	173	Po	236	Vefsna
48	Elbe	111	Livenza	174	Ponoy	237	Venta
49	Emän	112	Ljungan	175	Pregolja	238	Vilaine
50	Ems	113	Ljusnan	176	Prinses Margrietkanaal channels	239	Vinalopó
51	Erne	114	Llobregat	177	Pyhäjoki	240	Vizhas
52	Escaut / Schelde	115	Loire	178	Råneälven	241	Volga
53	Evros / Maritsa	116	Loudias	179	Ranelva	242	Volturno
54	Eya	117	Lough Corrib	180	Reisaelva	243	Von'ga
55	Foyle	118	Luga	181	Reno	244	Voronya
56	Ganyushkino salt marshs	119	Luleälven	182	Rep. Kalmykiya wetlands	245	Vyg / Belomorsko-Baltiyskiy kanal
57	Garonne	120	Målselva	183	Rhine	246	Warnow
58	Gauja	121	Malyy uzen' / Ashshiözek and swamps	184	Rhone	247	Weser
59	Gaula	122	Mat	185	Sado	248	Wisla
60	Gideälven	123	Megra	186	Salaca	249	Witham
61	Glomma	124	Meuse / Maas	187	Salgir	250	Wye
62	Göta älv	125	Mezen	188	Sarata-Cogalnic	251	Yare
63	Great Ouse	126	Mijares	189	Segura		

Table S4: Percent variance explained by significant interaction terms including anthropogenic stressors (urban area, agricultural land, socio-economic activity) in the final GLM models. If more than one interaction was significant, the explained variance (%) of each interaction is provided. Geo-climatic drivers interacting with anthropogenic stressors are provided in brackets; ateyr = actual evapotranspiration; long = longitude; avrange = altitudinal range in the catchment.

	Species richness			Taxonomic distinctness			Endemicity		
	Urban	Agricultural	Socio-economic	Urban	Agricultural	Socio-economic	Urban	Agricultural	Socio-economic
Fish			0.5 (aetyr)					0.6 (avrange)	
Odonata		2.9 (aetyr)						9.7 (long)	
Amphibia		1.8 (aetyr) 3.8 (long)						3.7 (avrange)	
Birds		0.3 (long) 0.7 (avrange)						2.1 (avrange)	
Molluscs								2.9 (long)	

Table S5: For each faunal group we conducted separate Spearman rank correlation tests; pairwise for the three biodiversity metrics. Correlation values (ρ) are calculated using raw data of the 251 river catchments. The significance of (ρ) is indicated as follows: ***p< 0.01, *p<0.1, ns (p>0.1). Sr: Species richness; TaDi: Taxonomic distinctness; Endm: Endemicity.

	Fish	Odonata	Amphibia	Birds	Molluscs
Sr vs. TaDi	-0.37 ***	0.59 ***	0.33 ***	0.65 ***	0.76 ***
Sr vs. Endm	0.45 ***	0.51 ***	0.69 ***	0.59 ***	0.8 ***
Endm vs. TaDi	-0.63 ***	0.46 ***	0.12 *	0.43 ***	0.69 ***

Chapter III
The Danube River Basin

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2009

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NS compiled the paper and authored sections 1, 3, 4, 5, 7 (7.1, 7.2 jointly with JB, 7.4 jointly with MP), 8 (jointly with JB), 9, 10 (jointly with KT).

1 Introduction

The Danube is the European river par excellence; a river that most effectively defines and integrates Europe. It links more countries than any other river in the world. The Danube River Basin (DRB) collects waters from the territories of 19 nations and it forms the international boundaries for eight of these (Figure 1). The river's largely eastward course has served as a corridor for both migration and trade, and a boundary strongly guarded for thousands of years. The river's name changes from west to east from Donau, Dunaj, Duna, Dunav, Dunărea, to Dunay, respectively. The names of the river (Danube, as well as Don, Dnjeper, and Dnjester) most likely originate from the Persian or Celtic word Danu, which literally means flowing. It also may stem from the Celtic "Don, Na," or "two rivers," because the Celts could not agree on the source of the Danube (Wohl, 2010).

In this chapter, we provide an overview of the DRB, including the three main sections (Upper, Middle, Lower Danube), the delta and 11 major tributaries (Figures 1 and 2, Table 1). This chapter builds upon several textbooks on the Danube, including Liepolt (1967) and Kinzelbach (1994) and, among many other sources, on information derived from the International Commission for the Protection of the Danube River (ICPDR).

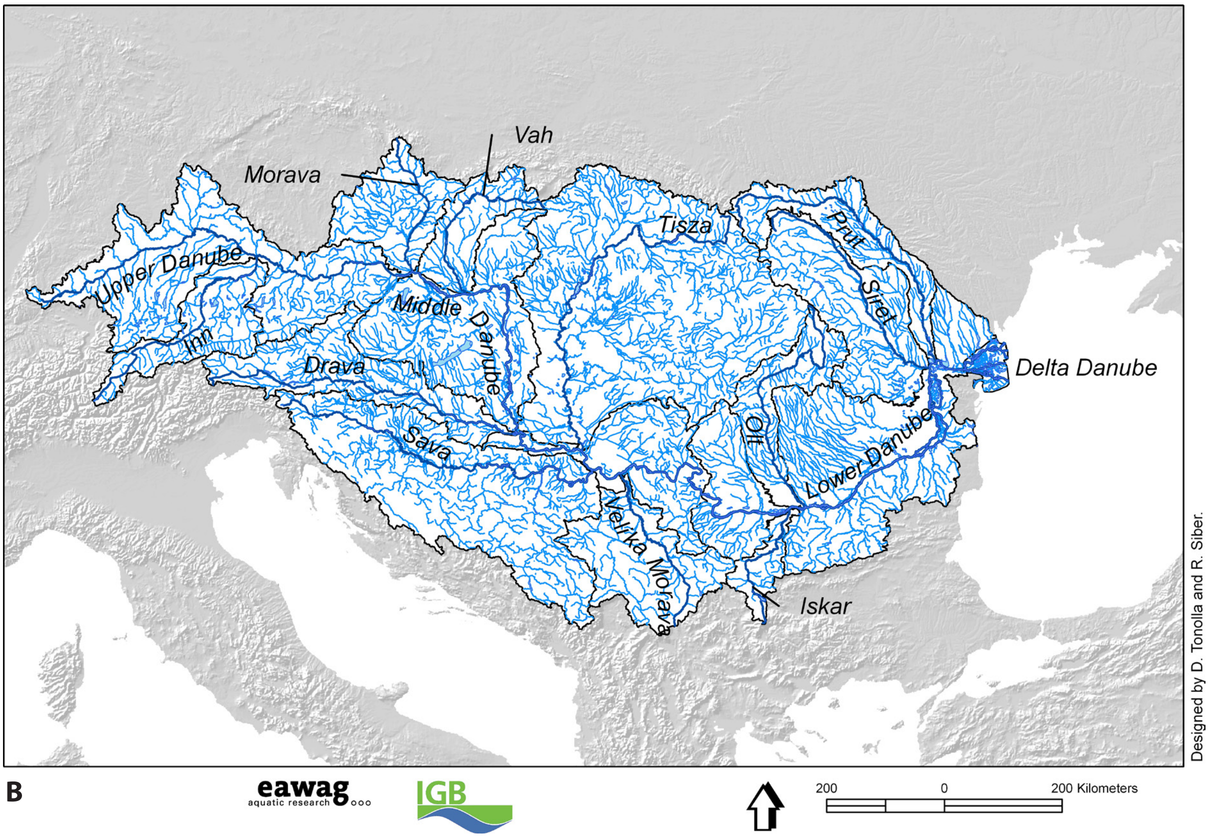

Figure 1: Digital elevation model (A) and drainage network (B) of the Danube River Basin. Major sub-basins are delineated. The Iskar River is not discussed in detail in the text. Data sources: Digital elevation model (DEM) is derived from the USGS' 30 arc-second DEM of the world (GTOPO 30), resolution: 1000 m × 1000 m, http://edcdaac.usgs.gov/gtopo30/hydro/index.asp. Delimitation of the Danube catchment and sub-catchments is based on the CCM river and catchment database JRC/IES European Commission, 2003, http://agrienv.jrc.it/activities/catchments/ccm.html. Drainage network is based on the HYDRO1k basins database http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html; data checked by co-authors and changed if necessary.

Table 1: General characterization of the Danube River Basin. Catchment boundaries: see Figure 1a. The Iskar River is not treated in detail in the text. n.d.: Not determined.

	Upper Danube	Middle Danube	Lower Danube	Delta Danube	Inn	Morava	Váh	Drava	Tisza	Sava	Velika Morava	Iskar	Olt	Siret	Prut
Mean catchment elevation (m)	793	435	355	9	1260	378	473	760	350	541	631	655	621	485	267
Catchment area (km²)	104 932	473 214	218 387	4560	26 128	27 267	19 660	40 087	156 087	95 793	37 571	8860	24 439	46 289	28 568
Mean annual discharge (km³)	25,3	125,9	187,7	204,7	23,1	3,47	4,35	17,1	25,0	49,6	8,47	1,70	5,43	6,63	2,11
Mean annual precipitation (cm)	101,2	79,2	60,5	43,2	136,0	63,8	79,3	112,1	65,8	105,4	77,8	62,1	67,6	62,4	59,8
Mean air temperature (°C)	6,7	8,8	9,2	10,7	4,6	8,1	7,5	7,3	8,6	9,2	9,3	9,4	7,9	7,7	8,5
Number of ecological regions	4	8	7	1	2	4	2	3	2	4	3	2	4	5	4
Dominant (≥25%) ecological region(s)	2; 70	52	9	55	2; 70	52; 70	13; 52	2; 52	52	27; 52	9	9; 58	9; 13	13; 22	13; 22; 28
Landuse (% of catchment)															
Urban	4.7	4.1	6.0	2.4	2.9	6.0	6.4	3.5	4.9	2.1	1.7	6.3	5.0	7.7	4.9
Arable	31.5	44.8	54.1	22.9	14.7	59.4	45.6	28.7	48.1	36.9	38.8	42.2	36.5	38.8	57.3
Pasture	13.4	7.8	6.7	1.1	15.4	3.0	6.4	7.9	11.1	5.8	7.3	4.3	12.6	9.4	7.3
Forest	37.3	35.4	26.6	5.8	35.2	29.3	36.8	45.8	30.0	45.3	42.6	30.3	37.4	38.2	27.7
Natural grassland	6.4	5.9	4.1	4.6	13.5	1.8	3.8	9.0	4.4	8.4	8.8	14.6	6.7	3.9	0.6
Sparse vegetation	5,5	0.6	0.3	1.4	17.0	0.0	0.2	3.9	0.1	0.7	0.5	1.6	0.4	0.2	0.0
Wetland	0.3	0.5	0.7	49.0	0.3	0.0	0.2	0.3	0.7	0.1	0.0	0.1	0.4	0.5	1.2
Freshwater bodies	0.9	0.9	1.5	12.8	1.0	0.5	0.6	0.9	0.7	0.7	0.3	0.6	1.0	1.3	1.0
Protected area (% of catchment)	0,5	2,8	0,7	89,1	0,9	7,7	11,2	0,3	3,0	0,8	0,0	0,0	0,0	0,3	3,3
Waterstress (1–3)															
1995	2,0	2,0	2,0	2,2	2,0	2,0	2,0	2,0	2,0	2,0	2,0	2,1	2,0	2,0	2,0
2070	2,9	3,0	3,0	3,0	2,9	3,0	3,0	3,0	3,0	2,9	2,9	3,0	3,0	3,0	3,0
Fragmentation (1–3)	3	3	2	1	3	3	3	3	2	2	2	2	3	3	2
Number of large dams (>15m)	217	143	227	0	31	46	17	49	45	18	3	2	27	18	3
Native fish species	59	72	70	70	15	45	37	49	56	50	35	37	17	29	41
Non-native fish species	13	12	7	4	2	7	n.d.	14	12	5	7	3	6	5	5
Large cities (>100 000 inhabitants)	7	23	18	0	2	2	0	3	13	5	1	1	2	3	3
Human population density (people/km²)	140	95	101	34	84	129	133	91	85	92	116	170	87	75	112
Annual gross domestic product ($ per person)	27 726	4886	1746	2145	31 317	8771	4342	15 832	2876	3664	702	2763	2212	1703	943

Data sources: Catchment elevation is derived from the digital elevation model (DEM) USGS' 30 arc-second DEM of the world (GTOPO 30), resolution: 1000 m ×1000 m, http://edcdaac.usgs.gov/gtopo30/hydro/index.asp. Delimitation and areal extent of the Danube catchment and sub-catchments is based on the CCM river and catchment database JRC/IES European Commission, 2003, http://agrienv.jrc.it/activities/catchments/ccm.html. Discharge: data from co-authors. Precipitation and air temperature: derived from: CRU Global Climate Dataset. Monthly mean values from 1961 to 1990, resolution: 10 000 m × 10 000 m. http://www.ipcc-data.org/obs/get_30yr_means.html. Ecological regions: data derived from Olson *et al.* (2001), http://www.worldwildlife.org/science/data/item1875.html, resolution: 1000 m × 1000 m; numbers of ecoregions: 2: Alps conifer and mixed forests, 9: Balkan mixed forests, 13: Carpathian montane forests, 22: Central European mixed forests, 27: Dinaric Mountains mixed forests, 28: East European forest steppe, 52: Pannonian mixed forests, 55: Pontic steppe, 58: Rodope montane mixed forests, 70: Western European broadleaf forests. Land use: land cover derived from USGS with classification according to International Geosphere Biosphere Programme (IGBP), 1992/1993, http://edcsns17.cr.usgs.gov/glcc/tablambert_euras_eur.html; the original 17 classes were reclassified in 8 classes: urban, grasland, cropland, shrub, forest, barren, wetland, waterbody; resolution: 1000 m × 1000 m; data checked by co-authors and changed if necessary. Protected area: sum of % of the total catchment area of Ramsar sites, national parks, national nature reserves, and other nationally protected areas; modified data derived from the world database on protected areas (WCPA), 2005; http://sea.unep-wcmc.org/wdbpa/; resolution: 1000 m × 1000 m; data checked by co-authors and changed if necessary. Water stress: data derived from Alcamo *et al.* (2007); three water stress categories: Low (1), Middle (2) and Severe (3). Fragmentation: calculated after Dynesius & Nilsson (1994); Nilsson *et al.* (2005). Three fragmentation categories.1: Not affected; 2: Moderately affected; 3: Strongly affected. Large dams / fragmentation: dams higher than 15 m. Data from co-authors. Fish species: Data from co-authors and Kottelat & Freyhof 2007. Large cities: Cities with more than 100 000 inhabitants; derived from "Cities of Europe and cities of the world" (ESRI®Data & Maps, 2004). Human population density: derived from the population density grid for the year 2000 adjusted to match persons per square km; Gridded Population of the World, version 3 (GPWv3, 2005); Center for International Earth Science Information Network (CIESIN), Columbia University; Centro Internacional de Agricultura Tropical (CIAT), http://sedac.ciesin.columbia.edu/gpw/, resolution: 5000 m × 5000 m, data checked by co-authors and changed if necessary. Gross domestic product (GDP): Data derived from ESRI®Data & Maps, 2004, resolution: 1000 m × 1000 m.

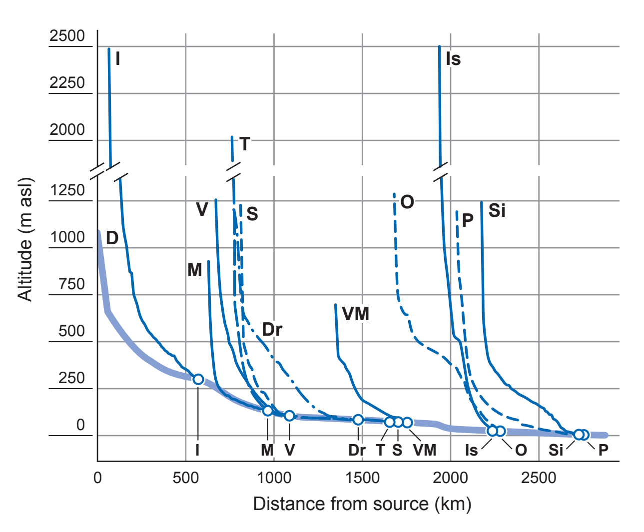

Figure 2: Longitudinal profile of the Danube River and its major tributaries. D: Danube, I: Inn, M: Morava, V: Váh, T: Tisza, S: Sava, Dr: Drava, VM: Velika Morava, O: Olt, Is: Iskar, P: Prut and Si: Siret.

2 Historical Aspects

In 1908, an 11-cm large statuette, the so-called "Venus of Willendorf", was excavated by the archaeologist Szombathy near the village of Aggsbach (Austria, Wachau valley), dating back 25 000 years BC. North of this place, in Dolvi Vestonica, a large meeting place of mammoth hunters from the same period was discovered 1924–1952. These two examples demonstrate that the Danube valley has experienced a long history of human occupation and cultural development that started during the Paleolithic period. Between 8500 and 500 BC, permanent fishery and hunting settlements were erected in Lepinski Vir (Iron Gate Gorge) and Vina (in the suburban sector of Belgrade) (Weithmann 2000). Starting >7000 years ago, farmers from Anatolia entered Europe and expanded throughout the continent. The Danube was most likely one of the major expansion pathways. There is evidence that a major flood that entered the Black Sea from the Mediterranean (i.e., the diluviam) probably forced the westward migration of these early farmers.

Between 750 and 500 BC, the Celts occupied the entire Upper Danube valley. The best known place was the Heuneburg near Riedlingen where a large Celtic wall circled the entire hill. The Celts respected the Danube as a bringer of life and death and their sole connection to the outside world. They called it the Great Mother of Gods – Danu. The Celts were stimulated by Greek culture. The Greek poet Hesiod first mentioned the Danube in about 700 BC as the "beautifully flowing Istros", the son of Tethys and Okeanos. Herodotus wrote in 450 BC that the (H)Istros is the largest river in the world, a river that "has its source in the country of the Celts near the city Pyrene, and runs through the middle of Europe, dividing it into two portions … before it empties itself into the Pontos Euxeinos". During the war against the Scythes in 513/12 BC, Dareis, the great Persian king, sailed up the Danube to explore a suitable location for constructing a bridge for his army. The first European waterway was established during the Greek period and connected the Adriatic Sea with the Black Sea via the Ocra pass, the Sava River and the Lower Danube. Today, there exist plans to re-establish this ancient Danube–Adriatic waterway for navigation.

The Danube was always both a migration corridor as well as a frontier. During the Roman Empire, the 'Limes' along the Danube as well as along the Olt River protected the Empire agains the 'Barbarians'. The Romans erected fortifications along the Danube such as Castra Regina (Regensburg), Juvavum (Salzburg), Lentia (Linz), Vindobona/Vindomana (Vienna) and Aquincum (Budapest), among many others. The Limes played an important role even long after the fall of the Roman Empire, for example, it was used as a fortification against the Mongolian invasion in 1241. The armies of Charlemagne also marched along the remnants of the Roman Limes, as did the Crusaders. The boundary between Orient and Occident is roughly just east of the Iron Gate and south of Belgrade. The division into two parts has remained for most of its history, making the Danube '*aqua contradictionalis*', the river of fatality as mentioned by Pope Innocent IV.

The Roman Empire influenced the Danube region for >500 years, starting with the expansion of the empire toward the Danube during the regency of Octavianus Augustus. The Upper Danube, down to the Iron Gate, then changed its name from (H)Ister (Istros) to Danuvius (Danubis). The Romans established several provinces along the Danube, including Raetia, Pannonia, Dacia, Moesia and Scythia. Dacia was the only province north of the Danube, but it was given up by Emperor *Aurelian* in 270 AD. The retreat of the Romans from Dacia created a power-vacuum and contributed to a global politcal and military crisis at that time. In the context of the Roman Empire, the Danubian provinces were primarily of military interest and the people in Rome and the Mediterranean area considered these provinces as culturally undeveloped.

The battle at Adrianopel (Edirne), 378 AD, marked the beginning of the end of the Roman Empire. An unstable period followed after the fall of the Empire and the subsequent invasion by the Barbarians. German tribes and later Turkic Avars ("Huns" is often used synonymously for Avars) entered the area and crossed the Danube; in particular during winter when the Middle and Lower Danube were frozen. The Goths left Pannonia at the end of 469 and crossed the frozen Danube north of Aquincum (Budapest). The Langobards replaced the Goths in Pannonia, remaining for >100 years. Moesia was the only Roman province along the Danube that remained for longer periods under the control of Constantinople, the capital of the Eastern Roman Empire. The Avars, a steppic tribe that forced the Langobards to leave the area (the Langobards settled in northeast Italy), established their Khangat in the Danube–Tisza area. For short periods, they expanded their area to near Constantinople. In the 7th century, Slavs (Croatians and Serbians) originating from north of the Carpathian Mountains and nomades (Bulgarians) from the Volga area entered the Danube region and replaced the Avars in the Sava–Drava and Lower Danube, respectively. Later, the Avars disappeared from the Pannonian plain, and in 895 AD the Magyars, originating from the northeast Ural Mountains and western Sibiria, arrived in the Pannonian plain and established their regency. The Upper Danube was mainly under the control of the Bavarians.

Up to 1050 AD, the Danube was primarily a migration corridor for warriers. During the 11th century, the river became an important route for pilgrims visiting the Holy Country and Jerusalem. However, the Crussards could not stop the loss of the Holy Country to the Ottoman Empire. The Ottoman Empire influenced the Danube region for ~500 years. The 'foreign' rule by the Turks has often been blamed for the present state of under-development in the Middle and Lower Danube. Bulgaria was the first country under Ottoman control (1393–1878). In 1389, Serbia lost at the memorable battle of Kosovo polje against the Ottomans. Soon after, the entire Danube downstream of Iron Gate became under Ottoman control. During the Ottoman Empire, the Danube was again a "Limes" but this time to protect the northern parts against the threats entering from the south. Hungarians (King Sigismund), together with French, Burgundian and German armies, tried to re-occupy these areas but were defeated by Sultan Bayezid at Nikopolis in 1396 AD. This battle stabilized the Ottoman occupation in the area for the coming centuries, until the Balkan wars at the beginning of the 20th century.

At the end of the 13th century, the Habsburg dynasty appeared for the first time in the Upper Danube valley after they had lost their stronghold in 1291 AD to the Swiss Federation. Until the 15th century, the Habsburg influence was restricted roughly to the area of present Austria. After the successful battle against the Ottomans in 1683 at Vienna, the Austrians, together with their allies, expanded their territories, re-occupied Budapest, freed Hungary and for a short period also Belgrade. The fight for the "golden apple" Vienna was a historic benchmark event for all of Europe. Kara Mustafa moved 200 000 men, the largest army Europe ever saw, along the Danube, devastating whole areas. During these battles, galleys constructed by the Dutch were successfully used on the Danube. In 1867, the Austrio-Hungarian Monarchy was formed, which was known as the "Danube-Monarchy" until the great political reconfiguration in 1918. Along the Lower Danube and delta, the Russians established their influence at the beginning of the 19th century. After World War II, the Iron Curtain again divided the Danube basin and increased the difference between the two parts.

The Danube has served as a major waterway since the Greek period. In Vienna, the Romans already erected a pontoon bridge during the war against the Markomans. And at Drobeta Turnu–Severin (Serbian/Romanian border), the Emperor Trajan erected in 105 AD a ~1000-m wide wooden bridge across the Danube (the famous Trajan bridge). The *Tabula Trajana*, a monument of the Roman frontier, marks a section of the Roman road along the Danube. The tablet honours Trajan for the construction of the road and bridge over the Danube. Along the Pannonian section of the Danube, the *Classis Pannonica*, the warship fleet of the Romans operated. These boats were 35-m long and 5-m wide, provided space for 120 people and reached a speed of 10 km/hr (Weithmann 2000; Landesausstellung 1994). In 1828, the "Donau-Dampfschiffahrtsgesellschaft" (DDSG) was founded. It soon became the world's largest inland shipping company, with a total length of navigable rivers and canals of 4100 km, a fleet of ~1000 ships, and ~12 000 staff members.

Early attempts to connect the Danube with the Main and Rhine Rivers date back to Charlemagne in 793, who tried to build a 2-km long canal between Altmühl and the Swabian Rezat, yet failed to complete it. In the following centuries, this idea was brought up several times but was never fully realised. The Bavarian King Ludwig I opened in 1845 a continuous waterway – the «Ludwig-Main-Danube-Canal» – which was in operation until World War II, but never gained importance because of limited capacity and the concurrent development of the railway network. Construction of the 177-km long Rhine–Main–Danube Canal started in 1960 and was completed in 1992.

Early attempts to coordinate the use of the Danube River led to the 1856 Treaty of Paris. Based on negotiations that started in 1848 (Congress of Vienna), the Budapest Commission was created to coordinate navigation. A convention on fisheries was signed among the lower Danube countries, but it took 2500 years after Herodotus and the fall of the Iron Curtain for Europeans to agree on the protection and sustainable use of the river. Based on the Danube River Protection Convention signed in 1994, the International Commission for the Protection of the Danube River (ICPDR) was founded.

3 Palaeogeography and Geology

Comprehensive introductions to the palaeogeography and geology of the Danube River Basin are given in Liepolt (1967), Hantke (1993), Blühberger (1996), Neppel *et al.* (1999), Domokos *et al.* (2000), Belz *et al.* (2004) and Kováč *et al.* (2006). The largest part of the basin belongs to the alpidic or neo-European geological macro-region in Europe. Smaller parts belong to the western and eastern Variscan subregions and to the pre-Palaeozoic Russian platform. In the tertiary, the basin was part of the Paratethys, a branch of the Tethys, the proto-Mediterranean Sea. During this period, the Alps, the Carpathian Mountains, the Dinarides, and the Balkan Mountains started to fold via plate tectonics. In the Miocene and Pliocene, the nuclei of these mountain chains formed islands in the shallow Paratethys. The rivers that exist today appeared for the first time in the Middle Miocene. They emerged as coastal rivers from the surrounding mainland and as streams on the Paratethys islands. It is worth noting that the basin boundary of the former Paratetys is almost identical to the present boundary of the Danube basin. Since that time, only local exchanges between neighbouring basins took place.

During the Pliocene, a strong uplift of the mountains occurred. Subsequently, massive debris and sediment erosion, conditioned by a sub-tropical climate, gradually filled the shallow Paratethys. A progressive subsidence of sub-basins, the Pannonian basin in particular, followed. At the end of the Pleistocene, the Paratethys became brackish, then freshened and finally formed a network of lakes, swamps and watercourses. This fluvio-lacustrine system disappeared when the residual lake Geta silted up completely in the first half of the Pleistocene.

Periodic cooling during the Pleistocene led to partial and complete (in the Alps) glaciation of the mountains that continued to rise. As a consequence, physical weathering generated vast amounts of solid material that filled the Danube basins to their present level. In piedmont zones, the rivers formed megafans and bedload ramps and the channels permanently shifted their course. In glaciation-free mountains, the rivers followed incised valleys.

Geologically, the Upper Danube is much older than the Rhine. In the Pleistocene, the Rhine started at the southwestern tip of the Black Forest, while waters from the Alps that today feed the Rhine were carried east by the so-called *Urdonau* (original Danube). Parts of this ancient riverbed, which was much larger than the present Danube at this location, can still be found as submerged canyons in the Swabian Alb. After the Upper Rhine valley had descended, rivers draining the northern slopes of the Alps changed their direction towards the Rhine. Because the Swabian Alb consists of porous limestone and the valley bottom of the Rhine is much lower than the Upper Danube, water from the Danube still continues to feed the Rhine via subsurface pathways (the so-called “Donauversickerung” or “loss of Danube” near Immendingen). Most of this water resurfaces at Aachtopf, Germany’s most yielding spring with an average production of 8000 L/s, north of Lake Constance.

In the Middle Danube, following the aggradation of the Vienna Basin, the river first followed the eastern margin of the Alps southwards, turned at the southern border of the Pannonian Basin eastwards, and finally reached the Iron Gate. At Visegrád Gate, it formed an immense alluvial fan that gradually filled the depression of the Great Hungarian Plain.

In the Lower Danube, the river course is more stable. Due to climate-induced low flow, tributaries exiting the mountains immediately deposited coarse bedload material and only small amounts of sediments, mainly as suspended material, reached the Danube valley. The Danube River valley, structured by several terraces, stretched along the southern margin of the Romanian Lowland. During the past 15 000 years, the Romanian section of the Danube valley has been mainly shaped by tectonic activities. Between Bazias and Drobeta Turnu Severin, the Danube flows for 130 km through a deep valley that links the Pannonian depression with the Dacic Basin ("Iron Gate"). The ongoing uplift of the Carpathian Mountains during the Pleistocene and Holocene resulted in intense erosion of the valley, which is <200 m wide. The evolution of the Danube floodplain in Romania is also strongly influenced by aeolian processes, which resulted in the formation of dunes. The thickness of the aeolian sands decreases progressively eastwards (Ghenea & Mihailescu 1991).

One of the most significant changes in flow direction was experienced by the River Olt, which originally had been a tributary to the River Mureş/Maros (a present tributary of the Tisza). It was captured by a smaller, yet direct Danube tributary that had cut deeply into the southern Carpathian Mountains, so that it was diverted towards the Danube. In this way, the Transylvanian Basin, that was originally uniform in hydrographic terms, became divided into the basins of the River Tisza/Tisa and Danube. The Danube first entered the sea south of the Dobrogea region, but due to a tectonic uplift of this area in the second half of the Pleistocene, it was forced to follow the northern margins of the Dobrogea. The water level of the Black Sea fluctuated by 70–80 m, shifting the river mouth forwards and backwards. The ancient Danube bed can still be traced on the Black Sea bottom.

At the beginning of the Holocene, the development of the present river system was nearly complete. Only three changes are notable. First, karstification of the Swabian Alb continued, with the consequence that a high proportion of the Danube flow entered the Rhine basin via subsurface sinks. This process will continue in the future and will lead to a further loss of Danubian headwaters. Second, a tectonic uplift of the northeast part of the Great Hungarian Plain forced the Tisza River to change its course. Third, the Black Sea transgressed into the debouchure area of the Danube valley up to the foreland of the Carpathian Mountains. This transgression, however, was limited in time, so that the Danube was then able to fill the embayment and to develop its present delta.

The main mountain ranges in the west of the basin (Black Forest, Bavarian Forest and Bohemian Forest) mostly consist of crystalline metamorphic rock. Crystalline bedrock also predominates in the central Alps, the central chain of the Carpathians and parts of the Stara Planina (Belz *et al.* 2004). Flysch sedimentary rocks extend from the German Prealps to the northern and eastern scarp of the Carpathian arc and to the northern part of the Stara Planina Mountains. In the Dinarids, Mesozoic limestone and dolomite covers the northern and southern limestone Alps. Near-surface quarternary sediments, mostly of alluvial origin, prevail along the river valleys. Sediments of aeolian origin (mainly loess and sand) dominate the non-alluvial zones of the basin.

4 Geomorphology

The Danube begins at the confluence of the Breg and Brigach Rivers in the Black Forest near Donaueschingen (Germany). It flows for a distance of 2826 km and enters the Black Sea east of Izmail (Ukraine) and Tulcea (Romania). The Danube is the second largest river in Europe and drains an area of ~801 093 km². Published information on the size of the basin varies depending on the source and whether the Black Sea coastal waters and river basins are included. The basin drains parts of 19 countries with a total human population of 83 million (census in 2002). Albania, Italy, Macedonia and Poland together contribute <0.1% to the area and <0.1% to the total human population within the basin (ICPDR 2005). The highest points are Piz Bernina (4052 m asl) on the western edge and Peak Krivan (2496 m asl) in the northern part of the basin. The average altitude of the basin is 458 m.

The Danube River Basin can be divided into three general sections and the delta (recently the Danube has been divided into up to 10 smaller zoogeographic sections, Birk & Sommerhäuser 2003). The Upper Danube extends from its source to the confluence with the Morava River near Bratislava (so called "Porta Hungarica"), the Middle Danube extends from Bratislava to the Iron Gate dams (border between Romania-Serbia), and the Lower Danube is formed by the Romanian-Bulgarian lowlands. Finally, the Danube delta, the 6th largest delta in Europe.

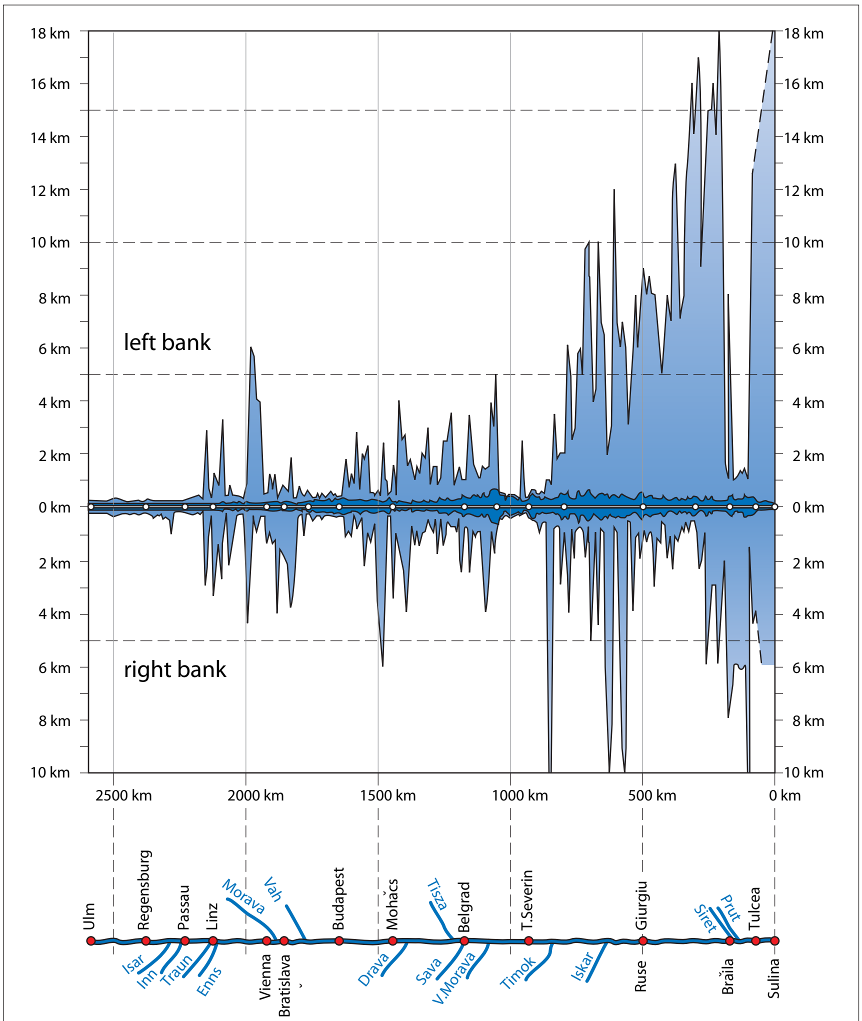

Figure 3: Extention of former inundation areas along the Danube River (area shaded in light blue) (from Ulm, Germany, downstream to the mouth). Dark blue band marks the average width of the main river channel based on Lászlóffy (1967) and modified after Tockner *et al.* (1998).

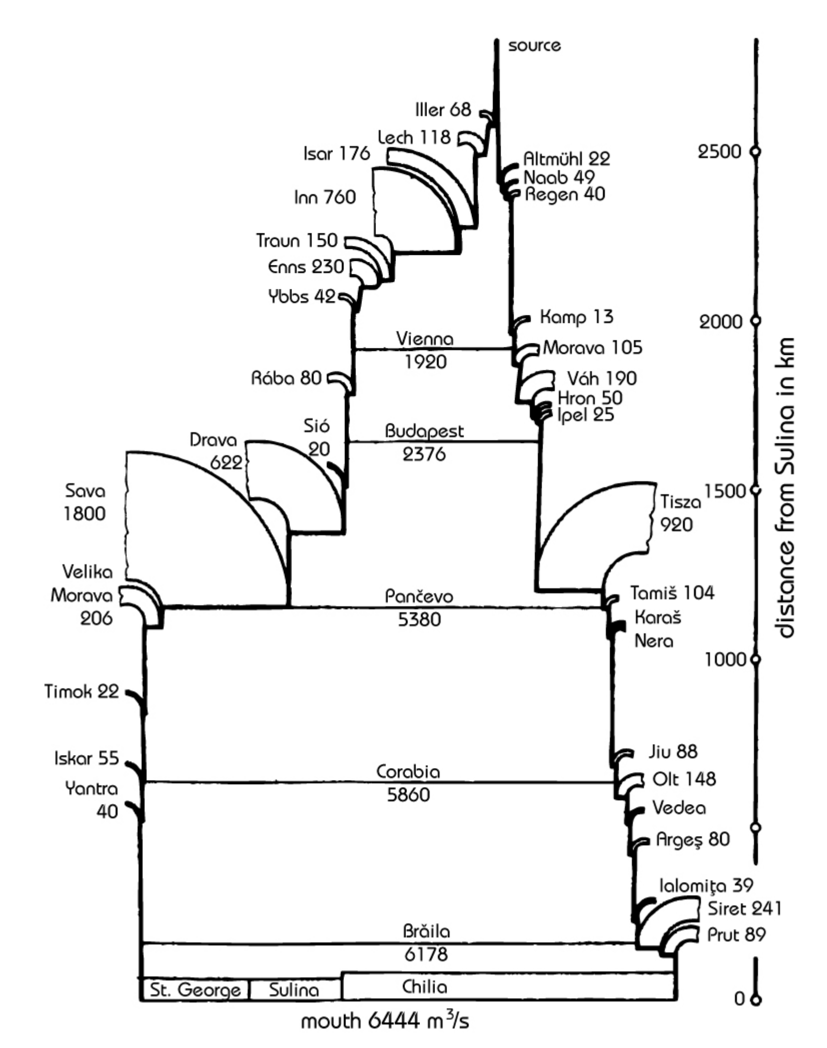

Figure 4: Average annual discharge (m^3/s) of the Danube River and its main tributaries. Note that major tributaries are from the right side (in flowing direction), especially in the upper part (alpine origin). The Tisza River is the main tributary from the left side. Redrawn after Liepolt (1967).

A characteristic feature along the entire river is the alternation between flat basins and deep gorges. The former floodplain width, before regulation, reached >10 km in the Upper Danube and >30 km in the Lower Danube (see Figure 3). Slope decreases from 0.4‰ in the upper valley to 0.004‰ in the final 250 km before it enters the Black Sea (Figure 2). The Upper Danube, after the confluence of the Brigach and Breg Rivers, follows the fault gap of the German Alb. Major tributaries in the south (Iller, Lech, Isar, Inn, Salzach, Traun and Enns Rivers) drain Alpine sub-basins increasing the discharge in the Danube substantially (Figure 4). The Morava River is the most important tributary from the north. The Upper Danube has an Alpine character with low water temperature, high velocity and coarse bed sediments.

Immediately downstream of the Porta Hungarica, the Danube forms a vast internal delta, and the slope decreases to 0.08–0.03‰. The Middle Danube is the largest of the three sections. It traverses the Pannonian plain and enters the 117 km long Iron Gate gorge where it flows through the Balkan and Carpathian mountains. The main left-bank tributaries are the Vah and Hron in Slovakia and the Tisza that enters the Danube in Serbia. The main right-bank tributaries include the Leitha, Raab, Drava, Sava and Velika Morava Rivers.

The Lower Danube is a typical lowland river fringed by (formerly) wide floodplains. In the 1960s, major floodplain sections (~5500 km^2, or 72% of former floodplains) were cut off from the river and

Table 2: Flood plain loss in the Danube River Basin. Data from Schneider (2002).

River stretch	Morphological floodplain (km^2)	Recent flood-plain (km^2)	Loss
Upper Danube	1762	95	95%
Middle/Central Danube	8161	2002	75%
Lower Danube	7862	2200	72%
Danube delta	5402	3799	30%
Total	23 187	8096	65%
in comparison: River Rhine	8000	1200	85%

transformed into agricultural land, poplar plantations, and fish ponds (Table 2). The Olt, Siret and Prut are the main tributaries entering from north, while only smaller tributaries, such as the Iskar, enter from the south. Despite the loss of floodplains ("balta" area), the Lower Danube represents an ecologically highly valuable section, with numerous islands, natural banks and floodplain remnants (Schneider 2002).

The Danube delta, including adjacent oxbow lakes and lagoons, covers some 5640 km^2 (about 20% in the Ukraine, 80% in Romania). Major changes took place between 1960 and 1989, when 1000 km^2 were poldered in the Romanian part for agriculture, forestry and fish culture. The fluvial backwaters in the Ukraine have been isolated from the river for aquaculture since the 1960s, whereas the frontal marine lagoons in the Romanian and Ukraine parts were isolated from the sea and used as a reservoir for irrigation purposes after the 1970s. The total length of channels in the Romanian delta increased from 1743 km to 3496 km (Gâștescu *et al.* 1983). Discharge from the river to the delta wetlands increased from 167 m^3/s before 1900 to 309 m^3/s during 1921–1950; 358 m^3/s during 1971–1980 and 620 m^3/s during 1980–1989 (Bondar 1994). Despite these engineering measures, over 3000 km^2 of the wetlands, including the Razim–Sinoe lagoon and the adjacent Ukrainian secondary delta (250 km^2), remain connected to the river and represent the largest nearly undisturbed wetland in Europe. About 50% of the area is permanently aquatic; the rest is seasonally flooded.

The Danube basin fully or partially covers nine ecoregions (Alps, Dinaric Western Balkan, Hellenic Western Balkan, Eastern Balkan, Central Highlands, The Carpathians, Hungarian Lowlands, Pontic Province and Eastern Plains). For the transitional and Black Sea coastal waters, Romania and Bulgaria have proposed to define a new ecoregion: The Black Sea ecoregion.

5 Climate and Hydrology

Due to its large size, its distinct west–east orientation, and its diverse relief, the basin exhibits a large climatic heterogeneity. The Upper Danube is influenced by an Atlantic climate with high precipitation and mild winters, whereas the eastern regions are under a continental influence with low precipitation and dry and cold winters. Parts of the Drava and Sava Rivers are influenced by a Mediterranean climate. The heterogeneity of the relief, especially the differences in the extent of exposure to predominantly westerly winds, as well as the differences in altitude, diversify this general climate pattern. This effect leads to distinct landscape regions that exhibit major differences in climatic conditions.

Precipitation ranges from <500 to >2000 mm. Average annual precipitation peaks in the highest parts of the Alps (~3200 mm) but is as low as 350 mm in the Black Sea and delta regions. Snowcover between November and February/March is expected at an elevation >1500 m asl (cited in Belz *et al.* 2004). Average peak precipitation occurs in July in the western part of the basin, in May/June in the southeastern parts, and in autumn in the areas influenced by the Mediterranean. The highest average annual temperature (+11 to +12 °C) occurs in the Middle and Lower Danube and in the lower Sava valley. Seasonal differences increase from west to east. In the Hungarian plains, the seasonal change in temperature (min./max.) can be as high as 74 °C.

Spatial and seasonal differences in precipitation have strong effects on the surface run-off and discharge regime of the Danube and its main tributaries (ICPDR 2005). For example, Austria (22% of total flow) and Romania (18%) contribute most to the total flow of the Danube, reflecting the high pecipitation in the Alps and Carpathian mountains. The average annual specific discharge decreases from 25 to 35 L/s/km² in the Alpine headwaters to 19 L/s/km² for the Sava, 6.3 L/s/km² for the Tisza and to 2.8 L/s/km² for the rivers draining the eastern slopes of the Carpathians (Belz *et al.* 2004). At its mouth at Ceatal Izmail (upstream end of the Danube delta), the mean annual discharge is ~6480 m³/s, corresponding to an annual flow of 203.7 km³ (range: 134 km³ in 1990; 297.1 km³ in 1941) (Table 3).

In the Lower Danube, the flow regime has been modified by the Iron Gate dams as well as by the large water management schemes along the Olt, Argeș, Siret and Prut Rivers. The suspended sediment load decreased from ~40 million tons/year (maximum of 106 million tons in 1940) to a low of 7.3 million tons/year today. The basin has experienced many disastrous floods. The flood in February 1342, associated with a big ice drift, caused the reported death of 6000 people. The largest flood during the past millenium was the memorable flood in August 1501. Peak discharge at Vienna was ~14 000 m³/s, and

Table 3: Flow regime (in m³/s) of the Danube River and its major tributaries (time period: 1931–1990). A: Catchment area upstream of gauging station; NQ: lowest measured discharge; MNQ: arithmetic mean of the lowest measured annual discharge; MQ: arithmetic mean annual discharge; MHQ: arithmetic mean annual flood discharge; HQ: highest measured discharge (data: Belz *et al.* 2004).

River	Station	A (km²)	NQ	MNQ	MQ	MHQ	HQ	MHQ/MNQ
Danube	Berg	4047	4,6	12,9	38,5	209	445	16,2
Danube	Regensburg	35 399	107	198	444	1468	2531	7,4
Danube	Vienna	101 731	504	832	1920	5547	9600	5,5
Danube	Bezdan	210 250	505	992	2372	4788	7689	4,8
Danube	Orsova	576 232	1060	2246	5611	10 604	14 813	4,7
Danube	Ceatal Izmail	807 000	1790	2901	6486	10 889	15 540	3,8
Inn	Passau-Ingling	26 084	195	267	732	2936	6359	11
Morava	Moravsky Jan	24 129	7,7	29	110	584	1573	20,1
Váh	Sala	10 620	0,5	22	138	861	1497	39,1
Drava	Donij Miholjac	37 142	166	234	541	1359	2281	5,8
Tisza	Senta	141 715	80	179	792	2142	3730	12
Sava	Sremska Mitrovica	87 996	194	401	1572	4154	6638	10,4
Velika Morava	Most Ljubicevski	37 320	17	55	277	1290	2355	23,5
Olt	Stoenesti	22 683	15	48	172	908	2320	18,9
Siret	Lungoci	36 036	16	52	210	1294	2825	24,9
Prut	Cernicvi	6890	1,5	10	67	1200	2170	120

flood marks can still be seen along the entire Danube. Since 1821, the water level has continuously been recorded at selected stations. The flood in 1862 stimulated the regulation of the main Danube (1869 to 1876) and the largest flood in the last century occured in 1954 (peak discharge at Vienna was 9600 m^3/s).

6 Biogeochemistry, Water Quality and Nutrients

6.1 General Characteristics

Physico-chemical and selected biological parameters are regularly monitored by contracting parties of the International Commission for the Protection of the Danube River (ICPDR). These data for the Danube and its main tributaries are mostly derived from the TransNational Monitoring Network (TNMN; monitoring period: 1996–2005). The biogeochemistry of the Upper Danube is mainly influenced by the Alps. The major tributaries Sava, Drava and Tisza dominate the chemistry of the Middle Danube, where alluvial deposits predominate, whereas the Iron Gate reservoirs influence the biogeochemistry and material transport in the Lower Danube (Garnier *et al.* 2002; Teodoru & Wehrli 2005). Last, the flux of nutrients and transported material to the Black Sea is influenced by the Danube delta, one of the largest European wetlands and covered by vast reed beds (UNESCO-MAB Biosphere Reserves Directory – http://www.unesco.org).

In general, the ion content increases along the course of the river. Calcium is the major cation, and carbonates, sulphates and chlorides are the main anions. Tributaries with the highest ion contents include the Prut and Siret, where elevated conductivity values result from high sulphate and chloride concentrations (Table 4). Suspended solid concentrations increase with drainage size and range from 27 mg/L to over 40 mg/L. Suspended solid concentrations are positively related to discharge with maximum concentrations during the rising limb of the hydrograph that can exceed 1000 mg/L (Zessner *et al.* 2005). The Siret and Prut as well as the Inn and Tisza Rivers exhibit the highest mean concentrations of suspended solids. In the Austrian Danube section, suspended solids are dominated by silt (70%) and clay (25%), mainly composed of silicates and secondary limestones of Alpine origin (Nachtnebel *et al.* 1998). The discharge-weighted annual load of suspended solids ranges from 0.7 to 3.1×10^6 t/year in the Upper Danube and from 3.5 to 6.3×10^6 t/year in the Lower Danube (TNMN yearbook 2000–2004). The Inn and Tisza contribute most to the annual load of the river with loads ranging from 0.7 to 2.5×10^6 t/year. The Iron Gate reservoirs cause a >50% reduction in suspended solids in the Lower Danube (Petschinov 1987; Friedl & Wüest 2002; Teodoru & Wehrli 2005; Kalchev *et al.* 2008). Reduced sediment input, in concert with other human induced impacts along the river, has lead to a decrease in recent Danube delta development. This change follows a 12 000 year evolution characterized by active progradation (Panin & Jipa 2002).

6.2 Water Quality

Over the last 50 years, water quality has become a key issue for the Danube and the coastal zone of the Black Sea (Schmidt 2001). The first attempt to map the water quality in the basin was made by Liepolt

(1967). Between the 1950s and 1970s, water quality was particularly impacted downstream of cities and industrial areas in the Upper Danube. In addition, the self-purification capacity of the river suffered from toxic industrial wastewater inputs. In the early 1980s, construction of wastewater treatment plants (WWTP) led to a major reduction of biodegradable organic matter and improved the water quality in the Upper Danube (Wachs 1997). Water quality in the Middle and Lower Danube remained relatively high (class II) between 1950 and the 1970s (Russev 1979; Kalchev *et al.* 2008), but deteriorated afterwards due to rapid industrial development, poor pollution control, and inputs from heavily polluted tributaries.

The total phosphorus (P) content, calculated using a model-based approach (MONERIS, see details in Kroiss *et al.* 2005), significantly decreased since the early 1980s due to the introduction of P-free detergents and P-retention in treatment plants in upstream countries. The economic breakdown in downstream countries also led to significant reductions from agricultural and industrial sources. In combination with the retention of P in the Iron Gate reservoirs, P loads decreased to levels found in the 1950s. The present total nitrogen (N) load into the river is still ~2.2 times higher than in the 1950s, although inputs have slightly decreased since the peak in the 1980s.

The total annual nutrient load in the river was estimated to be around 750 000 tons N/year and 68 000 tons P/y. For nitrogen, the main sources are groundwater (from agricultural inputs) and WWTPs (about 67% of all sources). For phosphorus, WWTPs and land erosion are the dominant sources (>80% of all sources), emphasizing the importance of point sources of phosphorus (Kroiss *et al.* 2005). The relative contribution of different countries and of different sub-catchments varies considerably for P and N. Todays total N and P loads are ~10 times above natural background values. Silica loads have only increased by 10% due to human impacts.

Long-term data demonstrated that during the past decades between 400 000 and 500 000 tons N/year, between 15 000 and 20 000 tons P/year (Kroiss *et al.* 2005) and between 150 000 and 300 000 tons Si/year are exported by the Danube into the Black Sea (Humborg *et al.* 1997). Peak loads for N and P occurred in the 1980s and early 1990s. Differences between loads from the basin and fluxes into the Black Sea are ~300 000 tons N/year and 50 000 tons P/year (Kroiss *et al.* 2005), and show the high retention and transformation capacity of the basin. In a recent study, Teodoru & Wehrli (2005) showed that the Iron Gate reservoirs are of relatively low importance in retaining sediments and nutrients. The numerous dams along tributaries and the mainstem upstream of the Iron Gate reservoirs may account for these differences, as well as the natural retention capacity of small tributaries. Friedl *et al.* (2004) showed that <4% of the dissolved silica in the river is retained in the Iron Gate reservoirs, pointing to the role of the large number of other reservoirs within the basin in nutrient retention. Regardless, the Iron Gate reservoirs still play an important role in the retention of suspended sediments and P.

Nitrate is the main component of N transported in the river (>70% of total N), and nitrate concentration decreases with increasing river size (Table 4). Ammonia and nitrite contribute <10% to the total N load. Nitrate shows a distinct seasonal cycle with peak values in winter. Organic N and P are positively related to discharge. During low flow, phytoplankton comprise a dominant fraction of the organic N (Literáthy *et al.* 2002). Phosphorus in transport is mainly bound to particles. In the Upper Danube, major floods (with a probability of once in 10 to 100 years) can transport between 25–65% of the total

Table 4: Physicochemical and biological parameters of the main Danube River sections and tributaries based on data from the TransNational Monitoring Network (TNMN) 1996-2005. Minimum, mean, maximum values and number of measurements (n) are shown. <dl: lower than detection limit; *: data from JDS 1 (Literáthy *et al.* 2002); n.d.: Not determined.

		Conductivity [µS/cm]	Dissolved oxygen [mg/L]	pH	Total nitrogen [mg/L]	Organic nitrogen [mg/L]	Ammonium (NH_4–N) [mg/L]	Nitrate (NO_3–N) [mg/L]	Nitrite (NO_2–N) [mg/L]	Total phosphorus [mg/L]	Orthophosphate (PO_4–P) [mg/L]	Silicates (SiO_2) [mg/L]	Calcium (Ca^{2+}) [mg/L]	Chloride (Cl) [mg/L]	Magnesium (Mg^{2+}) [mg/L]	Sulphate (SO_4) [mg/L]	Suspended solids [mg/L]	TOC [mg/L]	DOC [mg/L]	Chlorophyll a [mg/L]	BOD_5 [mg/L]
Upper Danube	Min.	247	3,7	7,5	1	<dl	<dl	0,6	<dl	<dl	<dl	4,4	24	7	6,1	<dl	<dl	<dl	<dl	<dl	<dl
	Mean	386	10,9	8,2	2,6	0,5	0,1	2,3	0,02	0,1	0,03	4,7	57,2	17,6	12,8	26,7	27,5	3,1	2,6	11,8	1,9
	Max.	641	28	9	5,2	2,1	0,7	5,3	0,09	0,8	0,12	5,2	101	53	30,4	55,8	1413	11	7	143	7,3
	n	1489	1501	1490	293	380	1578	1578	1325	1577	1464	10	1190	1577	1190	1345	1575	1455	810	1134	1571
Middle Danube	Min.	121	n.d.	6,2	0,7	<dl	<dl	<dl	<dl	<dl	<d	I0.2	6,7	2	0	3,4	<dl	0,4	2,9	<dl	<dl
	Mean	389	9,8	8	2,6	0,6	0,2	1,8	0,03	0,1	0,06	6,8	53,7	20,6	14,2	37,6	29	4,6	3,8	18,6	3,1
	Max.	8331	8,3	9	8	9,7	4	9	0,81	5,1	4,4	25	117	46	1067	108	286	15,2	4,9	156	16,8
	n	4279	4451	4393	1037	2198	4415	4421	4408	4218	4299	1576	3322	3273	3331	3243	3659	1319	12	2567	4317
Lower Danube	Min.	219	n.d.	n.d.	0,6	<dl	<dl	<dl	<dl	<dl	<dl	0,7	10,4	<dl	<dl	<dl	<dl	<dl	<dl	<dl	<dl
	Mean	397	8,6	7,9	2,4	1,1	0,2	1,5	0,03	0,1	0,09	7,8	55,9	27,7	17,6	42,6	43,7	4,9	2,6	6,7	2,7
	Max.	793	16,5	9	4,9	2,6	1,8	6,2	0,41	4,1	1,26	21,8	164	106	102	126,4	898	8,5	17,4	73	13,7
	n	1780	1787	1785	236	347	1772	1788	1799	1431	1670	842	1623	1720	1632	1533	1553	9	86	681	1758
Delta Danube	Min.	314	n.d.	n.d.	0,6	n.d.	<dl	0,1	<dl	<dl	<dl	0,4	9,2	<dl	7,3	<dl	1	n.d.	n.d.	<dl	<dl
	Mean	444	8,6	7,8	2,3	n.d.	0,3	1,6	0,04	0,1	0,05	8,4	53,1	36,3	20,5	39,4	36,1	n.d.	n.d.	2,3	2,4
	Max.	1353	14,5	8,7	4,7	n.d.	2,9	9	1,51	2,7	0,82	24,6	84,1	386,5	67,8	134	405	n.d.	n.d.	12,2	6,4
	n	1540	1653	1658	363	n.d.	1660	1661	1663	1489	1579	1404	1524	1609	1523	1495	1596	n.d.	n.d.	128	1633
Inn	Min.	131	8,1	7,3	0,6	n.d.	<dl	0,2	<dl	<dl	<dl	n.d.	20	<dl	5,6	<dl	<dl	<dl	n.d.	n.d.	<dl
	Mean	245	11,2	8,2	0,8	n.d.	0,1	0,6	0,01	0,1	0	13.4*	33,6	4,3	9,4	26,9	68	1,6	n.d.	n.d.	1,5
	Max.	4741	5,9	8,6	1,2	n.d.	0,4	6,1	0,02	1,8	0,06	n.d.	46,5	14	13,3	52	3211	6,6	n.d.	n.d.	6,1
	n	257	257	257	7	n.d.	255	252	12	256	253	1	22	254	21	22	247	256	n.d.	n.d.	249
Morava	Min.	271	6,2	7,5	1,9	<dl	<dl	<dl	<dl	<dl	<dl	n.d.	31,3	9,7	3,6	35	1	2	<dl	<dl	1,6
	Mean	484	11,4	8,1	3,3	0,9	0,3	2,9	0,04	0,2	0,13	7.5*	60,3	27,8	10,8	73	35,9	6,2	5,1	34,2	4,4
	Max.	693	14,8	8,8	5,1	2,8	3,3	6,8	0,17	0,6	0,34	n.d.	100	47,9	24,9	102,4	619	32,6	19,8	214	10,4
	n	119	119	119	11	107	119	119	119	119	119	1	119	119	119	119	119	107	106	107	119
Váh	Min.	316	5,2	7,5	1,3	<dl	<dl	0,6	<dl	<dl	<dl	n.d.	39,4	8,5	<dl	23,3	<dl	2,2	3,1	1	0,9
	Mean	458	9,8	8,1	2,8	0,5	0,4	2	0,03	0,2	0,11	3.1*	62,6	22	15,5	44	15,1	3,7	3,9	20,1	3
	Max.	704	13,8	9	4,8	2,7	1,2	3,4	0,12	0,7	0,24	n.d.	92,2	38,5	29,2	88,8	208	7,5	4,7	167,1	13
	n	146	146	146	72	146	146	146	146	146	134	1	146	146	146	146	146	133	12	121	145
Drava	Min.	22	6,1	6,2	<dl	<dl	<dl	<dl	<dl	<dl	<dl	2,1	12	1,3	2	5	1	0,6	0,8	<dl	<dl
	Mean	293	10,4	7,9	1,4	0,5	0,1	1,2	0,01	0,1	0,03	6,3	44,2	8,8	11,9	29	18,1	2,3	1,5	7,3	2,4
	Max.	585	16,4	8,8	3,7	3,8	0,6	3,2	0,21	0,6	0,21	8,7	72	27,6	26,2	56	172,5	8,5	4,6	94	9,6
	n	798	824	824	221	295	807	822	782	714	752	60	672	660	659	620	706	186	11	273	785
Tisza	Min.	<dl	3,5	n.d.	0,7	<dl	<dl	<dl	<dl	<dl	<dl	<dl	<dl	10	3,6	4,6	<dl	2,8	3	<dl	<dl
	Mean	413	9	7,8	1,6	0,3	0,2	1,2	0,02	0,2	0,06	6,1	49,1	38,5	10,3	49,2	76,6	6,8	3,9	15,5	2,2
	Max.	750	13,2	8,5	2,9	0,9	1	3	0,21	0,8	0,28	11,1	87	92	89	102	667	24,4	5,5	216	7,3
	n	653	651	644	174	435	645	647	647	60	864	660	534	524	523	524	447	233	9	428	632
Sava	Min.	232	3,3	6,6	0,5	<dl	<dl	0,1	<dl	<dl	<dl	n.d.	6,1	<dl	<dl	4	<dl	1,3	1	1,1	<dl
	Mean	391	9,4	7,9	1,9	0,7	0,1	1,3	0,02	0,1	0,07	4.7*	57,8	10,3	15	21,4	19,3	3,2	2,5	1,1	2,4
	Max.	641	17,3	8,8	5,6	6,3	3	4,2	0,57	1,2	0,8	n.d.	91,6	53,4	39,9	78,7	820	14,5	5,6	1,1	12,2
	n	1176	1182	1160	633	886	1173	1173	1169	880	1156	1	808	802	803	801	1169	170	189	1	1134
Velika Morava	Min.	266	7,9	6,9	1,5	<dl	<dl	0,5	<dl	<dl	0,01	n.d.	42,1	3,5	7	11,7	<dl	1,5	n.d.	n.d.	0,5
	Mean	431	11,3	7,7	2,8	1,1	0,1	1,6	0	0,1	0,1	0.2*	52,7	9,7	18,2	23,7	15,5	2,5	n.d.	n.d.	3,3
	Max.	670	15,2	8,8	6	4,2	0,4	4,6	0,05	0,3	0,26	n.d.	74	15,4	32,2	49	170	3,8	n.d.	n.d.	6,7
	n	93	95	79	57	57	93	93	93	32	91	1	39	32	39	33	93	10	n.d.	n.d.	72
Iskar	Min.	297	4,8	6,9	n.d.	0,1	<dl	<dl	<dl	0,1	0,02	n.d.	20	<dl	7	9,6	10	n.d.	n.d.	<dl	1,1
	Mean	453	8,9	7,9	n.d.	0,3	0,4	2,1	0,04	0,6	0,64	3.5*	55,7	34,5	17,5	54,5	33,4	n.d.	n.d.	18,8	3,5
	Max.	737	14,8	9	n.d.	0,5	2,7	8,1	0,17	1,6	3,36	n.d.	80	91	41,3	123,1	141	n.d.	n.d.	50,3	10,6
	n	71	70	71	n.d.	3	68	69	70	38	60	1	64	71	64	60	71	n.d.	n.d.	12	70
Siret	Min.	410	n.d.	6,7	0,8	n.d.	0,1	0,6	<dl	<dl	<dl	1,9	23,3	20,6	9,4	22,8	2	n.d.	n.d.	<dl	0,7
	Mean	660	8,3	7,9	2,9	n.d.	0,8	2,1	0,08	0,1	0,05	8,4	63,5	79	23,7	63,7	98,6	n.d.	n.d.	3	4,3
	Max.	1243	13,5	8,8	5,8	n.d.	3,4	7,6	1,2	1	0,23	16,8	113	196,8	59	176	762	n.d.	n.d.	14	8,4
	n	106	109	109	23	n.d.	109	109	109	100	109	98	109	109	108	106	108	n.d.	n.d.	9	108
Prut	Min.	298	n.d.	n.d.	1,1	n.d.	<dl	<dl	<dl	<dl	<dl	1,2	19,4	14,2	4,9	31	<dl	n.d.	n.d.	<dl	<dl
	Mean	672	8,6	8,1	2,8	n.d.	0,5	2	0,04	0,1	0,04	7,4	64,4	41,1	21,4	105,9	103	n.d.	n.d.	4,2	3
	Max.	1320	15,4	8,8	4,9	n.d.	4,5	21,9	0,7	0,8	0,28	16,6	153,2	186,7	65,6	270	2110	n.d.	n.d.	26	6,8
	n	199	277	284	22	n.d.	284	284	284	148	284	96	279	279	278	276	284	n.d.	n.d.	51	280

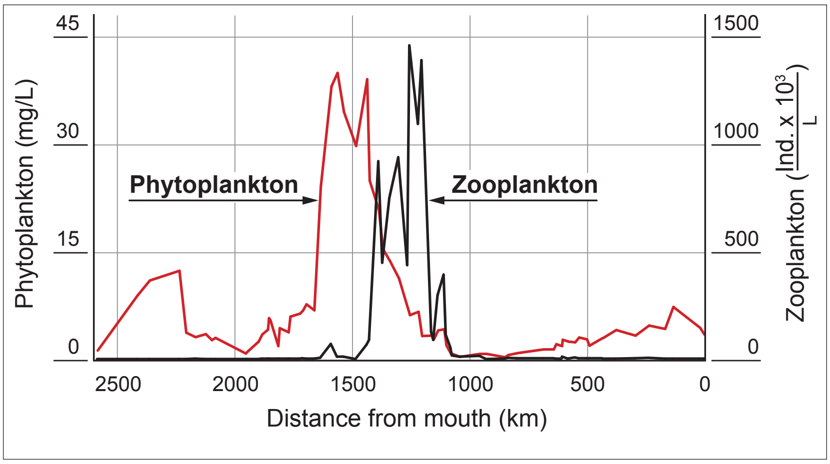

Figure 5: Phytoplankton biomass and zooplankton density patterns along the Danube River (data: Litheráthy *et al.* 2002).

annual P-load (Zessner *et al.* 2005). Dissolved silica, another key nutrient important for algal growth in aquatic ecosystems, exhibits a mean concentration between 4.7 and 8.4 mg/L in the Danube and increases with river size (Table 4). The molar ratio of dissolved inorganic P to N indicates that the river is generally P-limited for primary production when light is not limiting primary producers (Turner *et al.* 2003).

Today, the mainstem of the Danube has relatively good water quality (classes II to II–III). A few tributaries have water quality lower than class III for single nutrient parameters (e.g., Morava, Iskar, Siret and Prut Rivers). Since 2000, the organic carbon load (expressed as TOC) and the BOD_5 (biological oxygen demand during 5 days) have been monitored in the Danube and its tributaries. The TOC load increases from 70 000 tons/year to 550 000 tons/year from the Upper to the Lower Danube. The Tisza and Sava are main contributors of TOC. Excessive organic pollution can still be observed in some Romanian and Bulgarian tributaries such as the Olt, Iskar and Prut (Schmid 2004; TNMN 2000–2005) (Table 4).

Phytoplankton biomass and composition are included in the water quality assessment. Phytoplankton play an important role in the biogeochemistry and food webs of most large rivers (Thorp & Delong 2002). The highest phytoplankton biomass was found in the Middle Danube and in tributaries, biomass is highest in the Morava (Table 4). During 2001, a significant chlorophyll a peak was detected in the Hungarian section of the river, followed by a peak in zooplankton some 300 km downstream of the peak (Literáthy *et al.* 2002, Figure 5).

7 Biodiversity

The Danube River Basin is a "hot spot" for European freshwater biodiversity based on traditional zoogeographic as well as recent phylogeographic studies. The Danube is rich in biodiversity because of its orientation and history. The predominantly east–west alignment of the basin made it a corridor for migration and recolonization, both before and after the ice ages as freshwater organisms moved between the Ponto-Caspian and central Asian biogeographic regions to the east and the Alpine and Mediterranean regions to the west. The mainstem of the Danube was unglaciated, and served as a 'refuge'. As the ice sheets retreated, freshwater species expanded from this refuge to the rest of Europe. The Danube delta also is a meeting point of Palaearctic and Mediterranean biogeographic zones with a high number of wetland habitats and a rich biodiversity. Since sub-Mediterranean floristic and faunistic elements are common in northern Serbia and along the mainstem of the Danube up to the Iron Gates, it is assumed that the Vardar and Morava Rivers (the so-called "Vardar breach") played a major role in connecting the Danube with the Mediterranean (Matvejev & Puncer 1989; Lopatin & Matvejev 1995; Stevanovic 1995).

7.1 Riparian Vegetation

The riparian zone is a major part of most riverine systems, providing ecotones with high biodiversity. The main characteristic is the flow or floodpulse of the river and, hence, the periodic change from an aquatic to terrestrial ecosystem (Tockner *et al.* 2000). In particular, riparian vegetation features specific species adapted to such changes, and some root systems are interconnected to a variable groundwater table. Riparian vegetation also follows a natural geographic gradient from alpine headwaters to lowland floodplains.

Riparian zones provide many ecological functions and services. Riparian vegetation is a major source of allochthonous particulate organic carbon (POC) along the river continuum (Vannote *et al.* 1980). A major function of riparian vegetation is the adsorption and buffering of nutrients entering the river channel, especially from agricultural lands. Denitrification is promoted, mainly in floodplains, preventing excess nitrate in groundwater. The roots of trees and shrubs also stabilize river banks, hence, reducing erosion and sediment/soil transportation. Once partly eroded, roots and woody debris provide shelter and habitat for fish. In small streams, riparian vegetation provides shade and reduces irradiance, thereby ameliorating temperature extremes and preventing excessive macrophyte and algal growth. Riparian trees provide shelter for fish against predation and habitat to water birds for feeding, resting, hiding and breeding. Riparian vegetation along the river corridor can mitigate habitat fragmentation induced by man.

While much riparian vegetation has been destroyed in the course of deforestation and river regulation, especially in the Upper Danube, significant amounts of riparian vegetation are still present in larger floodplain areas in the Middle and Lower Danube, such as the Gemenc floodplains (Hungary), the Kopački rit (Drava confluence to the Danube), the Green Corridor (wetland protection and restoration programme along the entire Lower Danube; http://www.wwf.de/fileadmin/fm-wwf/Publikationen-PDF/DanubeDeclaration2000.pdf), and the delta. There are no detailed data available of how much riparian vegetation has been lost along the Danube and its tributaries. However, the loss of floodplains (including riparian vegetation) is significant, showing that only 5%, 25%, 28% and 70% of the original floodplains remain in the Upper, Middle, Lower Danube and delta, respectively (Schneider 2002).

Rehabilitation of riparian vegetation in the course of river restoration projects requires space. Providing just a small strip of trees („green tubing") may be aesthetic in terms of the landscape but is insufficient with regard to ecosystem function. River restoration needs botanical knowledge by choosing native species and fighting invasive species that can be a great nuisance (e.g., the Himalayan Balsam *Impatiens glandulifera* that presently "explodes" and suppresses other flora in Danube floodplains downstream of Vienna).

7.2 Vegetated Islands

Vegetated islands are key landscape elements along dynamic river corridors; at the same time they are among the first elements that disappear as a consequence of river regulation. Along the Danube corridor, a total of 349 islands occur of which 5 are >1000 ha, 63 are between 100 and 1000 ha, 117 between 10 and 100 ha, and 163 are <10 ha. Islands are particularly abundant in the Bulgarian/Romanian section of the Danube (Rkm 400–700) and in the middle reach in Hungary (Rkm 1200–1600). The combined total area of all islands is 134 000 ha (Tockner, unpublished data). The average area per island increases along the corridor, (Figure 6) and the remaining islands have high conservation value. Islands provide important ecotonal habitats, and they are on average less disturbed than adjacent floodplain areas. As such, vegetated islands play important stepping stones for aquatic and terrestrial floodplain organisms along the river corridor. Along the Bulgarian stretch of the Danube, 75 islands with a total area of 10 700 ha provide habitat for 1100 animal species including 65 fish species and 160 bird species. Along the Romanian stretch, 111 islands cover an area of 11 063 ha (http://www.panda.org/index.cfm). Along the Austrian section of the Danube, about 2000 islands were present before regulation, but only a few remain (Tockner, unpublished data).

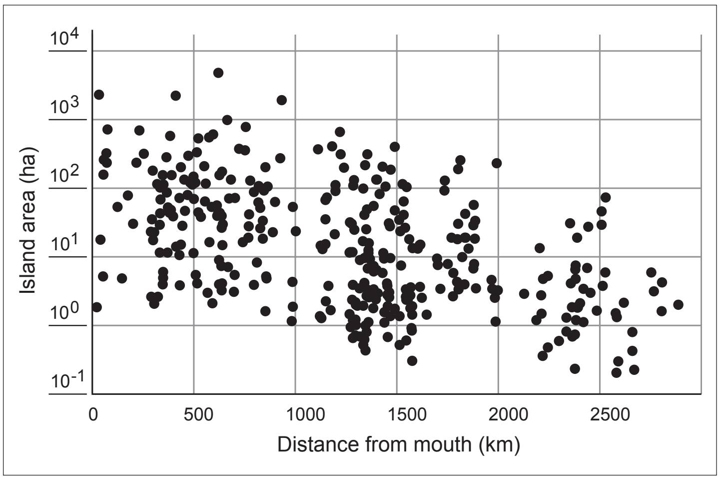

Figure 6: Present distribution of vegetated islands (location and average area) along the Danube River (Tockner, unpublished data).

7.3 Macrophytes

Liepolt (1967) and Kusel-Fetzmann *et al.* (1998) provide a comprehensive overview of the macrophyte flora in the basin. More recently, macrophytes were mapped along the entire Danube corridor, including selected floodplain waters in the frame of the Joint Danube Surveys (JDS1 in 2001 and JDS2 in 2007, Literáthy *et al.* 2002; Liska *et al.* 2008) and of the Multifunctional Integrated Study of the Danube Corridor (http://www.midcc.at, Janauer & Wychera 2002; Janauer *et al.* 2003). During JDS1, a total of 49 aquatic macrophytes was identified, including 14 mosses, 16 spermatophytes – submerged rhizophyte species, 9 spermatophytes – floating leaf and free floating plants, 6 amphiphytes, 3 helophytes and 1 Characeae (Phycophyta). In the Upper Danube, bryophytes (mosses) dominate (67–89% cover). Higher plants (11–28%) are mostly restricted to impounded sections. Spermatophytes – floating leaf and free floating plants dominate downstream Danube sections where water transparency and flow velocity are low. Submerged rhizophytes are present along the entire corridor.

A highly macrophyte rich section is the (former) inland delta downstream of Bratislava. In the impounded section of the Gabčíkovo hydropower plant, *Potamogeton pectinatus, Zannichellia palustris* and *Potamogeton nodosus* are dominant. Adjacent floodplain waters are primarily colonized by *Elodea nuttallii*, *Potamogeton* spp., *Batrachium trichophyllum*, *Ceratophyllum demersum* and *Lemnaceae* spp. The reed canary grass (*Phalaris arundinacea*) dominates littoral areas. Two seepage canals, built between 1979 and 1992, were rapidly overgrown by macrophytes (25 species in 2000), including several threatened species such as *Apium repens, Groenlandia densa, Hippuris vulgaris* and *Chara* spp. (Otahelova & Valachovic 2002; Janauer *et al.* 2003). In the "Gemenc" floodplain area in Hungary (Rkm 1498–1468), 21 species were documented in oxbow lakes, 27 species in canals and 12 species in the main channel.

7.4 Macroinvertebrates

The aquatic macroinvertebrate fauna of the Danube mainstem, its floodplain waters and its main tributaries have been studied for a long period. Most studies have been conducted to assess the environmental status of the river (Birk & Hering 2002; Birk 2003). The macroinvertebrate fauna of the Danube is highly diverse (Russev 1998; Literáthy *et al.* 2002; Slobodník *et al.* 2005; Csányi and Paunović 2006). This is a consequence of strong longitudinal and lateral hydrogeomorphic gradients (Literáthy *et al.* 2002; Sommerhäuser *et al.* 2003). Moreover, the headwater section upstream of the city of Kelheim (Rkm 2415) contains a macroinvertebrate community that significantly differs from all other river sections (Liska *et al.* 2008). Along the Austrian stretch, between 900 and 1289 macroinvertebrate taxa have been identified (Moog *et al.* 1994, 1995, 2000; Humpesch 1997). Most taxa have been found in floodplain waters (in total 683), compared to the free-flowing (306) and impounded sections (354). Diptera, Trichoptera and Mollusca are the most diverse groups along the main channel, while Coleoptera, Trichoptera, Mollusca and Odonata dominate floodplain waters.

Most recently, three international expeditions, namely the Joint Danube Survey (JDS1 in 2001), the Joint Danube Survey 2 (JDS2 in 2007) and the AquaTerra Danube Survey (ADS in 2004) have been completed. During JDS1, 98 sites were sampled along the Danube (from Rkm 2581 to Rkm 12). In total, 268 species were recorded, including Trichoptera (42 taxa), Gastropoda (30), Ephemeroptera (27), Coleoptera (22), Bivalvia (20) and Crustacea (18). Diptera were not considered. A total of 441 invertebrate taxa were recorded during JDS2 (between Rkm 2600 and the delta); including Diptera and Oligochaeta. During the ADS, which mainly focused on impounded sections, a total of 89 taxa were recorded from 30 cross-sections between Klosterneuburg (Austria, Rkm 1942) and Vidin-Calafat (Bulgaria–Romania, Rkm 795) (Slobodník *et al.* 2005; Csányi and Paunović 2006).

Based on these recent surveys, two distinct patterns were identified: (i) Diptera, Mollusca, Oligochaeta, Amphipoda and Trichoptera dominate the macroinvertebrate community along the Danube and (ii) taxon richness decreases longitudinally from the headwaters to the mouth (Literáthy *et al.* 2002, Slobodník *et al.* 2005, Csányi and Paunović 2006; Liska *et al.* 2008). The longitudinal decline in taxon richness may be explained by decreasing sediment grain size and heterogeneity in concert with increasing pollution. The Gabčíkovo and Iron Gate reservoirs contain particularly poor macroinvertebrate communities.

The Danube is under considerable pressure from the invasion of non-native species (Tittizer *et al.* 2000; Literáthy *et al.* 2002, Slobodník *et al.* 2005, Csányi and Paunović 2006; Liska *et al.* 2008). The opening of the Rhine–Main–Danube Canal in 1992 (also called Main–Danube Canal or Europa Canal) removed a natural barrier between the Rhine and the Danube; a bi-directional transfer of previously geographically isolated faunal elements and genetic potential followed. Today, the Danube serves as a "Southern Invasive Corridor" (Galil *et al.* 2007) and is an important branch of the Main European Invasive Network (Arbačiauskas *et al.* 2008), linking the Black Sea basin with the North Sea basin via the Danube–Main–Rhine waterway.

For the mainstem of the Danube, Arbačiauskas *et al.* (2008) reported 19 non-native macroinvertebrate species, mainly of Ponto-Caspian origin (14 species). The Ponto-Caspian invader *Litoglyphus naticoides* is today one of the most frequent and abundant species in the basin. In addition, species from New Zealand (mud-snail *Potamopyrgus antipodarum*) and Eastern Asia (Chinese pond mussel, Eastern Asiatic freshwater clam or swan-mussel – *Anodonta* woodiana, *Corbicula fluminea, C. fluminalis* and the tubificid worm *Branchyura sowerbyi*) have successfully established. Ponto-Caspian species like *Dendrocoelum romanodanubiale* (Turbellaria), *Hypania invalida* (Polychaeta) and *Jaera istri* (Crustacea) have rapidly spread into the Rhine–Main–Danube Canal and the Rhine basin. *Dikerogammarus haemobaphes* was found in the Main–Danube Canal just 1 year after its opening. Dikerogammarus *villosus* had already reached the Dutch Rhine by 1994/95 and arrived, via North-German canals, in the Elbe River in 1998.

The mussel C. *fluminea* (93% of all investigated sites during JDS2) and the crustaceans *Corophium curvispinum* (90%) and D. *villosus* (69%) are the most frequent nonnative species within the basin (Liska *et al.* 2008). C. *fluminea* has recently immigrated into the middle reaches of the Danube via the Main–Donau Canal (Csányi, 1998/1999) and has been sampled down to the delta. In the Middle and Lower Danube, it locally dominates macroinvertebrate communities (Csányi and Paunović 2006; Liska *et al.* 2008). Puky & Schád (2006) reported *Orconectes limosus* (introduced in the 1950s for farming) to be abundant in the Hungarian Danube. The occurrence of this species in the Serbian part of the Danube in 2004 (Pavlović *et al.* 2006) represents the most eastern habitat documented thus far. *Eriocheir sinensis* is known to occur in the Austrian, Hungarian and Serbian Danube sections. Moreover, it has been recorded in terrestrial habitats during its migration (Puky & Schád 2006).

The Zebra mussel (*Dreissena polymorpha*), native to estuaries and coastal waters of the Ponto-Caspian and Aral Sea basins, is abundant within the entire basin, while the Guagga mussel (*D. rostriformis bugensis*), native to the Dnieper and Bug Limans (North Black Sea) is limited still to the Lower Danube (Liska *et al.* 2008; Arbačiauskas *et al.* 2008). Today, about 40% of all documented species along the Danube are non-native, underlining their potential impact on native biodiversity and ecosystem functioning (Liska *et al.* 2008). In numbers, non-native species represent up to 90% of all macroinvertebrates in the Upper Danube valley and even up to 100% in the middle section. For example, C. *curvispinum* can reach densities of 450 000 individuals/m^2 and biomass can be as high as 450 g/m^2.

7.5 Fish

The Danube is the most species-rich European basin. About 20% of the European freshwater fish fauna, that is, 115 native species, occur in the basin (Kottelat & Freyhof 2007). For comparison, about 60 native species are reported in the Rhine basin. Diversity is also high at the local scale because of distinct longitudinal and lateral environmental gradients. For example, more than 45 species occur in the alluvial section between Vienna and Bratislava and 74 species are found in the delta (Oel, 2007).

The Danube fish fauna was already studied in the 18th and 19th centuries (Marsilius 1726; Heckel & Kner 1858; Antipa 1912). More recent summaries are provided by Banarescu (1964), Balon (1964), Schiemer *et al.* (2004) and through the JDS2 (Liska *et al.* 2008). Records of Danube fisheries date back to 335 BC when Greek traders commercialized the fishery in the Lower Danube. The oldest domesticated fish is *Cyprinus carpio*, which was exploited by Romans in the Pannonian area already 2000 years ago (Balon 2004). Cultivated stocks are assumed to be derived from the wild population in the Danube.

Balon (1964) reviewed the longitudinal distribution of Danubian fishes. The number of species increases longitudinally. High diversity is reported in the Hungarian section, the transition zone between foothills and lowlands, with up to 55 native species. Further downstream, the species number remains constant but peaks again in the downstream sections of the Lower Danube and delta. During JDS2 (Liska *et al.* 2008), *Alburnus alburnus* was the only species caught along the entire corridor (65 sampling sites) and accounted for almost 50% of all fish captured. Eurytopic species predominated in impounded sections.

There are about 30 endemic fish species in the basin, including *Hucho hucho*, *Zingel streber*, *Sabanejewia bulgarica, S. romanica*, *Coregonus austriacus*, *Eudontomyzon danfordi*, *Gobio carpathicus* and *Romanogobio vladykovi*. Some endemics are restricted to single rivers or single lagoons (*Romanichthys valsanicola, Scardinius racovitzai, Cottus transsilvaniae, C. haemusi* and *Knipowitschia cameliae)* (Kottelat & Freyhof 2007). *Salvelinus umbla* is restricted to Alpine and sub-alpine lakes.

The ecological status of the Danube and its fisheries is influenced by river regulation schemes that commenced in the 19th and early 20th centuries. Today, 18 major dams intersect the navigable Danube from Kelheim to the Black Sea. At only two dams (Melk and Wien-Freudenau), fish migration facilities are in operation (Liska *et al.* 2008). Hydromorphological alterations, in concert with pollution, land reclamation, navigation as well as the introduction of non-native species, have affected the Danube fish fauna. Out of 13 European freshwater fish and lamprey species that have gone extinct since 1700, two species were from the Lower Danube (*Alburnus danubicus*, *Romanogobio antipai*), one was endemic to the sub-alpine lake area (*Salmo schiefermuelleri*) and one occurred in a coastal lake near the delta (*Gasterosteus creonobiontus*) (Kottelat & Freyhof 2007). About 25 species native in the basin are globally threatened (http://www.iucnredlist.org), including all sturgeons and the endemic *Hucho hucho*, *Coregonus bavaricus*, *Umbra krameri*, *Alburnus sarmaticus* and *Scardinius racovitzai* (Kottelat & Freyhof 2007).

About 30 fish species have been introduced during the past century in the basin. Four established non-native species are frequent: *Pseudorasbora parva*, *Ameiursus nebulosus*, *Carassius gibelio* and *Lepomis gibbosus*. Other established non-native species like *Oncorhynchus mykiss*, *Micropterus salmonides* and *Perccottus glenii* are frequent in certain regions (Kottelat & Freyhof 2007). In many cases, introduction took place via the aquaculture trade; that is, decoupled from waterway transport (Copp *et al.* 2005). From the 1970s onwards, the invasion of several Ponto-Caspian gobies (*Proterorhinus semilunaris, Neogobius melanostomus, N. fluviatilis* and *N. kesslerii*) into Danube stretches upstream of the Iron Gates and thus beyond their native Danubian distribution limit have been reported, coinciding with the general change in the character of the Danube. Moreover, *N. kesslerii*, *N. melanostomus* and *P. semilunaris* have invaded the Rhine and subsequently the North Sea basin through the Rhine–Main–Danube Canal. Since the opening of this canal in 1992, a natural barrier between the Danube and Rhine has been removed and a bi-directional transfer of previously geographically isolated faunal elements and genetic potential followed. Thus the Danube serves as a “South Invasive Corridor” for fish just as for Ponto-Caspian invertebrates (Arbačiauskas *et al.* 2008). It is a dispersal corridor with *Gasterosteus gymnurus* invading the Upper Danube, and *Syngnathus abaster* invading the Danube mainstem and reaches on the Romanian-Hungarian border (Kottelat & Freyhof 2007).

Today, approximately 30 000 tons of fish are caught each year by commercial and sport fishermen (Wohl, 2010). Thirty species native to the basin are commercially important. The Danube catch yield has undergone serious regional cutbacks. Construction of the Gabcíkovo River Barrage System near Bratislava, opened in 1992, led to a decline in the annual fish catch by >80% already in 1993 compared to the pre-dam period (1961–1979) (Holcik 1995). Many phytophilous spawners lost their spawning, nursery and wintering grounds. Economically important species such as *Cyprinus carpio, Esox lucius*, *Sander lucioperca*, *S. volgensis*, *Aspius aspius*, *Tinca tinca* and *Silurus glanis* decreased in numbers.

In the Lower Danube, the strongest cutback in fishery occurred during the 1960s. Some 72% of the former floodplains downstream of Iron Gate II and upstream of the delta have disappeared or became functionally extinct (Table 2). These floodplains served as key habitats for semi-migratory species like *C. carpio*, *Leuciscus idus*, *Sander lucioperca*, and *Silurus glanis*. Moreover, strong declines have been reported for the delta in response to the (i) transformation of connected backwaters into isolated ponds for aquaculture (Ukraine) since the 1960s, (ii) isolation of the frontal marine lagoons from the sea for irrigation purposes from 1970 onwards (Romanian and Ukrainian parts of the delta) and (iii) poldering of about 1000 km² of the Romanian part of the delta (Schiemer *et al.* 2004).

No description of the Danubian fish fauna would be complete without highlighting the importance of the Danube as one of the last refugia for anadromous sturgeons (family Acipenseridae). The river provides access to almost the last spawning habitats in the Black Sea basin (Reinartz 2002; Reinartz *et al.* 2003). Two Danube sturgeons are resident species and four species migrate to the river for spawning. However, five out of six sturgeon species native to the basin are critically threatened by extinction and one species, the Atlantic sturgeon, *Acipenser sturio*, is already extirpated in the basin. The ship sturgeon, *A. nudiventris*, is on the verge of extinction in its natural range and is only occasionally reported in the Lower Danube. All other sturgeons still have self-sustaining populations in the river. *A. ruthenus* has undergone a massive decline and anadromous populations have been extirpated. It has self-sustaining populations in the Lower and Middle Danube as well as large tributaries such as the Tisza. It is stocked mostly in the Upper Danube. The spawning success of *Huso huso* is mostly a result of the relatively uninterrupted Lower Danube stretch (863 km from the mouth to the Iron Gate II) (Lenhardt *et al.* 2006). *A. gueldenstaedtii* and *A. stellatus* are extirpated upstream of the Iron Gates. Overfishing in

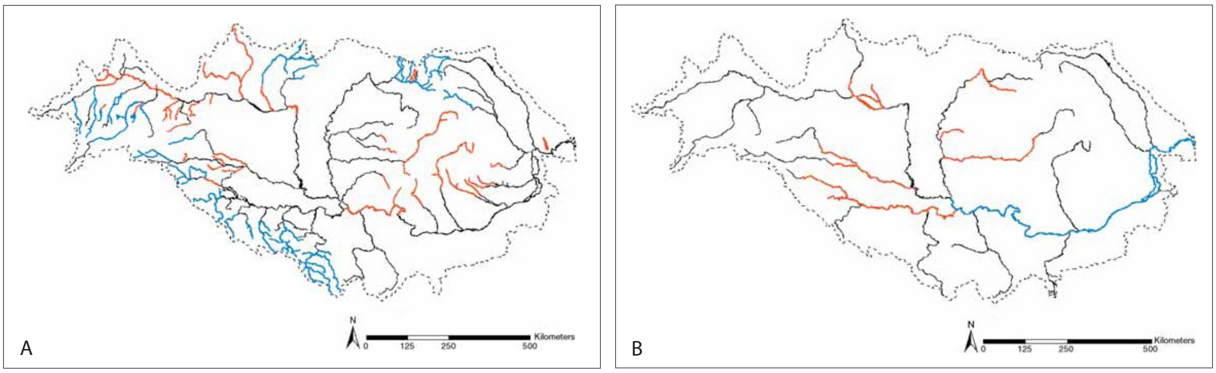

Figure 7: Present (in blue) spatial distribution of huchen (Hucho hucho) (A) and sturgeon (Acipenseridae) (B) within the Danube River Basin, lost distribution range shown in red; after Holík *et al.* (1989) and Reinartz (2002). Maps produced by D. Tonolla.

the Danube and at sea is predicted to lead to extinction of natural populations in the near future (Kottelat & Freyhof 2007).

In the Lower Danube, sturgeons were already exploited by ancient Greek colonies in the 5th and 6th century BC for meat and caviar (Reinartz 2002). A decline of *Huso huso* (beluga) and disputes between upstream and downstream parties about the share of these valuable resources date back as early as the 16th century. During the 18th century, the fishing of migratory sturgeons collapsed in Austria. At the beginning of the 19th century, *H. huso* was already rare in the Middle and Upper Danube. The construction of the Iron Gate hydropower stations (1972, 1984) had a great impact on sturgeon populations in the Middle Danube (Figure 7). Further, over-exploitation at the end of the last century has led to a dramatic decline in sturgeon catch. Although poaching and unreported fishing (up to 90% of the total catch, Reinartz 2002) seems to have decreased lately in the Lower Danube, there is a remaining pressure due to the high commercial value of sturgeon products like meat and especially caviar (Reinartz *et al.* 2003).

Unintentional escapes (e.g., during floods) of exotic sturgeons from hatcheries have been frequently reported. Hybridisation of native sturgeons with escapees can cause serious threats to native populations, as recently demonstrated in the uppermost population of the sterlet (*Acipenser ruthenus*) which hybridises frequently with introduced Siberian sturgeon (*A. baerii)* (Ludwig *et al.* 2008). Recently, single paddlefishes (*Polyodon* spp., living in North America and China) have been spotted in the Danube reach of Serbia. Since 1998, all sturgeons have been included in the Convention on International Trade of Threatened Species (http://www.cites.org), which regulates the trade of endangered species and has been signed by all countries in the Lower Danube. In April 2006, Romania banned commercial fishing and the trade of all wild sturgeon products for a 10-year period. In the same year, an Action Plan for the conservation of Danube sturgeons was agreed (AP 2006; Bloesch *et al.* 2006). It aims to secure viable populations of all Danube sturgeons by sustainable management and restoration of their natural habitats and migratory corridors. Hopefully, it will succeed to preserve at least the "Danubian" Ponto-Caspian sturgeons.

7.6 Avifauna

The Danube forms one of the most important bird migration corridors in Europe. In addition, the corridor and its adjacent near-natural areas provide resting and breeding sites to 330 bird species. In the Upper Danube, the 100 km² large Alluvial Zone National Park east of Vienna and the 550 km² floodplains along the Lower Morava (March) and Dyje (Thaya) Rivers form transboundary wetlands of international importance. The adjacent Lake Neusiedl and Fertö-Hanság National Parks (Austria and Hungary) contain extensive reed belts, small lakes and traditional pastures and thus provide resting sites for countless migrating birds. Common kingfishers (*Alcedo atthis*), little ringed plovers (*Charadrius dubius*), black tailed godwits (*Limosa limosa*), common sandpipers (*Actitis hypoleucos*), purple herons (*Ardea purpurea*), great egrets (*Casmerodius albus*), black kites (*Milvus migrans*), white tailed eagles (*Haliaeetus albicilla*), great bustards (*Otis tarda*), corn crakes (*Crex crex*), little bitterns (*Ixobrychus minutes*), black-headed gulls (*Larus ridibundus*), common terns (*Sterna hirundo*) and tufted ducks (*Aythya fuligula*) are among the birds that occur in these areas. Many of these birds are classified as rare in the Upper Danube due to the massive conversion of wetlands into cropland. For example, only a few little ringed plovers remain in Donauauen National Park, although they had been very common at the beginning of the 20th century (http://www.donauauen.at). Many of the above mentioned rare birds are still abundant in the downstream sections of the Danube.

In the Middle Danube, the Kopački Rit Nature Park in NE Croatia, the Gornje Podunavlje reservat in NW Serbia, and the Gemenc and Béda-Karapancsa areas of the Duna–Drava National Park in Hungary form an alluvial wetland complex of ~650 km². Some areas lack adequate protection status. The area hosts almost 300 bird species, including 140 breeding species. Little egrets, grey-, purple- and night herons (Areidae), whiskered terns (*Chlidonias hybridus*) and cormorants (Phalacrocorax) breed in large colonies in these wetlands. Moreover, birds that are endangered at both European or even global levels, like whitetailed eagles (*Haliaeetus albicilla*), black storks (*Ciconia nigra*), ferruginous ducks (*Aythya nyroca*), lesser spotted eagles (*Aquila pomarina*) and saker falcons (*Falco cherrug*), are reported in this area. Additional particularities are the Montagu's harrier (*Circus pygargus*) in the cultural landscape and sand martins (*Riparia riparia*) along the natural banks of the river.

Islands in the Lower Danube host intact floodplain forests, sand bars, marshes, and natural river channels. They provide habitats for numerous plant and animal species, including pelicans (Pelecanidae) that breed in the delta but use the islands as well as fish ponds to feed and rest when migrating.

The Danube delta has a tremendous variety of terrestrial and aquatic habitats. Mediterranean, Eurasian and Black Sea palearctic faunal elements meet in the delta. About 330 bird species have been inventoried. The delta is a nesting place for white pelicans (*Pelecanus onocrotalus*); about 3500 breeding pairs have been reported in 2001/2002, which is a large share of the western Palearctic population. The Dalmatian pelican (*Pelecanus crispus*) was represented by about 100 pairs in the 1980s and about 450 pairs in 2001/2002. The latter equals the majority of the European and about 10–15% of the global population of this species. Moreover, about ⅓ of the world population of pygmy cormorant (*Phalacrocorax pygmeus*, 9000 breeding pairs) is known to occur in the delta (RIZA 2004). There are also important colonies of spoonbill (*Platalea leucorodia*) and several breeding pairs of the white-tailed eagle (*Haliaeetus albicilla*). For millions of birds, especially ducks, white storks (*Ciconia ciconia*) and numerous predators the delta is a major stopping place during spring and autumn migration. During winter, the region hosts huge flocks of swans and geese, including the globally threatened red-breasted goose (*Branta ruficollis*) with almost 95% of its world wintering population (http://www.ddbra.ro/en). Piscivorous birds of the delta have been heavily reduced by fishermen during the 1950s and 1960s. The eutrophication of waterbodies has increased fish food availability and has led, together with protection measures, to a major increase in piscivorous birds since the late 1980s (RIZA 2004).

7.7 Wetland Mammals

In 1879, the Archduke Rudolf, ornithologist and Crown Prince of Austria, reported dense populations of the Eurasian otter (*Lutra lutra*) in the floodplains of the Danube east of Vienna (Lobau). Today, this species is extirpated in this area, although the large floodplains could serve as important habitats for otter. Extirpation of the otter was a result of habitat loss as well as dispersion of synthetic pesticides DDT/DDE that decrease fertility. Due to the ban of DDTs and conservation actions, otter populations are recovering across most of Europe (IUCN 2007). Red fox (*Vulpes vulpes*), wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*) are common along the entire Danube.

European beaver (*Castor fiber*) were intensely hunted for their fur and castoreumoil in the past. In the Danube, this key species was extinct for over a century. Reintroductions have enabled its return to much of the former range. Since the 1970s, beaver have been reported in the Austrian Donauauen National Park, since 1991 in the Middle Danubian Szigetköz area, a 375 km² wetland between Slovakia and Hungary, and since 1996 in the southern Hungarian sections of the Duna–Drava National Park. Recently, a beaver dam blocked the famous fish by-pass of the hydropower plant Freudenau near Vienna. The occurrence of beaver is reported for the Kopački Rit Nature Park since 2002. Beaver are being reintroduced to the Gornje Podunavlje Special Nature Reserve along the Serbian Danube (Rkm 1366 to 1433) by a joint Bavarian-Serbian programme.

The Danube floodplains are important habitats for 12 bat species (Microchiroptera) such as the pond bat (*Myotis dasycneme*). European pine martin (*Martes martes*), stone marten (*Martes fiona*), root vole (*Microtus oeconomus*), wildcat (*Felis silvestris*), red deer (*Cervus elaphus*) and otter (*Lutra lutra*) are reported to occur in protected areas along the Middle Danube. Golden jackals (*Canis aureus*) are among the most recent colonialists (Ramsar 2007). About 40 mammal species, including marbled polecat (*Vormela peregusna*), European ground squirrel (*Spermophilus citellus*), Romanian hamster (*Mesocricetus newtoni*), Eurasian harvest mouse (*Micromys minutes*), Southern birch mouse (*Sicista subtilis*), steppe polecat (*Mustella eversmanni*) and least weasel (*Mustela nivalis*) have been reported on the Ibisha and Belene Islands in the Lower Danube.

The delta supports a diverse mammal fauna (42 species), including species of high conservation value such as the otter (*L. lutra*) and European mink (*Mustela lutreola*). Since 1850, the European mink has undergone a dramatic decline. It is now extinct in most European countries, occupying <20% of its original range. The most viable population in Western Europe is in the Danube delta, although it is also rapidly declining here. In 2006, only one individual was caught per 250 trap nights compared to one individual per 20 trap nights in 2003 (IUCN 2007). The non-native American mink (*Neovison vison*) and raccoon dog (*Nyctereutes procyonoides*) are reported to compete with the European mink. Poaching of otters (*L. lutra*) has recently increased in the delta (IUCN 2007), and the muskrat (*Ondatra zibethicus*) and wild boar (*Sus scrofa*) are commercially important species (fur and hunting). Other predatory mammals in the delta are the ermine (*Mustela erminea*), fox (*Vulpes vulpes*) and wild cat (*Felis silvestris*).

7.8 Herpetofauna

About 27 amphibian and 37 reptile species are recorded in the basin (Mezzena & Dolce 1977; Engelmann *et al.* 1986, Nöllert & Nöllert 1992; Günther 1996; Gasc *et al.* 1997; Cabela *et al.* 2001; Kwet 2006, http://www.amphibiaweb.org, http://www.globalamphibians.org, http://www.tigr.org/reptiles/search.php). Two thirds of the amphibians and ⅓ of the reptiles prefer riverine landscape elements; the remaining species occur in adjacent hillslope and upland areas. Only three reptiles are truly aquatic: *Natrix natrix*, *N. tessellata* and *Emys orbicularis*. *Vipera ursinii* prefers steppic landscapes with moist areas and waters. *Salamandra atra* can live independent from water, while *Salamandra salamandra* and *Alytes obstetricans* are dependent on water in the larval life stages.

The amphibians *Lissotriton* (*Triturus*) *vulgaris*, *Hyla arborea*, *Bufo bufo*, *Bufo viridis* and *Rana* kl. *esculenta* (*Pelophylax* kl. *esculentus*) and reptiles such as *Lacerta agilis*, *Natrix natrix*, *Coronella austriaca* and *Anguis fragilis* are widespread in the entire basin. *Triturus dobrogicus* is the only endemic amphibian in the basin, and inhabits valleys and floodplains below 300 m asl. Considering the total size of the basin, it is surprising that no reptile species are endemic. Along small rivers, a distinct sequence of alpine, mountainous and planar species occurs. The main Danube corridor crosses several deep gorges (e.g., near Vienna, Iron Gate). Hence, mountainous species such as *Rana temporaria* and *Bombina variegata* are common along some sections of the river corridor. The close link of mountains with lowlands leads to the separation of geographic ranges of lowland species like *Triturus dobrogicus* and *Bombina bombina*. Reptile richness peaks in the hilly regions in the southeast of the basin. Along the Croatian, Serbian, Bulgarian and Romanian Danube sections, 20–31 reptile species occur; compared to 7–15 species in the other sections. In contrast, amphibian richness does not change considerably along the entire corridor, remaining at ~12 species.

Hybridisation is a widespread phenomenon and occurs in half of the Danube basin amphibians; that is, *Lissotriton vulgaris* x *L. montandoni*, *L. vulgaris* x *L. helveticus*, *Triturus carnifex* x *T. cristatus* x *T. dobrogicus*, *Bombina bombina* x *B. variegata*, *Bufo bufo* x *B. viridis* x *B. calamita*, and the well-known hybrid complex with *Rana* (*pelophylax*) *lessonae*, *R.* (*P.*) *ridibunda* and *R.* (*P.*) kl. *esculenta* with different levels of polyploidy. The closely related species *B. bombina* (yellow-bellied toad) and B. *variegata* (fire-bellied toad) hybridise in overlapping areas in Austria, Hungary, Bulgaria and western Ukraine. The high proportion of hybrids, although often not abundant, demonstrates the ongoing speciation process in the basin.

Despite the enormous interest in keeping exotic amphibians and reptilians as pets, which can result in abandoned or escaped animals, no introduced alien species have established reproducing populations in the basin until now. Nevertheless, there are problems with the ongoing introduction of *Trachemys scripta elegans* and other pond turtles, especially in Germany and Austria, because they most likely compete with the native turtle *Emys orbicularis*.

Most amphibians and reptiles are listed in Appendix II of the Convention on the Conservation of European Wildlife and Natural Habitats (Convention of Bern, 1979, http://www.lcie.org/res_legal.htm) and in the IUCN red list (http://www.iucnredlist.org). Many species are protected also by national laws (e.g., Puky *et al.* 2005). Destruction of wetlands is the most serious threat to amphibian populations. Even common species like Lissotriton *vulgaris* is locally threatened due to drainage, pollution, and destruction of breeding ponds and adjacent terrestrial habitats. In recent years, *Triturus dobricus* populations suffered from lower spring rains in the south, probably as a result of climate change (IUCN 2006).

8 Human impacts, conservation and management

Rivers are the „veins" of the landscape and as such they shape landscapes even more prominently than lakes. Rivers have long been used by man as ways of migration and transportation (shipping), collectors of waste, sources of drinking water and food (fish) and hydropower. Conversely, running waters have impacted humans through catastrophic floods and as carriers of disease. Lepenski Vir in the Iron Gates gorge in Serbia, a historical site with tracks of the earliest settlers in Europe (20 000 BC), illustrates the importance of the Danube River for humans. While poets and painters have glorified riverine landscapes as lovely places of nature, only in the last century has river protection become an important social endeavour, mainly initiated by severe pollution and subsequent health and aesthetic issues, and later triggered by water abstraction and morphological changes from impoundments and damming. Recently, droughts (2003) and floods (2002, 2005, 2007) became a priority in the Danube basin, especially since peak flows need space used traditionally for agricultural and urban development.

Since the 1990s, limnological concepts have incorporated a catchment approach to better understand the function of aquatic ecosystems, the ultimate foundation of sound river basin management for the implementation of sustainable use of running waters (Bloesch 2005a). Today, river and wetland conservation and management have become standardized and scientifically founded actions (Boon *et al.* 2000; Bobbink *et al.* 2008). In the Danube River Basin, they are implemented by the European Water Framework Directive (WFD) with the overall goal to achieve „good ecological status" by 2015 (EC 2000), and in various Directives and Conventions such as the EC Birds Directive 1979 (http://eur-lex.europa.eu/LexUriServ/site/en/consleg/1979/L/01979L0409-20070101-en.pdf), the EC Habitats Directive for Flora and Fauna 1992 (http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:31992L0043:EN:HTML), the UNESCO World Heritage Convention 1972 (http://whc.unesco.org/en/conventiontext), and the Ramsar Convention on Wetlands 1971 (http://www.ramsar.org). The latter two Directives formed the basis for the creation of the Natura 2000 Networking Programme on behalf of the European Commission (http://www.natura.org). Basic elements of river basin management include the ecoregion, the river type and reference state, and biodiversity (ICPDR 2005).

In respect to the general framework for conservation and management, the Danube River is an interesting and special case study for several reasons. First, the basin officially encompasses 19 countries, of which four have only small areas of headwaters (Albania, Macedonia, Italy and Poland). This is by far the largest number at the global scale, featuring a great variety of cultures and mentalities. The multicultural setting makes transboundary issues extremely difficult and challenging, although people in the basin have developed a kind of solidarity as „Danubian countries". Whether country borders are along the river (>800 km between Romania and Bulgaria) or across the river (creating the well-known upstream downstream situation) make a significant difference for management. For example, a meandering river does not respect political borders established in the middle of the channel because the channel often shifts from one country to another (e.g., the lower Mura/Drava floodplains).

Fortunately, some of these problems are being solved at the political level by bilateral border commissions and governmental mapping agencies. Since 1998, the International Commission for the Protection of the Danube River (ICPDR, http://www.icpdr.org) is the official forum where issues of water protection and conservation are treated. Using its expert groups, the ICPDR jointly prepares projects and documents for ratification and implementation by national governments. It fosters public participation programmes and is actively supported by many NGOs that have observer status. Through the ICPDR, the WFD is being implemented in the Danube basin. The Espoo Convention 1991 on Environmental Impact Assessment (http://www.unece.org/env/eia/documents/conventiontextenglish.pdf) also may help to solve environmental problems across political borders.

Second, the basin lies in the historical „political fault" between the East and West, reflecting the battles between Asian and Turkish empires and European states, and finally represented by the „Iron Curtain" between capitalist and communist countries. The different political systems have greatly influenced social behaviours, technical developments, as well as water use and protection. Today, this history is illustrated by the situation in the Upper Danube (former West) where mostly „clean water flows through heavily modified channels", while in the Middle and Lower Danube (former East) polluted water flows in more intact channels" (Bloesch 1999).

Third, as a consequence of recent political developments, the Middle and Lower Danube countries in transition have become or are gradually becoming members of the European Union. Hence, economic pressure in these countries will dramatically increase. Subsequent development may severely impact near natural stretches and floodplains of the Danube River and its major tributaries (Sava, Drava, Tisza). Last, the Danube River is the geographical/biological border between east and west, and Ponto-Caspian relicts are still an important part of the natural fauna. However, invasive neozoans and neophytes that threaten native species are prominent, as the trans-European waterway network links the Danube with the Rhine and promotes the exchange of plants, zoobenthos and fish across river basins (Bloesch & Sieber 2003).

The Danube pressures and stressors reflect the present state of the Danube River and its tributaries. To initiate and promote conservation and restoration, human impacts must be analyzed to identify ecological deficits. The ICPDR has made an inventory of physical, chemical and biological data, and compiled and described the pressures and stressors in the so-called "Roof Report 2004" (ICPDR 2005). Following a steady increase since the 1950s, nutrient concentrations have decreased since the 1990s due to new wastewater treatment plants in the Upper Danube (by Germany and Austria) and the economic breakdown in the Lower Danube countries (Schreiber *et al.* 2005; Behrendt *et al.* 2005). Since dilution of pollution by high discharge plays an important role in the Lower Danube, nutrient concentrations are relatively low and a biological assessment indicates moderate pollution.

Some major tributaries are still heavily polluted (Schmid 2004). The high nutrient concentration in the Danube, combined with the loss of 400 000 ha of wetlands along the Lower Danube (drained for agricultural purposes before the 1990s), caused strong eutrophication in the Danube delta lakes after 1980 and a drastic decrease in biodiversity (Vdineanu *et al.* 2001). The recent decrease in N and P load by 18% and 38%, respectively, has improved the situation along the Black Sea coast, but more efforts are needed to lower pollution. Apart from pollution by nutrients and other substances, hydromorphological alterations for hydropower and navigation, and dykes (flood protection) are the main pressures today (WWF 2002; ICPDR 2007a).

In total, about 600 major hydraulic structures (dams and weirs >15 m) including 156 hydropower dams have been built along the Danube and in the catchments of its major tributaries, not including the countless smaller dams (Reinartz 2002; Bloesch 2003; ICPDR 2005, Table 1). Along the mainstem of the Danube, 69 dams have been built and 30% of its total length is impounded. Upstream of Bratislava, only about 15% (Straubing-Vilshofen: 69 km, Wachau: 28 km, Vienna-Bratislava: 45 km) out of ~1000 Rkm remain free-flowing (Figure 8). Further, there are 34 dams along the Lech River, Austria/Germany (encompassing 90% of its total length). In contrast, the Isar River (tributary in Bavaria, Germany) represents one of the last natural alpine rivers in Europe.

The largest dams are Iron Gate dams I and II at Rkm 943 and Rkm 842 (opened 1972 and 1984, respectively). Each dam is equipped with two navigation locks, an earthen non-outflow dam, two hydroelectric power plants, and an overflow concrete gravity dam, among other facilities. The reservoir of Iron Gate II extends to the upstream Iron Gate I dam. During low water, Iron Gate I has a backwater zone of 312 km on the Danube mainstem (up to the city of Novi Sad), 102 km on the Sava, 65 km on the Tisza and 20 km on the Serbian Morava. Together with Gabčíkovo dam (built in the 1980s, diversion channel at Rkm 1835 to 1811), the Iron Gate dams disrupted fish migration in the Lower and Middle Danube and significantly changed sediment transportation and the groundwater regime (Zinke 1999, Klaver *et al.* 2007).

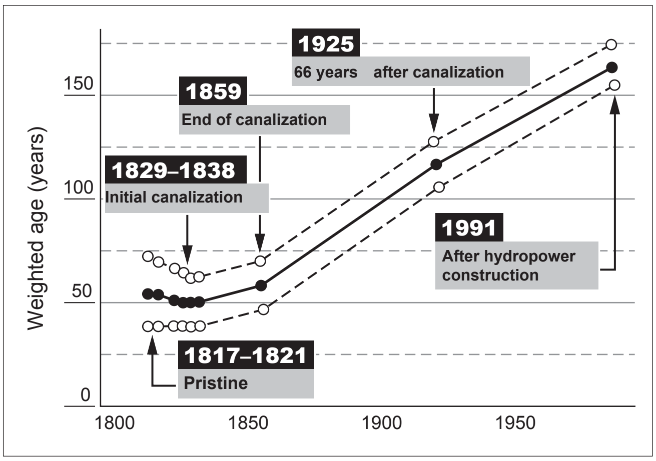

Figure 8: Historical development of the Marchland floodplain in Upper Austria (Rkm 2094-2098): age (average, minimum, maximum) development of the active zone from 1817 to 1991 based on weighted average ages of different habitat types (after Hohensinner *et al.* 2005). Depending on the modelling method, the age values generally represent maximum values calculated based on the maximum possible cell ages. Minimum and maximum values refer to the range of the potential start age of raster cells that are older than 1715 AD in the habitat age model.

The Danube is navigable up to the city of Ulm. From Kelheim (Rkm 2411) to the delta, it serves as an international waterway (87% of the total river length) and navigation is of international importance. In the Upper Danube, navigable tributaries are the Morava (~30% of its total length), Raba (29 km at the mouth) and Váh (71 km, 20% of its river length). The Drava is navigable along ~20% of its length. The Tisza River serves as a waterway from the Ukrainian-Hungarian border to the confluence with the Danube, about 70% of its total river length. On the Sava, navigation is possible on >50% of the river from Croatia (Kupa confluence) to its mouth in Serbia (see Section 9.6.4.). Additional man-made waterways were built along the Danube for transport purposes, including the Main–Danube Canal in Germany that links the Rhine and the North Sea, the Danube–Tisza–Danube Canal System in Serbia, and the Danube–Black Sea Canal in Romania.

Presently, a major controversy for the Danube is the European Union's plan to develop the Trans-European Networks for Transport (TEN-T) Corridor VII along the Danube. The project aims to remove navigation bottlenecks along the Romanian-Bulgarian section, the entire 379 river-km from Mohács to Palkovicoko in Hungary, the 48 km free-flowing section east of Vienna in Austria, and the 80 km free-flowing section between Vilshofen and Straubing. Another goal is to improve navigation between eastern and western Europe through the construction of hydraulic modifications and canals. The proposed Danube–Odra–Elbe Canal is another threat to the Danube. If realized, it would affect 46 000 ha of 38 protected areas, including two national parks, six Ramsar sites and two biosphere reserves (Baltzer 2004). Other major projects are the Bystroe Channel in the Ukrainian part of the Danube delta for navigation (Bloesch 2005b), the Braila–Calarasi section in the Green Corridor for navigation, the Drava and Sava floodplains for hydropower, navigation and gravel extraction and the construction of a Danube–Adria waterway through the Sava River (http://www.euronatur.org/Sava.sava.0.html). Further plans intend to connect the Vardar River (Macedonia) with the Danube. It is a great political challenge to protect "vaste" land against all these economic pressures.

An estimation of the total floodplain area in the Danube basin is 60 000 km² (~7.5% of the total area). Historically, this area would have been affected by regular and periodic inundation in the absence of flood defences. About 65% of the former floodplains have been lost or are now functionally extinct (Figure 3, Table 2). Canalization of the Danube has also truncated the natural balance between succession and rejuvenation processes. Before regulation, the average age of different floodplain habitats in the Upper Danube was 50–60 years and remained relatively constant over time. Following regulation, habitat age has increased and there has been a loss of early succession habitats (Hohensinner *et al.* 2005).

Some 6% of the total human population in the basin lives in areas below flood level. An even higher share of national assets and infrastructure can be affected by floods or is protected by flood defences (ICPDR 2004). The total length of flood embankments exceeds 13 000 km. Deterioration of morphological structure and riverine habitats, the longitudinal disruption of fish migration, the lateral disconnection of floodplains and wetlands, as well as navigation effects have reduced the abundance and biodiversity of biota (Schneider 2002; Schneider-Jacoby 2005). In particular, the endangered Danube sturgeon is near extinction, and 72 actions for their conservation have been proposed in the Sturgeon Action Plan in the framework of the Bern Convention (AP 2006; Bloesch *et al.* 2006). In comparison with other large European rivers such as the Rhine, the Danube still has comparatively larger near natural sections with intact ecological functions (Bloesch & Sieber 2003).

Major actions and measures are needed to protect and properly manage the Danube River and its tributaries. The big question is which comes first: conservation or restoration? From the ecological deficits identified above, measures for remediation can be derived. Mapping the hydromorphological structures according to CEN-Standards provides a powerful tool for managers (Schwarz 2007). The scaling within the river basin must be used to define the appropriate goals and to implement concrete actions (sensu Frissell *et al.* 1986). Pollution problems are shifting from nutrients to „priority substances" such as persistent organic compounds (PAHs and PCBs) and hormone active substances (endocrine disruptors). Heavy metals are accumulating in the sediments and mercury (Hg) is subject to bio-accumulation through the food chain. A principally "sustainable" approach is to tackle the causes or sources of pollution rather than the effects (known as „end-of-pipe-solutions"). It is clear that modern technology must play a major role in solving these problems (see also WFD recommending the combined approach of rigid Environmental Quality Standards, Emission Limit Values and Best Available Techniques). Low-tech solutions using wetlands as a purification step can be an effective and cost-efficient alternative.

Former and future hydrological and morphological alterations require an even stronger use of management measures as they include the riparian areas and ecotones along the aquatic–terrestrial interface, both hotspots for biodiversity. Numerous ecological restoration projects, mainly in the Upper Danube, illustrate the success of interdisciplinary measures (e.g., Donau–Auen-National Park, Vienna). An innovative approach was presented for Nature Park Lonjsko Polje (Sava River) by Schneider-Jacoby (2007) using riverine floodplains not only for flood protection, but also for sustainable forestry and agriculture.

Boon (2005) discussed the strategic problem whether conservation of what is left from technical impacts has priority over restoration of what has been morphologically altered and destroyed. In the long-term, both from an ecological and economic point of view, conservation has a much better cost-benefit ratio than restoration. Hence, the few large lowland floodplains in the Danube and larger tributaries like Sava, Drava and Tisza, must be conserved and used in a strictly sustainable way. This is „soft" eco-tourism that shows goods and services of nature reserves, restricted fishing, moderate shipping, flood protection by using the retention potential of natural floodplains (as recommended by the EU Flood Directive – Directive 2007/60/EC on the assessment and management of flood risks – and the EU Floods Action Programme), and a strong political regulation for proper landscape planning. Where the river has already been altered by damming and impoundment, restoration should be performed by creating new habitats, giving more space to the river, and reconnecting floodplains in particular.

A good conservation example is the UNESCO Biosphere Reserve in the Danube delta where outdated management practices such as the capture fishery period (1903–1960), the reed exploitation period (1960s), the fish culture period (1971–1980), and the agriculture-polder period (1983–1989) have been replaced by more sustainable uses (Gâştescu & Ştiucă 2006, see Section 9.11). Core areas and restoration zones represent only ~9% and 3%, respectively, of the total delta area (4560 km^2), while buffer zones cover 39% and economic zones 53% (Baboianu 2002). Ştiucă *et al.* (2002) showed that hydrological and ecological restoration is beneficial for the economy. For instance, restoration costs of flushing the Babina and Cernovca polders (3680 ha) amounted to 100 000 USD and yielded an annual benefit of 140 000 USD via lower labour costs. The importance of integrated management measures at the catchment scale has been emphasized by the adoption of River Basin Management Plans at the EU level. Increasing attention is being given to wetlands because their multiple ecological functions are regarded invaluable (e.g., water storage, connectivity of surface and ground waters, biochemical cycling of nutrients, retention of suspended and dissolved materials, and hotspots of biodiversity).

An ultimate goal of river conservation and restoration is to ensure ecosystem functioning and to maintain naturally high biodiversity. This is in general contradiction to the often irreversible ecological damage caused by flood protection, navigation and hydropower development. When applying an open discussion and using clever strategies, a paradigm change can yield acceptable solutions, as shown in a recent restoration project on the Danube near Vienna (Reckendorfer *et al.* 2005). Size matters in the Lower Danube, where the negative impact of technical measures may be recognized only after a long period such as in Gabčíkovo where the floodplain forest is changing over time due to lost flood dynamics and a lower groundwater table. Similar long-term effects occur along the Green Corridor where the floodplains were disconnected by longitudinal damming by Romania.

Sustainable river management theoretically provides the balance between use and protection. Use and protection (conservation) are the focus of most conflicts of interest and need to be balanced in river management. While sustainable use is propagated by almost all politicians, the real problem is its implementation (Bloesch 2005a). The definition of this term is still far from being clear and our society is still far from behaving in a sustainable way (Jucker 2002). Implementation is made further difficult because not only methods and strategies but also legal aspects need to be harmonized among the Danube countries (Bogdanović 2005). Besides those legal documents for Danube protection listed earlier, the Danube River Protection Convention, the Danube Navigation Convention and the Danube Sub-Basin Commissions on the Sava and Tisza are to be mentioned. Danube River Basin management is an ongoing and dynamic process that must be based on sound scientific knowledge and must be implemented pragmatically.

9 Major tributaries and the Danube delta

9.1 Inn River

The Inn River (*En* in Romansch; *Oenus* or *Enus* in Latin) has a catchment of 26 128 km², is 515 km long, and drains parts of Austria, Switzerland and Germany (some 254 km² is in Italy). In Passau, at its mouth (Danube Rkm 2225), the Inn carries for the most part of the year more water than the Danube River; during snowmelt the discharge of the Danube might exceed the discharge of the Inn. The Salzach River is the main tributary of the Inn. Around 35% of the basin is covered with forests, 15% is arable land (Table 1), and the remaining area mainly consists of alpine grasslands and bare rock. The Inn basin contains >800 glaciers with a total area of 395 km² (Tirol 2006); all are receding due to global warming. The Inn has been an important floatway for timber to Innsbruck and even Vienna. Today, navigation is of limited importance (Inn 2002). The basin is inhabited by 2.2 million people. The largest cities along the Inn/Salzach are Salzburg and Innsbruck (150 000 and 120 000 inhabitants, respectively).

9.1.1 Geomorphology

The Inn starts as the outlet of Lake Lughino in the Swiss Alps near St. Moritz (2484 m asl), runs north-east through the lake chain in the Engadin valley as it passes over crystalline, schist and quartz phyllite units. In Austria down to Innsbruck (570 m asl), the Inn valley forms the border between the northern limestone and the central crystalline Alps. The slope of the upper Inn ranges between 2 and 11‰ (Inn 2002). Geology of the western Salzach valley mainly consists of quartz phyllite, crystalline and wacken. Downstream of Innsbruck, the Inn flows through a wide valley before it traverses the alpine belt at Kufstein, enters the alpine foothills, and crosses the Bavarian plateau. Here the slope decreases to 1‰. After the confluence with the Salzach, the Inn forms the border between Bavaria and Austria. Its morphology has been heavily regulated with most banks fortified with riprap and short groynes. Natural riverbanks are restricted to short gorge stretches in the upper Inn and natural bedrock sections (Inn 2002). Less than 20% of the total length of the mainstem is free-flowing and in a near-natural state (ICPDR 2005), although some man-made floodplains have been established in the lower Inn.

9.1.2 Climate, Hydrology and Biogeochemistry

The average annual air temperature in the catchment is 4.6 °C (Table 1). The average water temperature is 7.3 °C (1991–2005). The hydrology is mainly influenced by a high alpine character and exhibits a nivo-glacial regime. Peak flows occur in early summer when heavy rain falls on snow. Some 80% of the upper and middle catchment is in the dry central Alps ("Inner valleys" such as the Engadine valley), and ~20% is in the precipitation rich northern limestone Alps (Inn 2002). At Innsbruck, average discharge from December to March is 50 m^3/s and increases to ~130 m^3/s by July (Tirol 2008). The average discharge at its mouth is 732 m^3/s, and peak discharge (1% probability of occurrence) is 5600 m^3/s (Table 3, ICPDR 2004).

Starting in 1920, the mainstem was converted into a chain of 19 hydropower plants. The tributaries are intensely trained as well; along the Ziller and Sill tributaries there are, for example, ~40 power stations (Inn 2002). Especially in the upstream sections, hydropeaking through pulse releases causes daily water level fluctuations of up to 1.4 m. In Innsbruck, the fluctuations are still up to 0.75 m. Bedload transport decreased from 540 000 tons/year before the 1920s to 180 000 tons/year in 1960, and is near zero today (ICPDR 2005). Snow-water from tributaries delivers glacier silt and mud, causing a high load of suspended matter and a milky, green water colour in the Inn. Thus, at its confluence with the Danube, the algal content (chlorophyll a levels) of the Danube is reduced by almost 50% (Bergfeld *et al.* 2001). The average dissolved oxygen concentration is 10.5 mg/L, and BOD_5 ~3 mg/L. Nitrate–nitrogen (NO_3–N) is as low as 1 mg/L. Total P is around 0.15 mg/L. Low nutrient and organic matter levels in the Inn (and Upper Danube) are the result of high elimination efficiency by municipal and industrial wastewater treatment plants (ICPDR 2005).

9.1.3 Biodiversity

Along the Austrian Inn, >50% of the former fish fauna (35 species) have disappeared mostly due to habitat loss and hydropeaking. Many of the remaining 17 species are restricted to small sections, although grayling (*Thymallus thymallus*) and brown trout (*Salmo trutta*) still occur along the entire section. After construction of the first hydropower plant at Jettenbach in 1921, the commercial fishery collapsed (ICPDR 2005). In the year 2000 fish biomass averaged 54 kg/ha, which is a rather low value for a river of this size. Downstream of Innsbruck, fish biomass can be as low as 10 kg/ha. Without stocking, fish abundance and biomass would even be lower because natural reproduction is limited.

Spindler *et al.* (Inn 2002) examined the hydro-morphological status of 116 tributaries of the Inn. Only five are considered as near natural, and 14 have undergone only minor anthropogenic impacts. Twenty-six (22.4%) are classified as considerably degraded and 11 are strongly altered. The majority of tributaries (60 equaling 51.7%) are classified as non-natural, their integrity has been permanently altered along their entire length. More than 35% of all tributary junctions are impassable for fish, and inaccessible for spawning fish. In tributaries with fish, rainbow trout and brown trout are most common. Graylings, once very common, account for only 3% of the total fish biomass. Minnows (*Phoxinus phoxinus*), another former common species in smaller tributaries, are rare. Quantitative fishing in 47 tributaries of the Inn revealed that 11 are without any fish. Almost 50% of the catch yield can be assigned to small brooks along meadows, as they serve as important breeding habitats (Inn 2002).

Along the lower Inn in Austria and Germany, two contiguous Ramsar sites with an area of 2865 ha were designated in 1976 and 1982. This ~25 km long stretch of the Inn comprises four storage lakes, sediment banks, riverine forests, muddy banks, successional vegetation of various ages, a series of islands and extensive reedbeds that support a wide variety of rare plants, the reintroduced European beaver, as well as the re-immigrating European otter (http://www.ramsar.org). The lower Inn reservoirs and floodplains are important areas for resident and migrating birds. In autumn and spring, up to 25 000 limicolae, other shorebirds, and birds from the high-arctic tundra are present.

9.1.4 Human Impacts and Management

Regulation of the Inn started as early as in the 15th century. The aim was to gain agricultural land in the river valley and to facilitate navigation. Up to 1940, over 700 groynes were constructed (often along both banks). In the late 1960s and early 1970s, the course of the river was partially moved to allow the construction of motorways. In 1855, floodplains covered about 1600 ha, today only 210 ha remain as altered floodplain forests (Bloesch & Frauenlob 1997). Beginning in the 1920s, many tributaries were used to generate hydropower. Reservoirs are flushed about two times per year and clogging (colmation) of bed sediments is an issue for benthic communities and fish spawning.
River restoration has been implemented in the upper Inn in Switzerland (4 km stretch from Celerina to Bever and 6.5 km from La Punt Chamues-ch to S-chanf). Along a 31-km stretch between Mühldorf and Waldkraiburg in Bavaria, restoration works were started in 2003 and should be finished in 2014. Further mitigation measures include the installation of retention reservoirs to lower the negative effects of hydropeaking, and additional fish passes are necessary to enhance the migration for rheophilic

species such as the barbel (*Barbus barbus*) and nase (*Chondrostoma nasus*). Riverbed widening and an active management of the bedload are required to restore spawning habitats (Inn 2002).

9.2 Morava River

The 354-km long Morava River (German: *March*, Latin: *Marus*) is a Central European lowland river that originates in the Králický Sněžník mountains at 1275 m asl in the northwestern corner of Moravia, near the border between the Czech Republic and Poland. It drains an area of 27 267 km². In the lower section, the river forms the border between the Czech Republic and Slovakia and between Austria and Slovakia. The Morava enters the Danube near Bratislava at Devín. The Thaya River (in German) or Dyje (in Czech), forming the border between lower Austria and Moravia, is by far the largest tributary of the Morava River (area: 13 400 km², length: 305 km, discharge at mouth: 43 m³/s). Brno, an industrial and trade town (390 000 inhabitants), and the historic town of Olomouc (160 000 inhabitants) are the main cities in the basin. The Morava River basin has a human population of 3.5 million.

The Morava forms an important natural corridor in Central Europe, allowing migrations of both animals and humans between the Danube valley and the northern European Plains. As such, it has a long history of human occupation and influence. The village Stillfried, along the Austrian Morava, has been occupied by humans for 30 000 years. Agriculture expanded into the area ~7000 years ago and the first fortified settlements were founded during the Neolithicum. Since the 8th century BC, the area has seen a continuous turnover of tribes and cultures: Celts, Marcomanns, Quads, other German tribes and Slavs, among many others.

9.2.1 Geomorphology

The Morava is a lowland river with an average slope of 1.8‰ that enters the Upper Danube (slope: 4‰ at the confluence). Plains cover 51% of the basin, highlands 35% and mountains 7%. The upper valley belongs to the Western Carpathians and is predominantly montane pasture. The basin geology mainly consists of crystalline bedrock (Bohemian Massif) and flysch. The lower Morava traverses the Neogene sedimentary Vienna Basin. Fluvisols predominate along alluvial sections of the Morava.

9.2.2 Climate, Hydrology and Biogeochemistry

The Morava River basin has a temperate continental (upper basin) climate with a pannonian influence in the lower section. Average annual temperature is 8.1 °C. The average annual precipitation in the Czech part of the basin is 635 mm, with up to 1200 mm in the mountainous parts. The average annual discharge at the mouth is 110 m³/s. Flow peaks in early spring (March/April) and can last for weeks to even months. In the downstream section, a second flooding period occurs in early summer when the Danube River impounds back into the lower Morava (up to ~35 km). The Vranov reservoir (length: 39 km, depth: up to >50 m), at the Czech-Austrian border, is the largest out of >20 reservoirs within the Dyje River basin (total storage capacity: 540 million m³), whereas only few reservoirs exist along the tributaries of the Morava (total storage capacity: 56 million m³).

Due to a highly developed industry and agriculture in the Czech part, rivers of the basin serve as recipients of both urban and industrial wastewater effluents. Today, >80% of the human population is connected to wastewater treatment plants. Agriculture is the largest source of nutrients and contributes >65% of the total nitrogen load and 30% of the total nutrient load in the river. During low flows, this imposes higher requirements on the quality of discharged wastewater and, consequently, the whole basin has been declared as a sensitive area. Nevertheless, water quality in the Morava has improved during the past decades. Once it was one of the most polluted tributaries along the Danube with oxygen concentrations frequently dropping to <1 mg/L and fish kills often occurring.

9.2.3 Biodiversity

The Morava floodplains are among the most diverse ecosystems in Europe. With an estimated 12 000 animal and plant species, it ranks 2nd after the Danube delta. In the Slovakian floodplains, 118 nesting bird species, 48 fish species (out of 52 for the entire basin, Lusk *et al.* 2004) and 850 higher plant species have been recorded. Hohausova & Jurajda (1997) identified 22 fish species from the upper river. *Gobio obtusirostris, Barbatula barbatula* and *Carassius carassius* were the most common species. In the lower section, *Abramis brama* and *Alburnus alburnus* dominate assemblages (Umweltbundesamt 1999). However, seven fish species are non-native and 5 species have disappeared in the basin. Beran (2000) found 43 species of aquatic mollusca (28 gastropods, 15 bivalves) in the Litovelské Pomaraví Reserve, near Olomouc, including endangered species such as *Anisus vorticulus* and *Spaerium rivicola*. Hasler *et al.* (2007) recorded 542 phytoplankton species along the Morava and Dyje Rivers. In the lower Morava, both cold- and warm-water adapted species co-occur because of the bimodal flooding regime from the Morava and Danube Rivers. For example, 12 out of 16 large branchiopods (Anostraca, Notostraca, Conchostraca) known for Austria occur in this area, making it an international priority area for these "living fossils" (Eder *et al.* 1997). During inundation, floodplains are used by several fish species for spawning and feeding grounds (Reimer 1991). During the dry phase, these wetlands are colonized by a diverse terrestrial arthropod community, many of them listed as endangered (Zulka 1991).

9.2.4 Human Impacts and Management

Downstream of Litovel, the river has been regulated from the 1930s to 1960s. Along the lower Morava, 17 meanders have been cut off, the length of the mainstem has been shortened by 11 km (14% of this section), and the slope has increased from 0.15 to 0.19‰. Lateral embankments have led to a reduction in the inundation area by ~80%. Similarly, the Dyje River has been channelized during the 1970s and the natural flooding regime was lost because of upstream flow regulation.

The central Morava, near Olomouc, has maintained its natural character for considerable stretches. An important floodplain area is the Litovelské Pomaraví Landscape Reserve, which covers an area of 9600 ha (57% forests, 36% periodically wet fields, 7% permanent wet fields) (Kostkan & Lehky 1997). A transboundary national park has been established along the Dyje River, and floodplains along the lower Morava are protected by the Ramsar Convention. Recently, major plans exist to reconnect meanders along the Morava. The Morava floodplains contain the largest semi-natural alluvial meadows in Central Europe (in Slovakia: 20 000 ha; Cnidion vegetation type predominates) (Ružičková *et al.* 2004). These wetlands are under threat by land use change, flow modification, recreational fishery and gravel mining. Several important measures have already been implemented to improve the situation: rehabilitating watercourses, increasing protection of existing waterbodies and wetlands, and terminating unfavourable agricultural practices (http://www.icpdr.org/icpdr-pages/czech_republic.htm).

9.3 Váh River

The 378 km (360–410 km, depending on source) long Váh River (Hungarian *Vág/Wágh*, German *Waag*, Polish *Wag*) is a left-side tributary of the Danube that flows entirely in Slovakia. It drains an area of 19 660 km² (38% of the total territory of Slovakia). The largest cities in the basin are Nitra, Žilina, Trenčín, Považská Bystrica and Komárno (Komárom) (86 000, 85 000, 57 000, 42 000 and 36 000 inhabitants, respectively).

9.3.1 Geomorphology

The Váh rises in the Carpathian Mountains as the Čierny Váh beneath the Kráľová hoľa peak in the lower Tatra Mountains (1948 m asl) and as the Biely Váh beneath Kriváň peak in the higher Tatra Mountains (2026 m asl). The catchment is characterized by long and narrow river valleys. The Váh and its tributary Orava flow partially through the Pieniny Klippen Belt (PKB). The PKB is composed of several layers of limestone covering a time-span from Early Jurassic to Paleogenic (Oszczypko *et al.* 2004). It represents the topographic contact zone of the External Western (Flysch) and the Central Western Carpathians. The CentralWestern Carpathians consist of Alpine crustal-scale basement and cover sheets (Tatric, Veporic and Gemeric superunits, comprising pre-Alpine amphibolite to greenschist facies basement, granitoids and Late-Paleozoic and Mesozoic sedimentary cover sequences) topped by several superficial nappes (Faryad 1999; Plašienka 2001; Kováč *et al.* 2002).

Along its course, the Vah takes up 11 large tributaries before it enters the Danube in the Western Hungarian Plain (Danube Rkm 1766): Revúca, Turiec, Rajčanka, and Nitra Rivers from the left and Biely Váh, Belá, Orava, Kysuca, Biela voda, Vlára and Malý Dunaj Rivers from the right (Banas *et al.* 1996). The Nitra is the largest tributary (catchment area: 4084 km²) and drains Central Slovakia. The Nitra meets the Váh twice, via a channel some 30 km before and within its natural riverbed at the confluence of the Váh with the Danube. The Malý Dunaj (Small Danube) is a former natural branch of the Danube that separates from the Danube downstream of Bratislava. In the first 15 km, it flows in an artificial channel, and undulates for 120 km parallel to the Danube before it enters the Váh at Kolárovo (25 km upstream of the Vah–Danube confluence). The Small Danube contains numerous vegetated islands. Together with the Danube main channel, it forms the area Žitný ostrov ("Rye Island") that spans 1890 km² and is an important agricultural and drinking water abstraction region.

9.3.2 Climate, Hydrology and Biogeochemistry

The Vah River basin ranges from cold mountainous to warm dry climates with moderate winters. Long-term average annual air temperature varies from 0 to 9 °C. Long-term average annual precipitation in the upper Váh is ~2000 mm and decreases to 550–600 mm in the lower Váh (WFD Report

2004). Average discharge of the Váh, including Nitra and Malý Dunaj tributaries, is 138 km^2 (ICPDR 2007b), and peak discharge (1% probability of occurrence) is 2000 m^3/sec (ICPDR 2004). Due to some storage lakes in the Tatra Mountains, the Váh has a flashy flow regime (maximum discharge range is 62:1; SAZP 2000). Discharge peaks in March and April during snowmelt, while minimum discharge occurs at the end of summer, in autumn and in winter.

The most important industrial areas in Slovakia are in the Váh and Nitra valleys (predominantly machine, food and chemical industries). In addition, the Nitra basin is an important agricultural region. The average annual BOD_5 at the mouth of the Váh has decreased by 50% between 1985 and 1998 to about 2.8 mg O_2/L. Similarly, NH_4–N emissions from wastewater treatment plants have decreased from 1990 onwards (SAZP 1997, 2003), but the lower Váh and Nitra are still seriously polluted.

Average phosphorus values range between 0.24 and 0.26 mg/L and NH_4–N averages 0.63 mg/L at the mouth of the Váh. The Nitra is classified as very polluted to extremely polluted (SAZP 2003), and chlorobenzenes and chloroform are reported to occur (DPRP 1998). At only 10.4%, the municipalities in the Nitra region have the lowest connection to wastewater sewage systems throughout Slovakia (OPBI 2003), and point sources account for about ⅔ of the total organic matter, phosphorus and nitrogen emissions to the river. Diffuse inputs from agriculture are less significant despite being an important land use (IIASA 1996), and there are some local effects from using chromium (Cr^{3+}) contaminated sludge as fertilizer (DPRP, 1998).

9.3.3 Biodiversity

Information about aquatic biodiversity of the river is mostly absent. However, the upper tributaries Turiec (66-km long, catchment area: 934 km^2), Belá (22-km long, catchment area: 244 km^2) and Orava (60-km long, catchment area: 1992 km^2) have been intensively studied during the past decades (Ertl 1983; Krno *et al.* 1996; Ramsar 1998; Ramsar 2006). Channel conditions, the hydrological regime and vegetation of the Turiec are near-natural. Adjacent wetlands have been designated as a Ramsar site in 1998, and were even enlarged in area in 2006 (area: 750 ha) (Ramsar 2006). The wetlands contain a large number of rare or endangered plants, including *Sesleria uliginosa* and the orchid *Dactylorhiza maculata transsilvanica*. The site is also important for algae, fungi, and mosses, as well as for 170 bird species (e.g., the yellow wagtail *Motacilla flava*) and mammals such as the Eurasian otter *Lutra lutra* and the Northern birch mouse *Sicista betulina*.

Benthic communities of the Turiec basin were studied from 1986 to 1990 (Krno *et al.* 1996). In total, 616 benthic invertebrate taxa have been recorded (442 macroinvertebrates), including 40 for Oligochaeta, 7 for Hirudinea, 54 for Ephemeroptera, 64 for Plecoptera (i.e., ⅔ of the stonefly fauna of Slovakia), 62 for Trichoptera, 48 for Coleoptera, 102 for Chironomidae, and 58 for other Diptera (excluding Chironomidae and Simuliidae) – among them are 54 species not found elsewhere in Slovakia. The Turiec and its tributaries support important populations of indigenous lamprey (*Eudontomyzon vladykovi*) and native fishes such as *Hucho hucho*, *Thymallus thymallus*, *Cobitis elongatiodes*, *Alburnoides bipunctatus*, *Chondrostoma nasus*, *Leuciscus leuciscus*, *Lota lota*, *Phoxinus phoxinus*, *Cottus gobio*, *Cottus poecilopus*, and *Zingel streber*. For the Belá River, 14 Oligochaeta species, 28 Ephemeroptera species, 58 Plecoptera species, 56 Chironomidae species and 12 fish species (brown trout, rainbow trout and grayling are the most important species) have been recorded (Ertl 1983).

The Orava River exhibits a near-natural state. Large forested peatlands, meadows, lakes, marshes, swamp forests, and open bogs occur in the basin. This area contains a rich terrestrial fauna and flora. For example, 37 fish species have been recorded, including *Phoxinus phoxinus*, *Cobitis elongatiodes*, *Lota Iota*, *Hucho hucho* and the Ukrainian brook lamprey *Eudontomyzon vladykovi* (Ramsar 1998). All four Newt species of Slovakia occur in the Orava basin (*Triturus alpestris*, *T. cristatuss*, *Lissotriton vulgaris, and L. montandoni*). The Orava is along a major bird migration route, including species of rare migratory species such as white-tailed eagles (*Haliaeetus albicilla*), fish eagles/osprey (*Pandion haliaetus*), black tailed godwits (*Limosa limosa*), black-throated divers (*Gavia arctica*), long tailed ducks (*Clangula hyemalis*), great egret (*Casmerodius albus*) and Eurasian cranes (*Grus grus*). Black storks (*Ciconia nigra*), common kingfisher (*Alcedo atthis*), common tern (*Sterna hirundo*), black-headed gull (*Larus ridibundus*), common redshank (*Tringa totanus*) and yellow wagtail (Motacilla flava) breed within the basin. There are good populations of the Eurasian otter (*Lutra lutra*) and water shrews (*Neomys fodiens* and *Neomys anomalus*) and in 1995 the European beaver (*Castor fiber*) was reintroduced into the tributary Jelešňa. The mouse *Alces alces* and the bat *Myotis daubentoni* also have viable populations. Since 1998, the Orava River and its tributaries have been designated as a Ramsar site (Ramsar 1998).

9.3.4 Human Impacts and Management

Twelve major dams (>15 m) are located along the mainstem of the Váh (17 in the whole basin, Table 1). Hydroelectric development on the Vah and its tributaries (Orava River, in particular) accounts for 48% of Slovakia's hydroelectric power potential. The most important hydropower plants are Čierny Váh in the upper Váh and Liptovská Mara forming the Bešenová reservoir (Rkm 336–345; total storage capacity is 360 million m^3). The nuclear power plant "Bohunice", which uses river water for cooling, is in the lower Váh.

To protect the middle and lower sections against floods, the building of dams commenced in the 1930s and intensified in the 1950s onwards. Today, the Váh and Nitra are regulated along 60–80% of their total length (ICPDR 2007b). Reservoirs on the Váh effectively reduce peak discharges of extreme floods through temporal storage/retention. However, during concomitant floods on the Danube and Váh, the discharge of the Váh escalates flood conditions in the Danube (ICPDR 2004). In former times, timber floating and rafting of mining products from central Slovakia were common on the Váh. Today, commercial navigation is restricted to the lower Nitra and lower Váh (for 74 km, up to the city of Sered), and mainly during higher water levels. Proposals exist (Project „Váh waterway") to make the Váh (European waterway E81) navigable up to Žilina (Rkm 242) and to eventually connect it with the Odra River (via the Kysuca River and various canals) and thus to the Baltic Sea (UNECE 2006). These plans would allow convoys carrying up to 6000 tons and a 22.8 m beam, and require the construction of new locks and the reconfiguration of existing ones.

9.4 Drava River

The 719-km long Drava River (German: *Drau*, Hungarian: *Dráva*, Slovenian, Croatian: *Drava*, Latin: *Dravus*) drains an area of 40 087 km². It is the 4th largest and 4th longest Danube tributary, and is shared by Italy, Austria, Slovenia, Croatia and Hungary. Its main tributaries are the Isel, Möll, Lieser and Gurk Rivers in Austria, as well as the Mura (German: *Mur*) River that joins the Drava River at the Croatian-Hungarian border. The Drava enters the Danube east of Osijek (Rkm 1382), and the basin is inhabited by ~3.6 million people (Schwarz 2007). About 30% of the basin is agricultural area and 46% is forested (Table 1). Graz, Osijek and Maribor are the largest cities (253 000, 121 000 and 116 000 inhabitants, respectively). Navigation is restricted to the lower Drava (~20% of its total length).

9.4.1 Geomorphology

The Drava originates in the Southern Alps in Italy near Dobbiaco (Toblach) on the Austrian border at about 1200 m asl. Within its first few kilometres, the Drava drops 400 meters in altitude. After entering Austria, it flows eastwards through Eastern Tyrol (Tirol) and Carinthia (Kärnten), thereby separating the central Alps from the limestone Alps. The Drava basin (Drautal) is the longest longitudinal valley in the entire Alps. Downstream of the city of Lavamünd, the Drava flows through northeast Slovenia, there the city of Maribor, and enters Croatia.

Upstream of its confluence with the Mura, 23 hydropower plants are in operation along the mainstem (12 in Austria, 8 in Slovenia and 3 in Croatia). Along the Mura, 26 hydropower dams have been built (Reeder *et al.* 2006). Downstream of the confluence, the Drava is a typical lowland river and unsuitable for effective hydropower production. Here, the Drava forms the border between Hungary and Croatia (for 145 km) before again entering Croatia and finally joining the Danube at 80 m asl (Rkm 1382). The lower Mura and Drava constitute a 380 km free-flowing and relatively natural watercourse. The confluence area of the Drava and Danube forms the internationally important Kopački Rit Nature Park.

The Drava crosses several ecoregions ranging from high Alpine mountains (Grossglockner is the highest peak at ~3800 m asl), Alpine basins, a Piedmont section, to finally the Pannonian-Illyrian plain. The river changes longitudinally from a straight to a braided and then to a meandering channel. In the lower reaches, sand and gravel bars as well as vegetated islands are still abundant (Schwarz 2007). The Drava basin consists of two terraces and a recent floodplain. The terrace sediments were deposited during the Upper Pleistocene and Holocene and consist of gravel and sands (Halamić *et al.* 2003), and its course follows geological basin fracture lines (e.g. high banks in Hungary) (Schwarz 2007). The southern Drava basin (and the Drava 'Graben') forms the Drava–Sava interfluve, the southwestern edge of the Carpathian region north of the area of the Dinarids (Földváry 1988).

9.4.2 Climate, Hydrology and Biogeochemistry

The Drava basin has a mild-continental and partly humid climate with an average annual temperature of 10.9 °C and an average rainfall of 600–750 mm/year. The Drava River has a glacial-nival flow regime with lowest flow in January and February and highest flow in May and June (Alpine snowmelt period). A second flow peak occurs in late autumn due to precipitation maxima in the Southern Alps (Mediterranean influence in the middle and lower course). Due to high precipitation rates in the upper basin, the Drava exhibits a high flood risk in the upper reach. Today, the construction of dams, reservoirs and lateral levees prevent the flooding of former floodplains. The downstream section, the Kopački Rit Nature Park area in particular, experiences long-lasting (~100 days of the year) floods. The natural water level fluctuation ranges between 5 and 6 meters in this lower section. Average discharge of the Drava is 541 m^3/s, and peak discharge (1% probability) is 2573 m^3/s (ICPDR 2004).

The Danube–Drava National Park in southwest Hungary is strongly influenced by the high natural water level fluctuations that are increased by hydropower peaking. Thus, the water level of the Drava near the dam fluctuates by about 1–1.5 m several times a day. Oscillations of a few centimetres are still observed in even Osijek, near the Drava–Danube confluence (Schwarz & Bloesch 2004). The hydromorphology also is affected by reduced sediment transport, canalization of the river course and sediment excavation, which lead to an incision of the riverbed by ~2.5 cm/year.

Erosion accounts for a large share of the phosphorus load (1479 tons/year in 2004) of the Drava to the Danube (~6% of the total load of the Danube). The nitrogen load of the Drava was 35 688 tons/year in 2004 (~8% of the total load of the Danube) (Behrendt 2008). Many cities (e.g. Osijek) and industrial areas discharge untreated wastewater into the Drava (Schwarz 2007). The heavy metal content in the topsoil of alluvial deposits exhibit elevated values of arsenic (As: mean value 12 mg/kg) and mercury (Hg: mean value 77 mg/kg) for the Croatian Drava. Elevated values of As and Hg are mostly a result of intense agricultural practices, fossil fuel combustion and traffic in urban areas. Elevated values for lead, zinc and cadmium (mean values for Pb: 76 mg/kg, Zn: 194 mg/kg, Cd: 0.8 mg/kg) are most likely due to former mining, smelting and floatation activities in the Slovenian and Austrian sections of the river (Halamić *et al.* 2003).

9.4.3 Biodiversity

The WWF-DCP Drava Inventory Project (Reeder *et al.* 2006) recorded 66 aquatic macrophytes in the Drava basin. In addition, 54 Odonata species, 27 amphibian and reptile species and 67 mammal species were recorded (Schneider- Jacoby 1994). In the Hungarian part of the Drava River, 113 caddisfly species were recorded, among them the strictly protected *Platyphylax frauenfeldi* which has locally stable populations (Uherkovich & Nógrádi 2005). A total of 63 fish species have been registered for the Drava basin (Sallai & Mrakovčić 2007). Most fishes are reophilic such as the abundant *Chondrostoma nasus, Alburnoides bipunctatus* and *Barbus barbus*. Other rheophilic species are less abundant and protected, including *Rutilus virgo*, *Romanogobio uranoscopus* and *Zingel zingel*. Eurytopic fish species like *Alburnus alburnus, Rutilus rutilus* and *Carassius gibelio* also were reported. In oxbows and backwaters, stagnophilic fish species like *Scardinius erythophtalmus, Tinca tinca* and *Carassius carassius* occur (Sallai 2002, 2003).

About 14 fish species have been introduced, of which the Prussian carp (*C. gibelio*) and Grass carp (*Ctenopharyngodon idella*) cause major impacts to native fauna. Nine species in the basin are endemic (*Rutilus virgo, Romanogobio uranoscopus, R. kessleri, Hucho hucho, Umbra krameri, Gymnocephalus baloni, Gymnocephalus schraetser, Zingel zingel,* and *Zingel streber*). A total of 24 species are protected and five fish species are listed as (critically) endangered (*Eudontomyzon vladykovi, Hucho hucho, Umbra* *krameri, Zingel zingel,* and *Z. streber*) (Sallai 2002, 2003). Four species, all sturgeons, are regionally extinct.

A total of 291 bird species are reported, 25% are listed as protected and include the little tern (*Sternula albifrons*, http://www.sterna-albifrons.net). It has been a characteristic breeding bird of the Drava in Slovenia, Croatia and Hungary, but has become nearly extinct due to the loss of gravel and sand banks as a consequence of hydropower dam construction in the 1970s and 1980s. Only 15 pairs remain in the lower free-flowing course of the Drava. The common tern (*Sterna hirundo*), common sandpiper (A*ctitis hypoleucos*) and the little ringed plover (*Charadius dubius*) require similar habitats. Seventy-nine colonies of sand martins (*Riparia riparia*) and 36 colonies of bee-eaters (*Merops apiaster*) found along the free-flowing Drava indicate active lateral erosion (Reeder *et al.* 2006).

9.4.4 Human Impacts and Management

Numerous groundwater well-fields for public water supply and hydro-technical melioration systems have been built in the Drava River basin. Human activities, which are often weakly controlled and poorly coordinated, have resulted in significant changes in the hydrological regime of the river. The Drava was regulated and dammed during the past century with a few semi-natural sections remaining in the lower part. In the upper part, intermittent hydropower generation (hydropeaking) causes major water level changes and impacts the aquatic fauna. In the Austrian part, a reduction of 50% of the fish stock and 80% of the benthic invertebrate community has been attributed to hydropeaking operations in the Möll and Malta tributaries (ICPDR 2005).

The lower Drava in Hungary has been protected as a National Park since 1991. In 2007, the lower section of the Mura was designated as a protected landscape, and Croatia has recently (March 2008) decided to establish the Regional Park Drava (total area: 1500 km^2). Its aim is to achieve transboundary protection status to allow for the implementation of joint monitoring programs, and to have this area included into the UNSECO Man and Biosphere (MAB) reserve network (Schneider-Jacoby 1996; SIFNP 2005). However, the park management is faced with a strong lobby of hydropower and navigation stakeholders.

9.5 Tisza River

The Tisza River (German: *Theiß*; Romanian, Slovakian, Serbian: *Tisa*; Ukrainian: *Tysa*) is in the geographic centre of Europe and drains parts of five countries (Ukraine, Romania, Slovakia, Hungary and Serbia). It is the longest (965 km) tributary with the largest catchment (catchment area: 156 087 km^2; Table 1) in the Danube basin. Mean annual discharge is 792 m^3/s, and it contributes ~13% to the total runoff of the Danube. The Tisza basin is home to 14 million people, and is mainly used for agriculture and grazing. Arable land covers 48% and forests cover 30% of the basin, mainly restricted to the north and east. Forestry is an important economic sector in the upper basin, particularly in Ukraine and Romania (ICPDR 2008). The largest cities in the basin are Cluj-Napoca, Timisoara and Kosice (320 000, 300 000 and 235 000 inhabitants, respectively). Some 3% of the basin is under legal protection.

9.5.1 Geomorphology

The basin is fringed by the ridges of the Carpathian Mountains (highest peaks in the Rodna Mountains at 2300 m asl and in the Retezat Mountains, Mures sub-basin at 2506 m asl) in the northwest to southeast. The eastern catchment is partly in the Transylvanian basin. The Tisza River network can be divided into three main parts: The mountainous upper Tisza extends to the confluence with the Szamos/Sumeş. The two headwaters, the Black and the White Tisza, originate in the Ukrainian Carpathian Mountains at ~1700 m asl. The slope in this section is 20–50‰. As a wild mountain river, the Tisza flows west through a sequence of alluvial and constrained sections, partly forming the Ukrainian-Romanian border. In this section, it receives the Visó/Vişeu and Iza tributaries, and the river changes to a braided style with numerous vegetated islands and extensive gravel areas. The slope declines to about 2‰. Before it enters the Hungarian Plain, the Tisza receives the Tarac/Tereszva, Talabor/Tereblja, Nagyág/Rika, Borsa/Borszava and Túr (in Hungary) tributaries. The channel changes from a gravel-bed to a sand-bed river. Along the first 260 km, from the source to the confluence with the Szamos/Sumeş, the Tisza has already dropped by 1600 m in elevation.

The middle Tisza extends to the confluence with the Mureş/Maros River which features an outstanding near-natural hydromorphology (Sandu & Bloesch 2008). The Bodrog and Sajó/Slaná Rivers are the largest tributaries in this section, and their catchments are in the Slovakian and Ukrainian Carpathian Mountains. The other large tributaries Körös/Crişul and Maros/Mureş drain parts of Transylvania in Romania. The smallest tributary of the middle Tisza is the Zagyva, which drains the Mátra and Cserhát Mountains in northern Hungary. In the middle Tisza, the slope is about ~0.09‰. In the upper Hungarian plain, the Tisza forms a great northward loop (the "Záhony bend") towards the Slovak-Hungarian border (Timár *et al.* 2005). The middle Tisza channel has an average width of 200 m, and the silt and clay proportion increases due to the fast loss in sediment transport capacity (average slope: 0.025‰).

The section downstream of the mouth of the Maros/Mureş River forms the lower Tisza. In this section, the Tisza receives the Béga/Begej, the Aranka and numerous smaller tributaries via the Danube–Tisza–Danube Canal System. The Tisza finally enters the Danube River in central Vojvodina, Serbia. In the Great Hungarian Plain, the Tisza is a typical lowland river with a meandering planform. The proportion of mountain areas in the Tisza catchment is about 1%, the area below 200 m is 46% (Szabó 2007; Zsuffa 2002). The Tisza is, together with the Inn River, the greatest supplier of loess sediments to the Danube. The loess is mainly composed of quartz silt and primarily originates from weathering of flysch bedrock in the Carpathian Mountains and Aeolian loess that is derived from fringing floodplains (Smalley & Leach 1978).

9.5.2 Climate, Hydrology and Biogeochemistry

The Tisza basin exhibits a temperate continental climate. Mean annual temperature is 6–9 °C in the mountainous sections, 8–9 °C in the Transylvanian basin, and 10–11 °C in the lowland catchment. Seasonal temperature ranges from 32 to 41 °C (Szabó 2007). Overall, the Tisza drains a relatively dry area. While precipitation exceeds 1700 mm in the high Carpathian Mountains (the Máramaros Alps), it decreases to <500 mm in the Great Hungarian Plain (Zsuffa 2002). Due to predominant northwest winds, the southeast slopes of mountains and basins behind are particularly dry (i.e., Zagyva catchment and the area east of the Bihar Mountains, where the Körös and Maros River catchments meet). About 25% of the annual precipitation falls in May/June, followed by dry summers. A second peak of precipitation occurs in October/November.

The Tisza exhibits a nival–pluvial flow regime with highest discharge in March/April and low flows in summer and early autumn. Discharge decreases rapidly at the end of the snowmelt period. Mean annual discharge at the mouth is 792 m^3/s (Tables 1 and 2) with a maximum of 3730 m^3/s and a minimum of 80 m^3/s. The Tisza and, in particular, tributaries such as the Bodrog and Körös, exhibit flashy flow regimes because of the lack of natural lakes functioning as retention basins, the predominance of fine soils, and deforestation in the headwaters. During the past 30 years, the river has experienced >100 major floods. The rate of occurrence and the magnitude of floods have shown an increasing trend, most likely in line with global warming. In 1998 and 2001, two devastating floods occurred in the Tisza basin (Szabó 2007).

There is a lack of municipal wastewater treatment facilities throughout the basin; in some areas <50% of the urban population is connected to the public sewerage system. Septic tanks are common. As a result, raw or only partially treated sewage is released into tributaries and the Tisza itself. Moreover, runoff from stockyards and animal wastes increase the organic load and microbial contamination in recipient waters. In 2004, the Tisza basin contributed 72 330 tons N (16%) and 4340 tons P (19%) to the total load of the Danube River (Behrendt 2008). Throughout the basin, the legal limits for nitrate concentrations in groundwater are often exceeded.

Major contamination of surface and ground waters by heavy metals (i.e., copper, iron, manganese, zinc, lead, cadmium) and other toxic substances such as cyanide from inadequately treated industrial discharges from mining and metal processing industries is prevalent in the upper basin. The Maramures mining region in Romania is the main risk spot in the basin. Recent major accidental spills in the basin have been the Baia Mare cyanide and heavy metal spill in January 2000 (release of about 100 000 m^3 wastewater containing up to 120 tons of cyanide within 11 h), the Baia Borsa heavy metal spill in March 2000 (release of 100 000 m^3 sludge with about 20 000 tons of solid tailings containing elevated amounts of heavy metals), and the oil pipeline incident on the Latorica River in September 2003 (resulted in a 5-km slick of oil).

9.5.3 Biodiversity

The Baia Mare spill (see section above) reached the Black Sea through downstream neighbouring countries within two months and caused a massive fish kill. Recovery was fast and after 1 year fish biomass was almost as high as before the accident. More than 95% of the killed fish belonged to non-native species *Ctenopharyngodon idella* (Chinese grass carp). In this respect, the disaster could be regarded as an ecological benefit for the indigenous fauna if the exotic carps would not have been restocked. There are still chronic consequences due to the accumulation of heavy metals in deposited sediments with potential long-term effects on biota and humans.

The Tisza River shows a high biodiversity, higher than most Western European rivers, mainly due to extensive natural or semi-natural floodplains along the mainstem and tributaries (>300 riparian wetlands are found in the catchment). Moreover, the Carpathian Mountains remain relatively unaffected from intensive agriculture and forestry. Thus, large carnivores including the brown bear (*Ursus arctos*), lynx (*Lynx lynx*), wolf (*Canis lupus*) and otter (*Lutra lutra*) are still abundant. About 60% of the total European brown bear population lives in the Romanian part of the catchment. Many vulnerable, threatened, and critically endangered species such as the Corn crake (*Crex crex*), Geoffroy's bat (*Myotis emarginatus*), European ground squirrel (*Spermophilus citellus*) and Russian sturgeon (*Acipenser gueldenstaedtii*) can be found.

The basin also contains the mayfly *Palingenia longicauda*, the largest European mayfly that shows spectacular synchronized mass emergence events. This species has been abundant in the middle and lower sections of larger lowland rivers up to the beginning of the 20th century. It has disappeared from Western Europe and has undergone a serious decline in Central Europe. Today, this species is only reported for the Tisza and some tributaries (e.g., Szamos, Körös) (Tittizer *et al.* 2008). The upper Tisza Basin is an important migration route for fish, notably nase (*Chondrostoma nasus*), barbel (*Barbus barbus*) and sterlet (*Acipenser ruthenus*). This river stretch supports a rich dragonfly fauna as well as many nesting water birds, including all 8 European herons (*Ardea cinerea*, *A. purpurea*, *Ixobrychus minutus*, *Botaurus stellaris*, *Egretta garzetta*, *Nycticorax nycticorax*, *Ardeola ralloides*, and *Bubulcus ibis*).

9.5.4 Human Impacts and Management

The present geomorphology and hydrology of the Tisza are the result of major human interventions, mainly between 1845 and 1910. The former extensive floodplains were drained or embanked to enable constant agricultural and industrial practices as well as to aid navigation and transport. Concurrently, the mainstem of the Tisza was shortened by 30–40%, while the channel slope increased from 0.02–0.04 to 0.04–0.08‰ in the Great Hungarian Plain (Lászlóffy 1982). Today, <1000 km² of the former 25 900 km² floodplains in the Hungarian Tisza basin remain, corresponding to a total reduction of 96% (UNEP 2004). In Hungary, 500 000 people, or 5% of the country's population, inhabit land reclaimed from the Tisza (ICPDR 2008). A total of 167 larger and numerous small oxbow lakes are now disconnected, except during major floods.

In the lowland section, the river traverses a 1400–1800 m wide corridor fringed by lateral embankments, and the riverbed is ~200 m wide (Szabó 2007). As a consequence of intense regulation and exploitation, the groundwater table along the Tisza has decreased, salinisation has increased, and soil-incrustination in the western area is prevalent. Following the strong droughts in the 1930s, construction of lowland reservoirs began in the Körös/Crisul River. Moreover, two large irrigation channels (98 and 70 km long, 10–30 m wide and 3–4 m deep) that branch off of the Tisza in northern Hungary were finished in the late 1950s. These channels have considerably enlarged the agricultural area and dampen floods. Due to their high water quality, they supply the second largest Hungarian city Debrecen as well as smaller cities with drinking water. These channels provide habitats for about 42 fish species.

Today, more than 60 reservoirs exist in the basin with a total reservoir capacity of ~2.7 billion m³. The Kisköre Reservoir (finished in 1974), so-called "Lake Tisza", is the largest artificial lake in Hungary with a storage volume of about 106 million m³. It provides recreational facilities and acts as a nature conservation site. A total of 37 hydropower stations (35 with an installed capacity >10 MW) have been built in the basin. The Tisza is used for 70% of its length, up to the Ukrainian border, for navigation (ICPDR 2008). However, the Tisza has lost its importance as a shipping route due to the decline in production and export of agricultural goods and building materials in Hungary. The water level of the Tisza still undergoes large fluctuations with low water levels of only 20–30 cm in fords along free-flowing sections between Kisköre and Csongrád during summer. Existing locks do not allow the passage of large vessels and the Tisza does not belong to the EU waterways of importance (Marton 2008). Some tributaries are navigable on shorter sections: Bodrog (Hungarian stretch and 15 km into Slovakia), Mureş (25 km, corresponding to <5% of its total length), Körös (115 km in Hungary) and Bega (117 km in Romania, Serbia and Montenegro, >48% of the total river length).

Land use changes in the upper Tisza catchment have increased runoff, soil erosion and diffuse nutrient inputs. As a consequence, floods, landslides and droughts (particularly in Hungary and Serbia) are more common today (ICPDR 2008). Efforts to reduce flood impacts by constructing higher dykes and continued riverbed regulation have led to the siltation of the main riverbed, which has inadvertently increased flood risks. The projected total annual water demand for the Tisza basin in 2015 is estimated to be ~1.5 billion m^3, or about 6% of the total annual runoff. Irrigation also is predicted to increase in all Tisza basin countries, which will add pressures on already threatened aquatic ecosystems; particularly during low water periods (ICPDR 2008). In Slovakia, major conservation areas exist along the Slaná River (50 000 ha) and a wetland is found along the Latorica River (10 000 ha). In Romania and Ukraine, protected areas total 195 000 ha. Along the middle and lower Tisza, five national parks (total area: 935 000 ha) and several protected areas exist.

9.6 Sava River

The 945-km long Sava River (*Save* in German, *Száva* in Hungarian) is the largest tributary of the Danube by volume (average discharge: 1572 m^3/s), and the second largest, after the Tisza, by catchment area (95 793 km^2). Today, the Sava basin is an international basin: 40% is in Bosnia and Herzegovina, 26% in Croatia, 15.4% in Serbia, 11% in Slovenia, 7.5% in Montenegro and 0.1% in Albania. Several tributaries such as the Kolpa/Kupa, Una and Drina Rivers cross international boundaries. About 8.8 million people live in the basin. Belgrade, Zagreb, Sarajevo, Ljubljana and Banja Luka are the largest cities (1.6 million, 780 000, 304 000, 280 000 and 225 000 inhabitants, respectively). Some 37% of the basin is arable land, and 45% is forested (Table 1).

9.6.1 Geomorphology

The Sava River is formed by the headwaters of the Dolinka Sava originating at the Italian-Slovenian border at 870 m asl and the Bohinjka Sava from Lake Bohinj (Bohinjsko jezero) in the Julian Alps. In Slovenia, the Sava is a gravel-bed river with an average slope of >0.7‰. The Sava and its tributaries have carved deep gorges into the cretaceous limestone. Eocene flysch forms the bedrock in northwest Slovenia. In Croatia, downstream of Zagreb, the Sava meanders through a wide valley covered with fertile soils and fringed by wetlands (average slope: 0.04‰) (Brilly *et al.* 2000). The Sava passes by the valley of the Kupa River and for 311 km the Sava constitutes the border between Croatia and Bosnia and Herzegovina (from the confluence of the tributary Una almost to the confluence of the Drina).

In Serbia, it remains a typical lowland river with a channel width of up to 1000 m before it enters the Danube in Belgrade (Rkm 1170). In the downstream section, alluvial sediments and igneous rocks with Neogene marls and shale prevail. The Sava drains the southeastern fringe of the Alps and the north-eastern Dinaric Mountains as well as the southern Pannonian lowland (Pandžić and Trninić 1998). Although most of the catchment is in the Alps and Dinarids, the river traverses a wide lowland valley. Most major tributaries enter from the right side. About 25% of the basin is karstic. Caves and underground rivers are common in the upper basin (Brilly *et al.* 2000).

9.6.2 Climate, Hydrology and Biogeochemistry

The Sava basin exhibits a mixture of Alpine and Mediterranean climates. Average annual air temperature is 9.2 °C and average annual precipitation is 1000 mm. Maximum precipitation is ~3800 mm in the Julian Alps and in the upper Kupa region (ICPDR 2004), minimum precipitation is 600–700 mm in the Pannonian Plain. The Sava has a nival-pluvial flow regime with a spring peak caused by snowmelt in the Alps and a second peak in autumn caused by heavy rainfall. The ratio of the highest to lowest monthly average discharge is ~10:1 (Brilly *et al.* 2000).

Average annual discharge of the river is 1572 m^3/s at its mouth, with an annual peak discharge of ~6400 m^3/s (1% probability of occurrence, ICPDR 2004). The Drina River is the largest tributary with an average discharge of 370 m^3/s (ICPDR 2004). The Sava contributes about 25% of the total Danube discharge (~15% of the Danube basin). Together with the Tisza, the Sava dominates the discharge regime in the Lower Danube, causing two distinct seasonal maxima. The impounded section of the Iron Gate I and II dams extends 100 km upstream into the lower Sava (ICPDR 2005).

Until the 1990s the Sava was affected by heavy pollution from metallurgical, chemical, leather, textile, food, cellulose and paper industries (Jovičić *et al.* 1989), as well as from agricultural activities (agrochemicals, pesticides and pollution from pig and poultry farms). These activities reduced during the war in the 1990s, but have been resumed since 2000. The Sava is the main recipient of wastewater from many cities, including Zagreb (Croatia) (Bosnir *et al.* 2003) and is impacted by polluted water of the tributaries Kupa and Bosna as well as smaller tributaries in the Zagreb region (Brilly *et al.* 2000). Thermal pollution from conventional powerplants and a nuclear powerplant (Krško in Slovenia) occurs along the Slovenian Sava sections. Today, the specific organic pollution in the basin is above Danube average (ICPDR 2005). The basin contributes 102 362 tons N (23% of the Danube basin) and 9829 tons P (43% of the Danube basin) to the total annual load of the Danube River (Behrendt 2008). In the lower Sava, the concentration of atrazine is ~0.78 µg/L (ICPDR 2005). Downstream of the Sava confluence, the Danube exhibits elevated concentrations of Al, As, Cd, Cu, Fe, Mn, Ni and Zn.

9.6.3 Biodiversity

For the Serbian river section, 62 macroinvertebrate species have been recorded (Paunović et al. 2008). Molluscsa (Gastropoda: 12 species, Bivalvia: 11 species) and Oligochaeta (16 species) dominate assemblages, and the community structure indicates habitat degradation and organic pollution. Five non-native species are reported to occur. The bivalve *Corbicula fluminea* (Asian clam) and oligochaete *Branchyura sowerbyi* show high frequencies, while the bivalve *Anodonta (Sinanodonta) woodiana* exhibits high abundances (Paunović *et al.* 2008). About 55 fish species, including the sterlet (*Acipenser ruthenus*), are found in the Sava River (Mrakovčić *et al.* 2006). The Nature Park "Lonjsko Polje" in the middle Sava forms the largest remaining inundation area in the entire Danube basin (510 km²). There, floodplain waters contain at least 35 fish species. This area is an important spawning area for wild carp (*Cyprinus carpio*). Further, 43 dragonfly species have been identified during a seasonal survey. The Nature Park provides breeding habitats for 22 bird species of special conservation concern in Europe, among them are rare birds such as the ferruginous duck (*Aythya nyroca*), white tailed eagle (*Haliaeetus albicilla*) and corncrake (C*rex crex*) (Schneider-Jacoby 1994).

9.6.4 Human Impacts and Management

Major sections of the river still exhibit a relatively natural geomorphic structure and hydrological regime and are fringed by large protected wetlands. The mainstem is navigable for almost 600 km (from the mouth up to the city of Sisak, 60 km downstream of Zagreb) for small vessels and for 377 km (up to Slavonski Brod) for large vessels. In the 18th century, the river was an important transportation route for crops. During the communist era, the Sava became the main transportation and shipping route of former Yugoslavia. The mainstem has been canalised for flood protection only in a very few and short sections (e.g. in Zagreb). In the central basin only about 40% of the alluvial wetlands were converted into arable land or drained. Large parts of the city of Zagreb were built on the former floodplain. In the 1960s, the city expanded to the southern banks of the Sava and floods became an increasing threat.

Regulation of high water by the central Posavina flood control system is carried out via three relief canals protecting the towns Zagreb (Odra Canal), Karlovac (Kupa-Kupa Canal) and Sisak (Lonja-Strug Canal), 15 distribution facilities and large alluvial retention areas for storage. This system has proven effective since its design in 1972, and the channels and facilities have been integrated into the existing limited flow river network. This is a system that, with the necessary retention and expansion areas in the lower central basin, and governed by the criteria established for the regulation of the water masses, ensures an unaltered water regime in the Makovac exit control profile (maximum: 3000 m^3/s) toward the lower Sava valley (Brundic *et al.* 2001). Only in the central basin around Zagreb 116 000 ha of floodplains have been preserved as retention areas and unique natural sites.

Two Ramsar sites – Lonjsko Polje and Crna Mlaka – and three important bird areas – Sava Wetlands, Odransko Polje and the Pokupsko depression – form a unique blend of natural landscape elements and European riverine lowlands. Further, large retention areas and alluvial wetlands are situated on the left Sava bank in the Spava-Bosut depression at the border with Serbia (Schneider-Jacoby 2005).

Along the Serbian section, a former large inundation area is separated by a 771-km long flood control dike (Brilly *et al.* 2000). In Slovenia, four large and several small hydropower plants are in operation along the mainstem, and nine are planned or already under construction. A chain of hydropower reservoirs is planned to be built in the Croatian section upstream of Zagreb, and additional multi-purpose reservoirs are foreseen. In Bosnia and Herzegovina, 12 hydropower plants are in operation along mountainous tributaries, greatly reducing sediment transport. Sediment management remains a key issue in the entire basin.

Increasing anthropogenic activities in the headwaters of the Sava and main tributaries, such as urbanisation, industrial development and agricultural monoculture, have increased the impact by organic, inorganic and hazardous pollutants. Bosnir *et al.* (2003) reported elevated mercury concentrations in fish caught in the Sava near Zagreb. The main economic industries in the basin are metal, chemical and food production as well as small family estates with extensive agriculture. During the dry season, water supply systems are sometimes unable to meet the water demands of consumers due to management and capacity problems. Today, most people are connected to the public water supply (e.g. 84% in Slovenia in 1991), but few are connected to wastewater treatment systems (e.g. 16% in Slovenia in 1991; negligible in Bosnia and Herzegovina) and urban sewage is directly discharged into the river. In Zagreb, a wastewater treatment plant has been in operation since late 2007, and another is planned for the Karlovač Province. In Serbia and Bosnia and Herzegovina, unprotected landfills along the river remain a permanent risk (http://www.inweb.gr/workshops/sub_basins/1_sava.html). Industrial pollution (leather, paper, oil and food industries) and pollution from agriculture cause major transboundary challenges for some city water supplies (e.g. Zagreb and Belgrade).

With its large alluvial wetlands and undisturbed lowland forests, the basin provides a major environmental resource. Four Ramsar sites have been designated: Cerkniško jezero (intermittent karstic lake, 7250 ha, Slovenia), Lonjsko Polje (500 ha, Croatia), Bardača (3500 ha, Bosnia and Herzegovina) and Obedska Bara (30 000 ha, Serbia). The headwaters of the Sava are in Triglav National Park and Plitvice Lakes National Park (UNESCO World Heritage site since 1979), and Croatian tributaries are found along the Risnjak National Park. Numerous important hotspots of biodiversity and Natura2000 sites exist in the basin.

Currently, flood protection in most parts of the middle and lower basin relies on flood-protection dikes as well as on natural retention areas in some parts. In particular, the Nature Park Lonjsko Polje in Croatia serves as a natural retention area and is a good example of how to link flood control measures with the conservation of natural and cultural landscapes of national and international importance (ICPDR 2005). The Tourism Masterplan for the Posavina is proposing an intergrated development for the whole central basin (http://www.euronatur.org/fileadmin/docs/projekte/Save/Save_bulletin_EN_KR.pdf). The Nature Park Lonjsko Polje is an outstanding place for tourism development for inland Croatia (Komatina & Grošelj 2008).

During the past two decades, pollution has decreased due to reduced industrial production and a weak economy. The riparian states of the Sava are presently in a post-war recovery period and pollution levels are slightly increasing (Brilly *et al.* 2000). The International Sava River Basin Commission (ISRBC) was established in late 2002 and held its constitutional session in mid 2005. The general objectives of the ISRBC are to strengthen transboundary cooperation for sustainable development of the region. Its specific goals are (i) the establishment of an international navigation regime along the Sava and its navigable tributaries, (ii) the implementation of a sustainable water management scheme and (iii) to undertake measures to reduce the risks of flooding, ice jams, droughts and pollution accidents (http://www.savacommission.org). The ISRBC works in close cooperation with the International Commission for the Protection of the Danube River (ICPDR). Currently the preparation of the Sava Basin Management Plan (in accordance with the EU WFD) and a Flood Risk Management Plan (in accordance with the EU Flood Directive) are under preparation (Komatina & Grošelj 2008). Unfortunately, there are plans to canalise the remaining near-natural meandering section in the middle Sava, and a navigation channel between the Sava and Danube Rivers in Croatia is under consideration. But there is hope as Croatia has proposed the Nature Park Lonjsko Polje as a Natural and Cultural World Heritage Site in 2008 (http://www.pp-lonjsko-polje.hr) and the ecological value of the alluvial forests and retention areas impacted by the proposed navigation channel would be much higher, if the application will be successful, and help to preserve the natural riverbed and its floodplains (Schneider-Jacoby 2005).

9.7 Velika Morava River

Two Morava Rivers are found in the Danube basin. The 'Slovak' Morava is a left-hand tributary that enters the Danube east of Vienna (see Section 9.2.). The Velika Morava ('Great Morava') corresponds to the lower section of the Morava basin in Serbia. The Serbian Morava is the lowermost large right-bank tributary of the Danube upstream of the Iron Gate. The Latin sources refer to the 'Slovak' Morava as *Marus* and to the Serb Morava as *Margus* (Sinor 1997). The Serbian Morava drains 40% of the entire country, in total an area of approximately 38 000 km². Small parts of the catchment are in Bulgaria (~3%) as well as in Macedonia and Montenegro (<0.5% each). The basin is inhabited by 4.5 million people and the catchment consists of 39% arable land and 43% forested area (Table 1).

9.7.1 Geomorphology

The Morava catchment has three sub-basins: (i) the catchment of the Velika Morava that extends from the confluence of the Južna (Southern) and Zapadna (Western) Morava near the city of Stalac (130 m asl) to its confluence with the Danube, (ii) the catchment of the Južna Morava and (iii) the catchment of the Zapadna Morava. The Velika Morava crosses densely populated and cultivated areas for ~180 km. It receives 32 tributaries before it enters the Danube near the city of Smederevo (Rkm 1105). The Velika Morava valley contains among the most fertile soils in Serbia and is therefore important for crop production (SEPA 2007). Alluvial terraces and marshy bogs fringe the mainstem. The alluvial sediments consist of a mixture of Quaternary loess, Neogene lacustrine sediments, Mesozoic flysch sediments and Paleozoic schists. Pockets of volcanic and plutonic igneous rocks also occur (Jakovljevic *et al.* 1997). The Velika Morava has an average channel width of 140 m (maximum: 325 m) and a water depth (surface to bottom) of 1–4 m. Height of the river banks (from bank edge to thalweg or water surface) is 3–16 m.

The 230-km long Južna (Southern) Morava drains southeastern Serbia (catchment area: 15 446 km²). Its two major headwaters originate from the Macedonian-Serbian and Rilo–Rhodope Mountains and merge near the city of Bujanovac at 400 m asl. The most important tributary is the Nišava River (length 218 km; area 4068 km², 25% is in Bulgaria) that originates on the southern slopes of the Stara Planina Mountains in Bulgaria and enters the Južna Morava near the city of Niš. Although the Južna Morava is considered a lowland river, it crosses a series of alluvial plains separated by constrained sections. Several of its tributaries are relatively natural with densely forested catchments and clear waters.

The 308-km long Zapadna Morava River drains southwestern Serbia (catchment area: 15 567 km²). Its headwaters are ramified, originating in the Golija (1350 m asl), Mučanj, and Tara Mountains in the Dinaric Alps (western Serbia). Its headwaters merge near the village Leposavić at 302 m asl. The largest tributary is the Ibar River (catchment area: 7500 km², length: 272 km). It originates in eastern Montenegro at 1360 m asl, flows eastwards to Mitrovica (Kosovo), then north until it meets the Zapadna Morava near the city of Kraljevo.

9.7.2 Climate, Hydrology and Biogeochemistry

The Morava River basin has a predominantly continental climate with an average annual temperature of 11–12 °C (January: 1 to +1 °C, June: 22–23 °C). Precipitation is highest in May and June and lowest in February and October. In the alluvial plains, average annual precipitation ranges between 600 and 700 mm. Precipitation increases to 800–1300 mm with increasing altitude. The Južna Morava flows through a dry valley with an average precipitation of <600 mm (SEPA 2007).

The average discharge of the Morava is 277 m^3/s (average low flow: 50 m^3/s; peak flow with 1% probability of occurrence: 2464 m^3/s; ICPDR 2004, Table 3). Discharge peaks during the short snowmelt period in spring. Major floods occur when snow melting and heavy rains coincide, and its tributaries exhibit a torrential character with frequent flash floods associated with landslides. Erosion is prevalent in the entire basin, in particular in the almost completely deforested Južna Morava sub-basin (UNECE 2007). High sediment yields reduce the flow capacity in the downstream Velika Morava River and increase flood risks. Flood protection embankments and chains of reservoirs have been constructed to reduce flood risks. All major cities as well as many industrial facilities and waste disposal sites are found in flood prone areas (ICPDR 2006).

About 60% of the phosphorus (P) input originates from point sources such as industrial areas, wastewater treatment plants, as well as through the prevalent use of P in detergents. Less than 10% of the rural population and ~30% of the urban population is connected to public sewerage systems (UNEP 2003; SEPA 2007). About 20% of the P-input originates from erosion, in particular from fertile arable lands (Schreiber *et al.* 2003). The annual load of P from the basin is 1841 tons/year (in 2004) and contributes ~8% to the total P load of the Danube (Behrendt 2008). Dominant pathways for nitrogen input are groundwaters (~40%) and point sources (i.e. urban areas; 25%). Topsoils in the basin have a high N-content resulting in an annual load of 28 246 tons/year (in 2004), 6% of the Danube basin (Behrendt 2008). Based on the saprobic index, the Morava River is classified as 'critically polluted' at its mouth (ICPDR 2005), and BOD_5 values are considerably higher compared to most Danube tributaries. Downstream of the confluence with the Velika Morava, Danube river sediments (bed and suspended sediments) contain elevated lead (Pb) concentrations (52–70 mg/kg, Klaver *et al.* 2007) and increased levels of faecal coliforms.

Recent changes in the Serbian economy have resulted in a significant reduction of pollutants. The economic decline and transformation to private ownership have resulted in a significant change in industrial production from 1998 to 2002 (ICPDR 2006). BOD_5 and ammonium (NH_4–N) concentrations show decreasing trends. Today, BOD_5 is as low as <4 mg O_2/L and NH_4–N has stabilised to 500 µg/L. Nitrate and orthophosphate concentrations range between 1.5 and 2 mg/L and <400 µg/L, respectively (SEPA 2007). The Zapadna Morava and its tributary Ibar are the most polluted rivers in the catchment as well as in Serbia. They receive large volumes of untreated wastewater that contain phenols, lead, zinc and nickel from non-sustainable industrial complexes such as lignite mines, power plants and sawmills (UNEP 2003; Spasojevic *et al.* 2005).

9.7.3 Biodiversity

In a recent survey, 42 fish species have been recorded for the Velika Morava River (MEP 2003). Cyprinidae predominate and Salmonidae, Esocidae, Cobitidae, Balitoridae, Siluridae, Ictaluridae and Percidae are also abundant. In the headwaters, cold-stenotherm invertebrates dominate the macroinvertebrate community, especially Plecoptera, Ephemeroptera, Trichoptera and Amphipods (mainly *Gammarus* spp.). Artifical ponds and reservoirs are mostly eutrophic and their benthic communities are represented by Oligochaeta (family Tubificidae, genera like *Limnodrilus, Potamotrix, Tubifex*) and Diptera (family Chironomidae, Chaboridae) (MEP 2003). Since 2005, the Chinese pond mussel (*Anodonta* (*Sinanodonta*) *woodina*) has been reported in the lower Velika Morava. Its abundance exceeds the native mussel *Unio pictorum* by a factor of 5, and is now spreading into other tributaries of the Danube such as the Sava (Paunović *et al.* 2006). The non-indigenous tubificid worm *Branchiura sowerbyi* has a scattered distribution in the basin (Paunović *et al.* 2005).

9.7.4 Human Impacts and Management

Between 1960 and 1995, the Morava basin has undergone major hydro-engineering activities. The Velika, Zapadna, Južna Morava Rivers as well as some of their tributaries have been regulated, meanders have been cut off, and the river courses shortened. Marshlands have been transformed into fish ponds (today: ~4000 ha), and comprehensive drainage systems have been put in place to increase the proportion of arable land (Jakovljevic *et al.* 1997). Extensive flood embankments (total length ranges between 1181 and 2015 km, depending on source) disconnect the floodplains from the river. Several multipurpose dams and reservoirs have been constructed that are used for flood protection, irrigation, municipal water supply (e.g. Prvonek, Barje, Gruža dams), and hydropower generation (e.g. Meduvršje, Gazivode reservoirs; volume: >10 million m^3). Moreover, dredging of sand and gravel has impacted the hydromorphology of the rivers, and predicted increase in industrial activities could further degrade water quality.

9.8 Olt River

The 615-km long Olt River in central and southern Romania drains a catchment of 24 439 km^2 and enters the Danube at Rkm 604. The human population within the basin is 2.13 million, of which 53% are living in urban areas (population density: 87 inhabitants/km^2, Table 1, Olt RD 2007). The largest cities along the river are Brașov and Râmnicu Vâlcea (285 000 and 110 000 inhabitants, repsectively).

9.8.1 Geomorphology

The source (~1800 m asl) of the Olt is near the headwaters of the Mureş River (tributary of the Tisza River) in the eastern Carpathian Mountains. The upper Olt crosses the intramontane basin between the eastern Carpathians and the volcanic Călimani–Gurghiu–Harghita Mountains, flowing through Miocene and Quaternary sedimentary bedrocks. Further south, the Olt drains the Gheorgheni–Ciuc basin (~700 m asl). There, bedrock consists of fluvial-lacustrine clastic deposits intermixed with volcano-sedimentary deposits derived from adjacent volcanic complexes. Then, the river flows through the Braşov Basin filled with fluvial-lacustrine clastics intermixed with lignite, carbonates–diatomites and alluvial fan deposits, as well as with volcanic clastics and extrusive volcanic rocks.

The river makes a northern bend around the Perşani Mountains, flows through the Făgăraş depression (400 m asl) that is filled with 100–150 m thick deposits of Pleistocene alluvial sediments derived from the southern Carpathians, and leaves the Transylvanian basin by cutting across the southern Carpathians in a steep gorge called "Pas Turnul Roşu" (350 m asl). Until this location, the Olt follows the main Carpathian divide. It is the only river of the Carpathian basin that crosses the Carpathian Mountains and discharges directly into the Danube. The lower section of the Olt passes the pericarpathian front as well as the outer limits of the foreland basin before it reaches the Moesian plain (Precambrian metamorphic rocks), and then enters the Danube (Sandulescu 1994; Fielitz & Seghedi 2005). The Olt basin mainly consists of siliceous bedrock. In the upper region (Călimani–Gurghiu–Harghita Mountains, Gheorgheni–Ciuc and Braşov basins), small outcrops of calcareous bedrock occur.

9.8.2 Hydrology, Climate and Biogeochemistry

The average discharge is 172 m^3/s and maximum discharge (1% occurrence probability) is 3400 m^3/s (Table 1, ICPDR 2004). The total length of the river network is 9872 km; and ~15% are temporary streams (Olt RD 2007). Starting in the 1970s, the hydrology of the Olt has been fundamentally altered by the construction of >30 reservoirs and 650-km lateral embankments that disconnect former floodplains from the mainstem. Hydromorphological alterations affect 74 out of 622 rivers in the catchment. In the lower 310 km (Făgăraş to Islaz), the river has been transformed into a cascade of 25 large reservoirs. These reservoirs, together with hydropower plants along the Lotru and Cibin tributaries, provide a hydroelectric potential of 4.44 TWh/year. The Olt and Siret Rivers account for 30% of the total Romanian electrical production (Zinke 1999; Nistreanu *et al.* 2002). Many reservoirs in the basin receive high sediment inputs and siltation is an important issue (areas with high sediment yields: >250 tons km^2/year; Rãdoane and Rãdoane 2005).

Average annual air temperature ranges from 0 to 4 °C in the upper, 6–8 °C in the middle and 10–11 °C in the lower river. Annual precipitation ranges from 700 to 1100 mm in mountainous regions (upper Olt, tributaries of the Braşov section, and the gorge crossing the southern Carpathians), averages 600 mm in the middle hilly sections, and decreases to ~400 mm in the lower section. The inner Gheorgheni–Ciuc and Braşov basins exhibit low precipitation rates as well.

Nitrate concentrations are elevated along the entire mainstem and peak in the reservoirs of Racovita (influenced by the city Sibiu) and Gura Lotrului (maximum: 19–22 mg/L NO_3–N). In the Făgăraş basin, NO_2–N concentrations reach 1– 2 mg/L and NH_4–N concentrations are ~3.4 mg/L. NH_4–N is also high near the city of Râmnicu Vâlcea (~2.2 mg/L) (Nistreanu *et al.* 2002). Microbial water quality at the confluence with the Danube is moderate, only faecal streptococci show high concentrations (Literáthy *et al.* 2002). The lower section exhibits high organic pollution. Preda *et al.* (2005) reported heavy metal concentrations for the Râmnicu Vâlcea valley that were <0.08 mg/L for copper, <0.13 mg/L for chromium, 0.213–0.69 mg/L for iron, 0.044–0.498 mg/L for manganese and <0.06 mg/L for zinc. Bravo *et al.* (2007) reported high contamination of reservoir sediments from mercury (Hg) with values of 44.5 µg/g in 1987, 30.3 µg/g in 1991 and 8–10 µg/g in more recent sediments.

9.8.3 Biodiversity

In the upper Olt, Bányász (2005) identified 124 (in 2002) and 91 (in 2003) diatom taxa, respectively. The most abundant species were *Nitzschia dissipata*, *Navicula lanceolata*, *N. radiosa*, *Meridion circulare* and *Fragillaria construens*. Mara *et al.* (1999) reported 15 amphibian and 12 reptile species from the upper and middle Olt. In the middle Olt, grey willow *Salix elaeagnos* and along the lower Olt ash (*Fraxinus holotricha*) and oak (*Quercus pedunculiflora*) dominate riparian vegetation (WWF 1999). Banarescu (1964) reported 46 fish species, including 3 non-native species (*Oncorhynchus mykiss*, *Carassius gibelio* and *Ameiurus nebulosus*), in the basin. The upper and middle sections exhibit richer fish diversity than the lower river (36 vs. 29 species). A recent survey (2005–2007) at 10 sites along the mainstem of the river reported four species as non-native to the Olt basin: *Oncorhynchus mykiss*, *Carassius gibelio, Pseudorasbora parva* and *Lepomis gibbosus* (AR Olt 2007) and only 17 fish species as native, that is, 50% of the species richness before the construction of hydropower plants. *Ameiurus nebulosus* most likely still occurs. High organic pollution and potentially toxic substances result in a low diversity of macroinvertebrates at the river mouth (Literáthy *et al.* 2002).

9.8.4 Human Impacts and Management

The Olt has a long history of human impacts. In particular during the last seven decades, the river has been dammed and embanked, floodplains and marshes have been drained, meanders have been cut off, tributaries diverted and banks reshaped. The river channel itself has been cleaned of riparian trees and bushes. Water abstraction, in combination with sporadic droughts, creates additional impacts on instream and riparian habitats. Domestic and industrial pollutants as well as accidental and continuous releases of hazardous substances from inactive and active waste disposal sites remain a key problem (Curtean-Bănăduc *et al.* 2007). Only a few wastewater treatment plants are in operation and illegal waste deposits impact remaining wetlands (NSAPBC 1996). Extensive gravel exploitation leads to a significant bedload deficit. In the course of the implementation of the WFD, it is aimed to apply new river restoration concepts that not only account for flood protection but also promote biodiversity through improving instream and riparian habitat quality (Olt RD 2007).

9.9 Siret River

The 599-km long Siret River (*Szeret* in Hungarian; *Seret* in Ukrainian) is the 3rd longest tributary of the Danube and drains a catchment area of 46 289 km² (Ukraine: 10%, Romania: 90%). Its major tributaries are the Suceava, Moldova, Bistrița, Trotuș, Râmnicul Seret, Birlad and Buzău Rivers. The Siret enters the Danube east of Galați at Rkm 155. The basin is inhabited by ~3.5 million people with about 40% living in urban areas. The main cities in the basin are Suceava, Piatra Neamț and Bacău (106 000, 110 000, 176 000 inhabitants, respectively). In medieval times, the Baltic Sea–Black Sea transportation route followed the Siret valley, and today it forms the main road/railway artery from Bucharest (Romania) to Moscow (Russian Federation) via Kiev (Ukraine).

9.9.1 Geomorphology

The Siret originates in the Ukrainian part of the Bukovina region in the northeast Carpathian Mountains (1250 m asl). Dominating bedrock in the headwaters is Paleogene flysch and the headwaters form typical mountain valleys. The Siret flows first north-eastward before entering the Moldavian Plateau. It reaches Romania and flows southward crossing the eastern Romanian plains until its confluence with the Danube. In the middle river, well-developed and fertile alluvial terraces occur (Ungureanu 2006). The lower river exhibits a meandering style with numerous backwaters and oxbow lakes. All major tributaries of the Siret originate from the eastern Carpathian Mountains that are dominated by flysch bedrock. Two tributaries, the Bistrița and the Moldova, originate from inner crystalline and volcanic bedrock. The Birlad River originates in the Moldavian Plateau and is a main left-bank tributary. It exhibits a semi-permanent flow regime. Despite the fact that the Siret flows through a hilly-lowland area over most of its length, it exhibits a strong Carpathian character in regard to its stream bed dynamics, longitudinal profile and thick alluvial deposits (Ichim & Radoane 1990). Agricultural area covers about 65% and forest 34% of the basin (Table 1).

9.9.2 Climate, Hydrology and Biogeochemistry

The Siret basin has a temperate climate with continental influence. The mean annual temperature is ~2 °C in the mountainous part, 8 °C in the hilly section and ~10 °C in the downstream plains. Mean annual precipitation ranges from 1200 mm (mountainous area) to 450 mm (Romanian lowlands). Precipitation peaks in May/June. Mean annual discharge is 210 m^3/s, and peak discharge (1% probability of occurrence) is 3950 m^3/s (Table 1, ICPDR 2004). The Siret and its tributaries exhibit flashy flow regimes with lowest rates from late summer until winter (lowest recorded discharge: 16 m^3/s at the mouth; Ungureanu 2006). Ice cover lasts from mid-December to mid-March. Snowmelt-induced spring floods are common, although rainfall-induced floods (such as the disastrous flood in July 2005 in the sub-basin of the tributary Trotuș) can exceed spring floods and cause major devastation.

At its mouth, biodegradable organic matter (BOD_5) averages 7 mg O_2/L and chemical oxygen demand (COD-Cr) averages 45 mg O_2/L (1996–2000). These values are well above the ICPDR-TNMN target values of 5 mg O_2/L and 25 mg O_2/L, respectively (ICPDR 2005). Saprobic values show critical organic pollution at the mouth of the Siret (ICPDR 2005). However, during the past decade, BOD_5 has shown a decreasing trend. Formerly, the Siret was among the most polluted Danube tributaries in respect to organic pollution at the mouth of the Siret (UNECE 2007). Because the basin is intensively used for agriculture, nitrogen through leaching and diffuse phosphorus emissions via erosion are prevalent (Schreiber *et al.* 2003). Only 30% of the population is connected to wastewater treatment plants (75% in urban areas, 3.3% in rural areas) (DAS 2004). In 2004, the basin contributed some 6996 tons N (2%) and 251 tons P (1.1%) to the total load of the Danube (Behrendt 2008).

The Siret has one of the highest suspended sediment loads of all Carpathian rivers, corresponding to a total annual load of ~10 million tons. Almost 50% of the total load originates from the Putna and Râmnicul

Sărat Rivers. The suspended solids of the Siret contain the highest DDT (dichlorodiphenyltrichloroethane; 0.05 mg/kg) and PBCs (polychlorinated biphenyls; 0.0069 mg/kg) contents of all Danube tributaries (ICPDR 2005). The Siret is exploited for hydropower and irrigation. In addition, the mining industry, primarily for copper, zinc, lead, coal and uranium, is a pressure in the upper basins of some of its tributaries. Cyanide spills from abandoned industrial sites were reported in January 2001 and March 2004 in the tributary Şomuzul Mare with cyanide concentrations temporary up to 4.0 mg/L (EU limit is 0.05 mg/L (EC 1998)). Nowadays, some projects for ecological rehabilitation of abandoned sites are underway.

9.9.3 Biodiversity

The Siret basin has experienced a profound change in its morphology and water quality, especially downstream of urban and industrial areas. The present fish richness (34 species) is lower compared to the 1960s (42 species). Five non-native species (*Ctenopharyngodon idella, Hypophthalmichthys molitrix, H. nobilis, Oncorhynchus mykiss* and *Salvelinus namaycus*) and three invasive species (*Pseudorasbora parva, Lepomis gibbosus,* and *Perccottus glenii*) are new since the 1960s (Battes *et al.* 2005). Unfortunately, further internationally published information on other organism groups is unknown at this time.

9.9.4 Human Impacts and Management

The most important hydromorphological pressures in the basin are caused by the construction of ~30 reservoirs, the building of extensive lateral embankments, as well as water diversions and abstractions. The Izvoru Muntelui reservoir (Lake Bicaz) on the Bistrița tributary is the largest reservoir within the basin (total volume: 1230 million m^3). During the last 50 years, most wetlands fringing the river have been disconnected by dikes or have been drained (DAS 2004). Uncontrolled deforestation, erosion and siltation of reservoirs increase the flood risk in the basin. In addition, river banks are often impaired by illegal gravel excavation. Regulatory monitoring is underway.

Today, there have been common undertakings among Slovakia, Hungary, Ukraine and Romania to inventory Accidental Risk Spots (ARS). The next steps agreed are (i) to assess the actual risk of accidents and (ii) to install an accident emergency warning system. The inventory of old contaminated sites in potentially flooded areas needs to be completed as well as the inventory of protected areas (GTZ 2007). Currently there are 30 areas designated as conservation sites to protect specific habitats or species (total area 102 300 ha or ~4% of the basin area). The entire basin is designated as a nutrient-sensitive area. The perimeter of 54 localities within the basin has been designated as a "nitrate vulnerable area" due to agricultural activities (DAS 2004).

9.10 Prut River

The 953-km long Prut, or Pruth, originates in the Chernogora Mountains in the southwestern Ukrainian Carpathians at ~1600 m asl. It drains an area of 28 568 km^2 before discharging into the Danube just upstream of the Danube delta, east of Galați (Danube Rkm 132). It is the second longest tributary of the Danube. It flows for the first 211 km eastwards in the Ukraine, then forms the border between

Ukraine and Romania (31 km) and the border between Romania and Moldova (711 km) while flowing south-southeast. Its main tributaries are the Ceremosh, Derelui, Volovat, Baseu, Corogea, Jijia, Chineja, Ciugur and Lapusna Rivers; most of them are regulated by reservoirs (ICPDR 2004, UNECE 2007). The largest city along its banks is Chernivtsi (Western Ukraine, 240 000 inhabitants), and the main industrial complex is at Iaşi, Romania. The total human population in the basin is ~3.2 million (Teodosiu *et al.* 2003).

9.10.1 Geomorphology

The Prut basin can be divided into three sections: (i) a mountainous section (20% of the basin), (ii) a piedmont section (12%), and (iii) lowland plains (68%) (Zeryukov & Pavlov 1968). The mountainous part consists of limestone rock and Paleocene flysch. The piedmont is covered by Miocene deposits of clay intermixed with argillite, conglomerate and sand as well as Torton and Sarmate bedrock. The lowland basin is filled with sedimentary and alluvial sediments. The basin drains three ecoregions according to Illies (1978), namely the Carpathians, Eastern plains and the Pontic Province. Formerly, the lower Prut was fringed by vast floodplains (total area: 1665 km²), but 75% have been lost or are now functionally extinct (WWF 1999).

9.10.2 Climate, Hydrology and Biogeochemistry

The Prut Basin has a moderate mild continental climate in the upper section and a harsher continental climate in the lower section. Average annual precipitation ranges from 1400 mm (upper section) to 600–440 mm (lowland plains). The average annual air temperature increases from ~ –2 °C to 9 °C from the headwaters to the mouth, and ice cover lasts for 60–65 days. Snowmelt starts in March and lasts on average for only 10–15 days (DAP 2004). The average discharge at the mouth is 67 m^3/s and maximum discharge (1% occurrence probability) is 2940 m^3/s (Table 1, ICPDR 2004). The upper section and tributaries exhibit a flashy flow regime, and flooding is an important issue in the basin. Major floods often occur in March when snowmelt and heavy rain coincide, although floods may occur at any time of the year.

The catchment of the Prut is intensively used for agriculture and vineyards, and is a major source of diffuse nutrients. In addition, ~98 000 ha of irrigated land (mainly in Romania; Teodosiu *et al.* 2003) contribute to the prevalent soil erosion and nutrient inputs. Although nitrate, nitrite and phosphate concentrations are lower today compared to the 1980–1990s, tributaries of the Prut as well as the upper and middle sections are still affected by urban wastewater discharge, waste disposal, and outdated industrial production modes. Chemical Oxygen Demand (COD-Cr; up to 40 mg O_2/L) and organic pollution remain high at the mouth and in the downstream Danube section (period 1996–2000; ICPDR 2005).

9.10.3 Biodiversity

Information on the biodiversity of the Prut is rather scarce. Usatâi (2004) has studied the composition of the fish fauna of the middle (Moldavian) and of the lower Prut and its main tributaries between 1996 and 2002. Between 24 and 30 fish species are reported for the middle Prut. Cyprinidae and Percidae are the dominant families; in total six families occur. About 35% of the species are of economic interest like *Aspius aspius*, *Vimba vimba*, *Esox lucius*, *Hypophthalmichthys molitrix*, *Cyprinus carpio* and *Stizostedion lucioperca*. Their relative abundance, however, ranges from only 12–19%. *Zingel zingel* and *Z. streber* occur in the middle Prut, and they are listed in the Red Book of Moldova and are protected. Some 37 fish species are documented in the lower Prut. *Leuciscus idus* occurs as a third protected species, and *Umbra krameri*, *Abramis brama* and *Carassius carassius* are species of high conservation value (Usatâi 2004). In summer 2007 Moldavian and Romanian scientists conducted a common survey of the fish fauna of the Prut River. They report the occurrence of 46 species (41 native, 5 non-native) (Davideanu *et al.* 2008 and personal communication).

In the lower Prut valley, 189 bird species, including 123 breeding species, are reported (Biodiversity Office MD 2007). The spreading of willows into the reed belts has created favourable conditions for some nesting birds such as *Ardeola raloides, Egretta garzetta, Ardea cinerea, Nycticorax nycticorax, Platalea leucorodia*, *Plegadis falcinellus, Casmerodius albus, Phalacrocorax carbo, P. pygmaeus* and *Ardea purpurea.* The water chestnut (*Trapa natan)s* still occurs along the lower Prut; due to water eutrophication it has dramatically decreased (WWF 1999).

The lower Prut floodplain lakes Beleu and Manta are the largest natural lakes in Moldova and have been designated as a Ramsar site since 2000 (http://www.wetlands.org). The Beleu Lake serves as habitat for 27 fish species. Economically valuable species include *Abramis brama*, *Rutilus rutilus*, *Cyprinus carpio*, *Sander lucioperca*, *Silurus glanus*, *Alosa immaculata* and *Esox lucius*. *Hucho hucho* and *Umbra umbra* are protected by Moldavian law. The ecological capacity of Beleu Lake for the reproduction of fish and for the development of sturgeon caviar has been strongly reduced during the past decades. The main reasons are the siltation of the Manolescu channel, construction of access roads to oil boreholes and water pollution caused by oil products (Biodiversity Office MD 2007).

9.10.4 Human Impacts and Management

Starting in the 1960s, the Prut and its tributaries have undergone major hydromorphological changes. More than 30 reservoirs have been built within the basin. The largest is the hydropower station of Stanca–Costesti in the upper Prut (total volume: 735 million m^3), jointly operated by Romania and Moldova (UNECE 2007). The lower Prut remains mostly free-flowing, although lateral embankments have disconnected the formerly vast floodplain from the main channel. Large alluvial areas in the lower section, near the Danube, have been drained. As a consequence, Lake Brateş (Romania's largest freshwater lake) has substantially decreased in area. The Ramsar site "Lower Prut Lakes" cover an area of 19 150 ha including 14 400 ha of wetlands. The lower Prut does not meander strongly. The floodplain is up to 6 km wide and includes wet meadows and riparian forests. Aquatic biodiversity is high in Lake Beleu (area: 1700 ha) and Manta floodplain lakes (a complex of interconnected lakes) (Ramsar 2000).

9.11 Danube delta

The Danube delta is located on the coast of the Black Sea and includes the area between the three main Danube branches Chilia, Sulina and Sf. Gheorghe. It covers an area of 4560 km^2 (Table 1); 82% is located in Romania, 18% in Ukraine. The delta starts at the first bifurcation of the Danube (Rkm 116) where the northern Chilia branch splits off, forming the boundary between Romania and Ukraine. The highly canalised middle branch Sulina serves as the navigation channel to the Black Sea (80-m wide, a minimum depth of 7.3-m is secured via dredging). The reported population of the Romanian part of the delta amounts to about 15 000 (RIZA 2000). The majority lives in rural settlements (64%) and one third in the port-town of Sulina. Fishing and agriculture are major sources of income. About 10 000 people are reported for the Ukrainian part of the delta and 110 000 people inhabit the cities Izmail and Vilkovo at the northern edge of the delta in Ukraine. The city of Tulcea at the entrance of the delta in Romania has about 90 000 inhabitants and is not included in the calculations of human population density (Table 1). Deviant indications of the size of the delta (4127 to 8800 km²) result from different delimitations, i.e. whether the Ukrainian part but as well whether lakes and lagoons, which are geologically and ecologically attached to the delta are accounted for. An area of about 6800 km² is under legal protection including floodplains, the Razim-Sinoe lacustrine system and marine areas.

9.11.1 Geomorphology

Deltaic conditions were initiated during the early Upper Pleistocene, when the Danube started to discharge into the Black Sea. It was a fluvial-dominated delta in an embayment of the Black Sea, which was sheltered by a barrier (initial cordon) in the late Pleistocene/early Holocene (Panin *et al.* 1983; Giosan *et al.* 2006). Subsequent clogging led to the successive formation of the Danube delta branches and its north- and southward expansion. The evolution of the delta occurred in five main phases: (i) the formation of the Initial Letea–Caraorman Spit (11 700–7500 years BC), (ii) the St. George I Delta (9 000–7200 years BC), (iii) the Sulina Delta (I and II) (7 200–2000 years BC), (iv) the St. George II and Kilia Deltas (2800 years BC to present) and (v) the Cosna–Sinoe Delta (3 500–1500 years BC) (Panin *et al.* 1983). The delta is formed on a sequence of up to 400 m thick detrital deposits that accumulated mainly during the Upper Pleistocene and Holocene (Panin *et al.* 2004). Histosols (27%), gley soils (22%), limnosols (17%), psammosols and sands (16%) and alluvial soils (13%) predominate. Smaller areas are covered by solonchaks, kastonozems and anthrosols (Munteanu 1996).

The delta consists of (i) a fluvial zone characterised by large sandy levees and small densely vegetated lakes and (ii) a fluvio-marine zone that includes marine levees as well as important lacustrine complexes and undergoes morphohydrographic changes at its contact zone with the Black Sea (RIZA 2000). The marine delta plain covers ~1800 km² and the delta-front unit ~1300 km² (delta-front platform: 800 km², delta-front slope: 500 km²). The maximum altitudinal difference in the delta is 15 m (−3 m to +12 m), although about 50% is at 0–1 m asl. The level difference between the apex and the Black Sea is 3.6 m (RIZA 2000). Since the northern part of the delta is slowly sinking, the discharge of the northern Chilia branch has increased (UNEP-WCMC 1991). The Danube delta is still expanding seaward at a rate of 24–30 m annually (http://www.icpdr.org/icpdr-pages/danube_delta.htm). Between the river branches, four lake complexes can be distinguished: Sontea-Fortuna (3705 ha), Gorgova-Uzlina (6848 ha), Matita-Merhei (5701 ha) and Rosu-Puiu (6519 ha) (RIZA 2000).

9.11.2 Climate, Hydrology and Biogeochemistry

The climate in the delta is temperate continental with some maritime influence. It experiences short, mild winters and hot, dry summers. The average annual air temperature is 11 °C (January: –9 to 5 °C; June: 22–23 °C). Minimum air temperature is –25 °C, maximum is 37 °C, and temperature slightly increases from west to east. The number of frost days (T_{min} <0 °C) ranges between 84 (western part) and 57 (eastern part). Long periods of ice cover are rare. Total precipitation is 300–400 mm, evaporation 800–1000 mm (RIZA 2000; 2002). The proximity to the sea and the humidity originating from numerous lakes and secondary branches influences precipitation patterns (UNEP-WCMC 1991).

Air humidity is ~80% (up to 90% in winter). Due to the high average discharge of the Danube (6486 m^3/s) at the delta entrance, aquatic environments prevail. Discharge peaks in summer (33% of the total annual discharge) and is low in autumn and winter. The total Danube discharge entering the delta splits into Chilia Branch (about 53–57%), Sulina Branch (about 19–22%) and Sf. Gheorghe Branch (about 23%). Major channelization of Sulina Branch has significantly altered the natural discharge pattern in the Danube delta: while the discharge of the Tulcea arm (Sulina and Sf. Gheorghe Branch) increased by 17% that of Chilia Branch diminished by 17% and now suffers from strong siltation due to reduced flow (Bloesch 2005b). The total annual suspended sediment load carried by the Danube at the mouth has decreased from 67.5 million tons (1921–1960) to 29.2 million tons (1981–1990) (RIZA 2000).

The Danube delta acts mainly as a sink of nitrogen (denitrification in reed beds) but is a source of phosphorus (Suciu *et al.* 2002). In general, the delta has a low retention capacity and is mainly a by-pass for nutrients which is enhanced in wet years of high discharge and less pronounced in dry years. Reconnecting wetlands will enhance retention capacity. The canalization has diminished the ability of the delta to retain nutrients; more nutrient-rich water flows through the main canals rather than being distributed through the wetlands and reed beds. The average concentration of dissolved nutrients is 1–4 mg DIN/L and 0.1–0.3 mg TP/L (1996–2003). The concentrations of iron, cadmium and lead are elevated in the Danube branches as well as in the Delta lakes (ICPDR 2005). A significant eutrophication of the Delta lakes in the 1950s–1990s has drastically reduced biodiversity (Vădineanu *et al.* 2001). This has been recently stopped due to reduced nutrient inputs and loads.

9.11.3 Biodiversity

The Danube delta comprises 23 natural and 7 man-made ecosystem types (Gâstescu *et al.* 1999). Extensive species lists of flora and fauna are found in Tudorancea and Tudorancea (2006), and a comprehensive fish atlas is presented in Oțel (2007). The Danube delta forms among the largest reed bed zone worldwide. The delta is a major hotspot of biodiversity where boreal species and species typical for Central andWestern Europe co-occur. A total of 1460 vascular plants and ~3500 animal species, including 473 vertebrate species (74 fish, 9 amphibian, 12 reptile and 325 bird species), have been reported. Since forests and forest-steppe habitats are decreasing, many of these species (e.g. >⅓ of the vascular plants) are included in the Red List of the Danube delta Biosphere Reserve (RIZA 2002). The delta provides habitat for 60% of the world population of Pygmy cormorant, 5% of the Palaearctic population of White pelican and 90% of the world population of the Red-breasted goose (RIZA 2000 and references therein). The five Danube sturgeons (*Huso huso, Acipenser gueldenstaedtii, A. nudiventris, A. stellatus* and *A. ruthenus*) are highly endangered, and *A. sturio* is already extirpated (AP 2006; Bloesch *et al.* 2006). The threat for sturgeons is not only poor water and habitat quality, but also overexploitation and poaching due to the economic value of caviar. Other fish listed as threatened include *Umbra krameri*, *Misgurnus fossilis* and *Carassius carassius* (Oțel 2007).

Within the Razim–Sinoe lacustrine system, *Sander lucioperca* is the only predator fish that has been able to adapt to the eutrophication conditions. Cyprinidae like *A. brama* increased in the lacustrine system along with the increased phosphorus content of the water. Moreover, the numbers of *Carassius auratus*, an exotic and invasive species, increased. *C. auratus*, together with extensive embankments of floodplain areas, impede the reproductive success of carp (ICPDR 2005).

9.11.4 Conservation and Management

The delta is impacted by catchment and local processes. An altered sediment regime, embanked floodplains and increased pollution are major catchment factors that affect the delta. Within the delta, an area of 1000 km² was embanked, drained and converted for agriculture, forestry and aquaculture between 1960 and 1989. It decreased the connectivity between the river and its wetlands. For example, 235 km² of the transitional Razim–Sinoe lake system has been embanked and disconnected from the influence of the Black Sea. The natural channel network has been artificially extended from 1743 km to 3496 km in the period 1920–1990 (Gâstescu *et al.* 1983). Despite these multiple human impacts, >3000 km² of wetlands and the adjacent Ukrainian secondary delta (250 km²) remain connected to the river and represent the largest almost undisturbed wetlands in Europe. Although near-natural in large parts, some ecosystem functions are still reduced due to former mismanagement, overfishing and polder constructions (Gâştescu & Ştiucă 2006). About 6800 km² are designated as a transboundary UNESCO Biosphere Reserve, shared by Romania and Ukraine. The area includes floodplain forests, coastal biotopes, sand dunes and >600 natural lakes. The core area (~3100 km²) was declared both as aWorld Natural Heritage Site and Ramsar site in 1991. Current restoration in the framework of the Biosphere Reserve may partly improve the situation while new impacts of navigation may disturb the system again (TEN-T, Bystroe channel). Between 1994 and 2003, ~15% of disconnected areas have been reconnected in the delta (ICPDR 2004).

Fish farming was introduced in the Danube delta in 1961. Cultured species are the common carp (*Cyprinus carpio*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Aspiorhynchus laticeps*) and gras carp (*Ctenopharyngodon idella*). Today, production costs in the often-oversized ponds (50–1000 ha) nearly exceed production values. The total catch of fish in the delta has declined during the past decades and shifted from piscivorous to less profitable non-piscivorous species due to changes in abiotic and biotic conditions (Figure 9). The commercial catch of migratory anadromous sturgeons (*Huso huso*, *Acipenser güldenstaedti* and *A. stellatus*) collapsed from 1000 tons/year at the beginning of 20th century to 10 tons/year in 1990 (Navodaru 1998). It is assumed that today's smaller nutrient loads in the Danube may counteract the eutrophication problems in the delta. Increasing attention for the restoration of wetlands should have a positive effect on the water quality of the delta via an intensification of hydrological contact zones (ICPDR 2004).

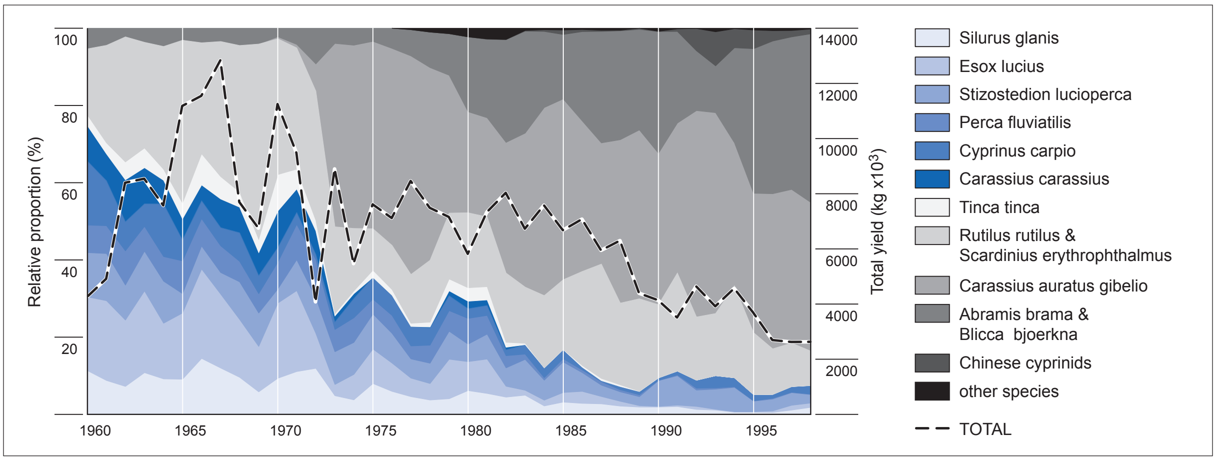

Figure 9: Total yield (dashed line; right axis) and relative proportion of species (left axis) of the commercial freshwater fishery in the lakes of the Danube delta (1960-1998; redrawn from Navodaru *et al.* 2002).

10 Conclusion

The Danube is the river that most effectively integrates and defines Europe. Culturally and biologically, the river has always been a separator as well as a connector. It served as a migration corridor for organisms and cultures, and has been an area of dispute as well as a major melting pot of cultures. It also is listed as one of the world's top 10 rivers at risk (Wong *et al.* 2007). The development of the Trans-European Network for Transport, the ongoing construction of small- and medium-sized hydropower plants along its tributaries, bed incision, truncation of sediment transport and rapid landuse change within the basin pose major threats. Nevertheless, the governments of Bulgaria, Romania, Ukraine and Moldova agreed in 2000 to establish the Lower Danube Green Corridor (http://www.wwf.de/fileadmin/fm-wwf/Publikationen-PDF/DanubeDeclaration2000.pdf). The agreement, which was facilitated by WWF, is one of the most ambitious wetland protection and restoration projects in Europe, with ~1 000 000 ha new and existing protected areas and 224 000 ha of floodplains to be restored to their near-natural state.

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13 Relevant websites

BSC – Commission on the Protection of the Black Sea against Pollution
 http://www.blacksea-commission.org

Danube-Black Sea Strategic Partnership
 http://www.blacksea-environment.org

DEF – Danube Environmental Forum
 http://def.distelverein.at

daNubs-Project
 http://www.danubs.tuwien.ac.at

IAWD – International Association for Water Works in the Danube Basin
 http://www.iawd.at

ICPDR – International Commission for the Protection of the Danube River
 http://www.icpdr.gs

IAD – International Association of Danube Research
 http://www.iad.org

MIDCC – Multifunctional Integrated Study – Danube River Corridor and Catchment
 http://www.midcc.at

International Sava River Commission
 http://www.savacommission.org

UNDP/GEP – Danube Regional Project
 http://www.undp-drp.org

WWF – Danube-Carpathian Programme Office (Vienna)
 http://www.panda.org/dcpo

Chapter IV
Managing the world's most international river: the Danube River Basin

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NS compiled the paper and authored sections 1, 2, 3, 4, 5 (jointly with CB), 6 (jointly with CB), 7 (jointly with MV and TH), 8 (jointly with MP), 10.1 (jointly with MP), 10.2 (jointly with MV), 10.3 (jointly with CB and MSJ), 10.4 (jointly with CB and MSJ), 11 (jointly with JB), 12 (jointly with JB and KT), accessory publication (jointly with CB, MSJ, TH, JB).

1 Abstract

Transboundary river-basin management is a challenging task emerging from lack of on-site expert knowledge, high administrative and socioeconomic complexity, various stakeholder interests, and difficulties enforcing international and national law. Therefore, an efficient 'science–policy interface' is a crucial ingredient for the successful development and implementation of adequate management strategies. The Danube River Basin (DRB) drains areas of 19 countries with different cultural, political, and environmental legacies. The European Water Framework Directive (WFD) has provided the guiding legal instrument for DRB management since 2000, supported by several multilateral agreements. The International Commission for the Protection of the Danube River (ICPDR) is responsible for the implementation of the WFD in the DRB. It stimulates management-oriented research and coordinates the various activities of the contracting parties and observers, including those of many NGOs and stakeholders. The development of the first DRB Management Plan in 2009 constituted a milestone of cooperation among scientific, political, and public organizations. Key stressors and pressures have been identified, a new basin-wide monitoring network has been established, and numerous conservation and restoration sites have been designated. A major challenge in DRB management will be to establish synergies among the competing interests of navigation, hydropower production, flood protection and nature conservation. This paper examines the strengths and weaknesses of DRB science–policy interactions and outlines future strategies for sustainable development of the DRB as a template for transboundary river basin management.

2 Introduction

The management of international water resources and large transboundary rivers is a challenging task because of the administrative and socio-cultural differences within the catchment, the spatiotemporal heterogeneity of the encompassing landscapes, the multiple and often competing water uses, and, not least, the difficulty of enforcing international laws at regional and local levels. Moreover, managing landscapes as complex as large river-floodplain networks requires a comprehensive understanding of the underlying ecological structure-function relationships at various spatiotemporal scales. Hence, tailor made water management strategies need to be properly selected, designed, and implemented based on sound ecological principles, the best available scientific knowledge, and stakeholder participation (Uitto and Duda 2002; Dudgeon *et al.* 2006; Hein *et al.* 2006a; Quevauviller 2010).

The Danube River Basin (DRB) is the most international river in the world, characterised by exceptionally diverse ecological, historical, and socioeconomic properties. Its unique biodiversity and high ecological potential make the DRB one of the Earth's 200 most valuable ecoregions (Olson and Dinerstein 1998). At the same time, the DRB is listed among the world's top 10 rivers at risk (Wong *et al.* 2007).

In this paper, we analyse the strengths and weaknesses of the DRB management strategies, in particular by focusing on science–policy interactions. We start with an outline of the key environmental and socioeconomic characteristics of the DRB. Then, we identify the main human pressures, discuss the legal frameworks, emphasise the role of governmental and nongovernmental organisations (NGOs) in implementing river basin management strategies, and present current and planned proactive and reactive management actions. We finish with a brief discussion of the future strategy for the sustainable development of the DRB, which may serve as a template for transboundary river basin management elsewhere.

3 Characterisation of the Danube River Basin

The DRB covers a total area of ~801 000 km² and collects water from the territories of 19 countries in Central and South-Eastern Europe (Germany, Austria, Switzerland, Italy, Poland, the Czech Republic, Slovenia, Slovakia, Hungary, Croatia, Serbia, Romania, Bosnia and Herzegovina, the Former Yugoslav Republic of Macedonia, Albania, Montenegro, Moldova, Bulgaria, and Ukraine) (Fig. 1). Today, ~83 million people inhabit the DRB, and ~60 cities in the DRB have a human population of more than 100 000 (Sommerwerk *et al.* 2009). Culturally, the DRB consists of a wide variety of languages, traditions, histories and religions. The political and social conditions and the corresponding economic status of the DRB countries are more diverse than those in any other European river basin. Although the countries in the Upper Danube are economically prosperous (Germany: GDP of ~36 000 EUR per capita and per year), the countries in the lower basin are among the poorest in Europe (Moldova: GDP of <1000 EUR per capita and per year). Ten countries are European Union (EU) Member States and one country (Croatia) is an Accession State. The steep socioeconomic gradient and the political divide into formerly communist and Western countries, once separated by the 'iron curtain', and the present separation into EU and non- EU countries challenge the establishment of joint basin-wide manage-

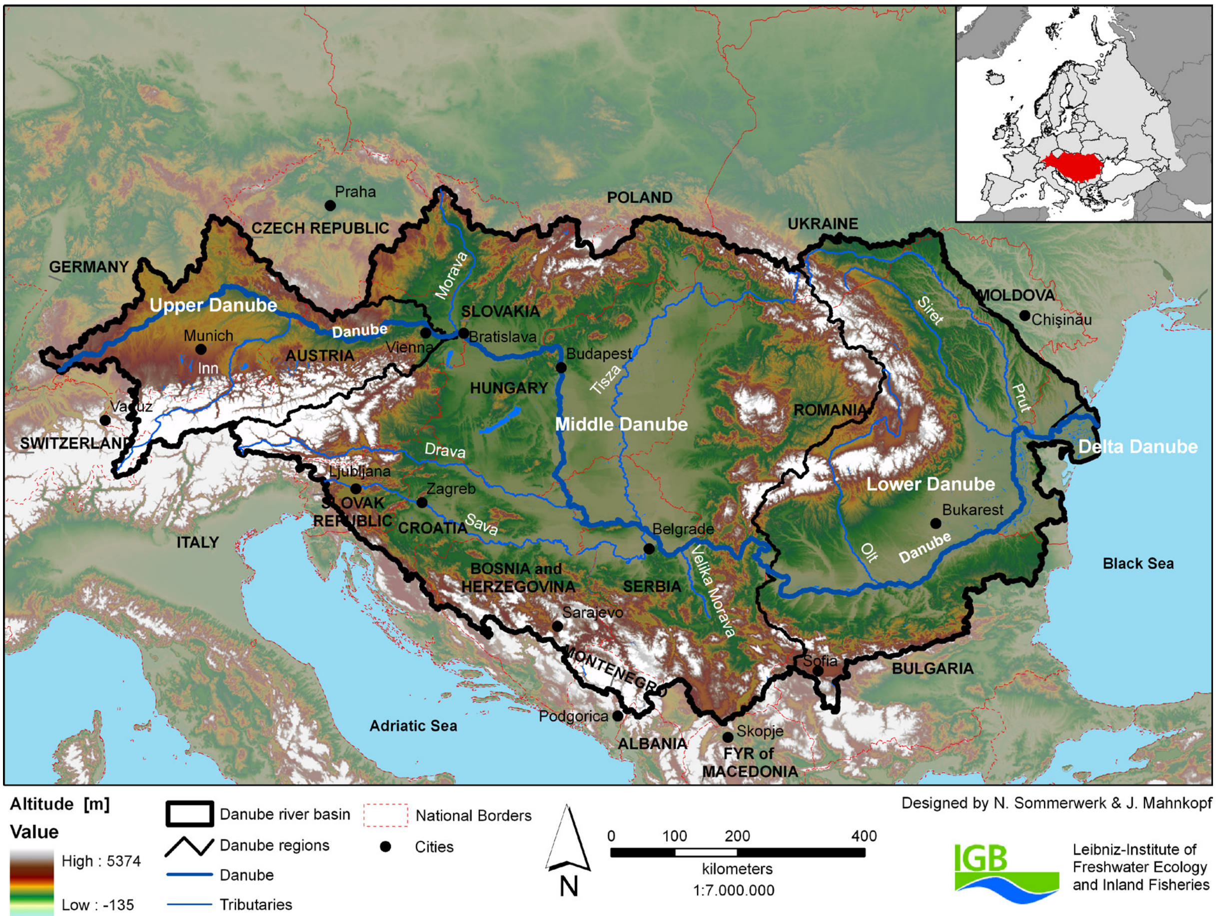

Fig. 1: Digital elevation map of the DRB, delineating the three sub-basins and indicating the location of the main cities.

ment strategies. Furthermore, there exists an immense variation in technical development and legal obligations within the basin. For example, the number and standards of wastewater treatment plants and associated sewage network decreases towards the downstream DRB countries.

The Danube is the second longest river in Europe (2826 km), and its large delta forms an expansive wetland (area: 5640 km^2) of global importance. The mean annual discharge of the Danube at its mouth is ~6480 $m^3\ s^{-1}$, corresponding to a total annual discharge of 204 km^3. The Danube is divided into three sections that are almost equally long, and separated by distinct changes in geomorphic characteristics: the Upper, Middle and Lower Danube (Fig. 1). A characteristic feature of the Danube is the alternation between wide alluvial plains and constrained sections along the main stem. Before regulation, active floodplain width reached >10 km in the Upper Danube and >30 km in the Middle and Lower Danube. In the Upper Danube, most floodplains and fringing wetlands have been converted into agricultural and urban areas, or have been isolated by dams and artificial levees, and therefore are functionally extinct. However, along the Middle and Lower Danube, large near-natural floodplains still remain. Vegetated islands form another (former) prominent landscape element in the DRB. Along the Austrian Danube, ~2000 islands were present before regulation; today, only a few remain. However, islands are still abundant in the Hungarian/Serbian (Middle Danube) and the Bulgarian/Romanian sections (Lower Danube). Remaining near-natural floodplains and vegetated islands may serve as important nuclei for conservation and management actions; at the same time, they are sensitive indicators to assess the ecological state of river corridors (K. Tockner, unpubl. data).

Zoogeographic and phylogeographic studies clearly pinpoint the DRB as a biodiversity hot spot region in Europe. For example, ~20% (115 native species) of the European freshwater fish fauna and 36% (27 species) of the amphibian fauna occur in the DRB today (Sommerwerk *et al.* 2009). Moreover, the Palaearctic and Mediterranean biogeographic zones overlap in the Danube Delta, resulting in an exceptionally high biodiversity, especially for birds (total: 325 species, ~50% are breeding species). The corridor of the Danube River remained unglaciated during the last ice age and therefore served as a substantial glacial refuge area, as well as an important expansion and migration corridor for many species. Today, the DRB drains areas of nine ecoregions (Illies 1978).

An updated and thorough compilation of historical and scientific information on geological, hydromorphological, physico–chemical, and biological features of the Danube River and its tributaries can be found in Sommerwerk *et al.* (2009).

4 Key water management issues

The Danube Basin Analysis in 2004 provided the first comprehensive characterisation of the entire DRB (ICPDR 2005). It comprised a basin-wide pressure and impact analysis to estimate the risk for water bodies of failing the management objective of the EU Water Framework Directive (WFD), i.e. to achieve 'good ecological status', by 2015 (European Commission 2000). Mitigating hydromorphologic alterations, and reducing organic pollution, nutrient loads, and hazardous substances, have been identified as the main targets for the Danube River Basin Management Plan (DRBM Plan, ICPDR 2009). However, transport and contamination of sediments, as well as the spread of invasive species, have not yet been given sufficient attention. Adaptive strategies that take future global change into consideration are also missing.

5 Hydromorphologic alterations

Hydropower generation, flood protection, land reclamation, and navigation are the main driving forces for hydromorphologic alterations in the DRB. Approximately 700 major hydraulic structures (dams and weirs >15 m), including 156 large hydropower dams, have been built in the DRB (Reinartz 2002; Bloesch 2003; ICPDR 2005). Approximately 30% of the length of the main stem is impounded through 78 major hydraulic structures. Less than 15% of the Upper Danube remains freeflowing. The largest dams in the DRB are the hydropower plants Iron Gate I and II (built in the 1970s) in the downstream part of the Middle Danube (Rkm 943 and Rkm 842). The Iron Gate dams, together with the Gabíkovo Dam in Slovakia (built in the 1980s), disrupt fish migration in the Lower and Middle Danube, and significantly alter the sediment and groundwater regime (Zinke 1999; Klaver *et al.* 2007). As of 2009, 22 of the 78 barriers are passable for fish (ICPDR 2009).

Notable areas of the Danube Delta have been embanked and drained, and the total length of the channel network in the delta doubled between 1920 and 1980 (at present 3500 km: Gâștescu *et al.* 1983).

The new Bystroye navigation-canal has cut through the Ukrainian part of the Danube Delta biosphere reserve since 2004.

Currently, the Danube is navigable for 87% of its total length (upstream to Rkm 2410). Approximately 1100 ships are registered along the Danube River (for comparison, River Rhine: ~10 000 ships; navigable for ~1000 km (http://www.icpdr.org, http://www.ccr-zkr.org). The registered vessels along the Danube are 40 years old on average. Therefore, emission standards are most likely not up-to-date. The remaining free-flowing river sections and their mobile beds have been identified as 'bottlenecks' for navigation. Hence, the creation and maintenance of a continuous shipping channel of 2.8 m water depth and 160–180 m width, for most of the year, has been proposed. Thus, the Trans-European Transportation Network (TEN-T, 'Corridor VII', http://tentea.ec.europa.eu) of the EU competes with the concurrent projects to conserve unique habitats and species along the Danube River.

6 Alteration of the sediment regime

The dams along the main stem have severely interrupted sediment transport in the Upper Danube. The Iron Gate dams retain approximately two-thirds of the suspended solids. Therefore, sediment delivery to the Delta decreased from 53 to 18 million t y^{-1}, resulting in severe coastal erosion (WWF 2008). River-bed incision further reduces low water levels and impedes the hydrological connection between the channel and its floodplains.

To mitigate the adverse effects of river-bed incision in the Upper Danube (downstream of Vienna, Rkm 1921–1880), the river bed will be stabilised by adding coarser gravel, and by widening the main channel by removing ~50% of the artificial bank protection (riprap) (Reckendorfer *et al.* 2005). In addition, the bedload sediment deficiency is balanced by annual additions of 160 000 t of gravel, corresponding to ~20% of the load in 1850. These joint measures should lead to an 85% reduction in bed incision (WWF 2008). This project, if successful, should serve as a template for similar projects in the DRB and beyond (SedNet 2007). Commercial dredging is mostly banned in the Upper Danube, and dredged material is returned to the main stem ('no-net-loss'). In the Middle and Lower Danube, stopping the ongoing sediment removal remains an urgent issue.

7 Water pollution

Despite an overall improvement in water quality over the past few decades, the Danube and its tributaries remain exposed to multiple point and non-point pollution sources (Schmid 2004; Behrendt *et al.* 2005; Liška *et al.* 2008). The construction and upgrade of wastewater treatment plants (WWTPs) have reduced the input of biodegradable organic matter in the Upper Danube during the past three decades (Wachs 1997). In the Middle and Lower Danube, water quality remained relatively high until the 1970s, but then deteriorated owing to rapid industrial development, poor pollution control, and inputs from heavily-polluted tributaries (Russev 1979; Kalchev *et al.* 2008). However, the high self-purification capacity of the remaining near-natural river sections and alluvial wetlands has buffered these adverse effects, and at the same time has maintained a relatively high biodiversity up to now (UNDP/GEF 1999). Large cities along the main stem, like Belgrade and Budapest, or Bucharest along the tributary Argeş, still lack WWTPs. In Budapest, a WWTP is under construction. The Budapest Central Wastewater Treatment Plant project is the largest environmental investment to be actually implemented in Central Europe (total costs € 530 million: ICPDR 2010a). Zagreb, located along the Sava River, has recently completed a new facility.

Nutrient concentrations are well above the level they were in the 1960s (the DRB management objective), and ~10 times higher than natural background values. The present total emissions into the DRB are 737 kt y^{-1} for BOD_5 (5-day biological oxygen demand) and 1511 kt y^{-1} for COD (chemical oxygen demand) (ICPDR 2009; reference years 2005 and 2006). In the Lower Danube, the TOC (total organic carbon) load is 550 kt y^{-1}. The Danube discharges ~29 kt y^{-1} of total phosphorus (TP) and 478 kt y^{-1} of total nitrogen (TN) into the Black Sea (Venohr and Behrendt, unpubl. data, mean of the years 2000–2005). Despite the achieved reductions, pollution loads are still high enough to threaten the unique biodiversity and affect the fishery and recreational value of the Black Sea (United Nations 1997).

Hazardous substances like heavy metals, persistent organic pollutants (pentachlorphenols, PCPs; polycyclic aromatic hydrocarbons, PAHs; and organochlorine pesticides), hormone-active substances (e.g. endocrine disruptors) and micro-pollutants are becoming an increasing issue in the DRB. Contamination of sediments with DDT (dichlorodiphenyltrichloroethane) is common in the Lower Danube. However, there is a lack of legal measures for obligatory monitoring of some of these hazardous substances. In the downstream DRB countries, adequate analytical equipment is also lacking. The International Commission for the Protection of the Danube River (ICPDR, http://www.icpdr.org) and the Black Sea Commission have put the reduction of hazardous substances as a high priority issue on their agenda. The improvement of WWTPs and the application of best-available techniques for the industrial and agricultural sectors are considered as the most efficient measures to reduce the emissions of toxic substances, as well as of nutrients and organic matter.

8 Non-native and invasive species

For centuries, European inland waterways have provided opportunities for the spread of non-native aquatic species. At present, a complex network of more than 28 000 km of navigable rivers and canals connects 37 European countries, creating a biological 'meta-catchment' that encompasses large parts of the continent (Panov *et al.* 2009). The Danube River belongs to the Southern Invasive Corridor that links the Black Sea with the North Sea via the Rhine-Main-Danube Canal.

At present, 141 non-native and cryptogenic taxa (41 fish, 67 macroinvertebrate, 24 aquatic macrophyte, 1 amphibian, and 8 parasite species) have been reported for the DRB (http://www.alarmproject.net). Several non-native species are true invasive species that currently represent prevalent components of the aquatic community: *Corbicula fluminea* (Asian clam); *Anodonta woodiana* (Chinese pond mussel); *Orconectes limosus* (spinycheek crayfish); and *Dreissena polymorpha* (zebra mussel) (Graf *et al.* 2008; Liška *et al.* 2008). New introductions are constantly recorded (e.g. Leppäkoski *et al.* 2002; Arbaiauskas

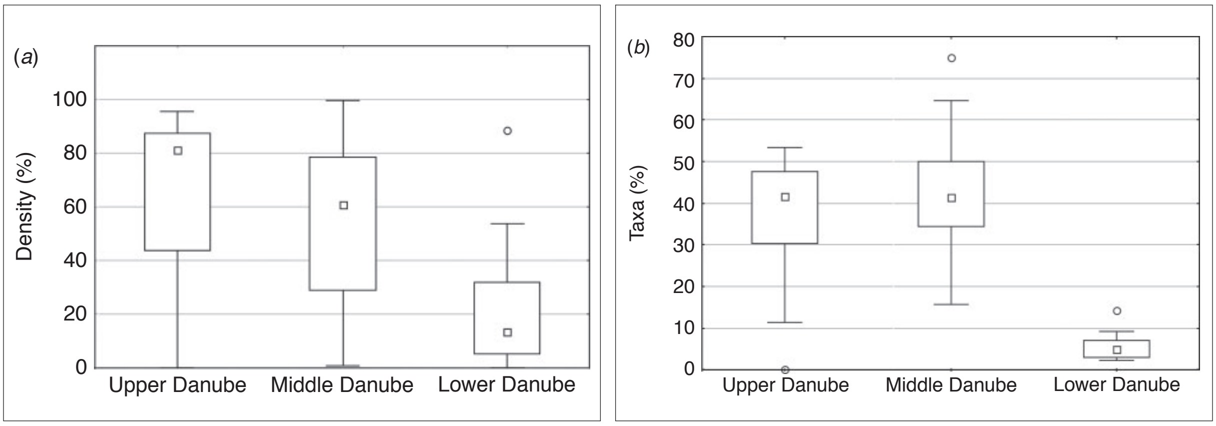

Fig. 2: Relative (% of total) density (a) and species richness (b) of non-native benthic invertebrates in the Upper, Middle and Lower Danube River sections (n = 78). Modified after Graf et al. (2008) in Liška et al. (2008).

et al. 2008). The Ponto–Caspian Region not only serves as a suitable recipient, but is also a key European 'donor area' for non-native species.

The quantification of non-native species was a key focus of the Joint Danube Survey 2 (Liška *et al.* 2008; Fig. 2). There is clear evidence that channel stabilisation and construction of artificial banks have favoured the establishment of non-native species. Therefore, restoring hydrogeomorphic dynamics is expected to mitigate the spread of invasive species, as pioneer habitats are less prone to the establishment of non-native species (Tockner *et al.* 2003).

Little is known about the ecosystem consequences of novel communities that are composed of a mixture of native and nonnative assemblages. In addition, there is the need to improve the understanding of the interactions of species invasion with other pressures in order to better manage invasive species in the DRB. It will be important to apply risk assessment procedures and use those results for priority actions to reduce the rate of aquatic invasions and to combine these actions with awareness-raising measures in water management and the public (Panov *et al.* 2009). It is also questionable whether all measures should be based on the *a priori* assumption that non-native species have a negative ecological and economic impact.

9 Legal frameworks of the Danube River Basin

A long history in developing and establishing national and international legal frameworks exists along the Danube River (Bogdanovic 2005; Table 1). However, to manage a river basin as diverse and complex as the DRB poses major legal and political challenges to the public and stakeholders at various hierarchical levels. Since 2000, the WFD forms the guiding legal principle for the management of the DRB. The ultimate goal of the WFD is to achieve good ecological (and chemical) status for all surface waters by 2015 (with possible extensions to 2027). Basic elements to define good ecological status are the ecoregion, river type, and reference state, as well as the composition of aquatic assemblages (Moog *et al.* 2004; ICPDR 2005). If restoring good ecological status causes disproportionate costs or adverse effects on the environment and human society, water bodies might be designated as 'heavily modified'. As such, 'good ecological potential' and 'good surface water chemical status' must both be achieved.

The ICPDR, founded in 1998, is responsible for the implementation of the WFD in the DRB. The Danube River Protection Convention (DRPC) forms the political framework that underpins the international cooperation within the ICPDR. Fourteen out of the 19 DRB countries are contracting parties and legal members of the DRPC. In addition, the European Commission is a contracting party. Italy, Switzerland, Poland, Albania, and the Former Yugoslav Republic of Macedonia, which have only minor shares in the DRB, cooperate with the ICPDR. The WFD implementation is legally binding for the EU Member States of the DRB. Further, contracting parties that are non-EU Member States have made a voluntary commitment to implement the WFD under the DRPC. This undertaking represents a major step forward to the overall DRB management strategy, as well as to the environmental administrations of the respective countries.

The secretariat of the ICPDR coordinates the work of national delegates (i.e. high-ranked governmental representatives) and technical experts, integrates the members of the public, and cooperates with the scientific community. The ICPDR jointly prepares the content and calls for project tenders, as well as the documents for the implementation of the water protection and conservation issues, to be ratified by the national governments. The Roof Report (ICPDR 2005), the Joint Danube Surveys (in 2001 and 2007), the Issue Paper on Hydromorphological Alterations (ICPDR 2007a), the Action Program on Sustainable Flood Protection (ICPDR 2004), the DRBM Plan (ICPDR 2009) and the establishment of public participation strategies (see below), are so far the main deliverables provided by the ICPDR. Nested within the ICPDR are sub-basin activities for the Danube Delta as well as for the Tisza and Prut Basins. An international commission has been established for the Sava River Basin (http://www.savacommission.org).

The Espoo Convention on Environmental Impact Assessment in a transboundary context (http://www.unece.org/env/eia) helps to solve environmental problems across political borders (e.g. for the Bystroye navigation-canal in the Danube Delta, bordering Romania and Ukraine). Finally, the Danube–Black Sea Joint Technical Working Group coordinates the work of the ICPDR and the International Commission for the Protection of the Black Sea, in particular to develop strategies for reducing nutrient inputs into the Black Sea.

The Belgrade Convention on Danube Navigation, the EU Flood Directive, and the Floods Action Program aim to further expand inland navigation and to implement flood control programs (European Commission 2004; European Commission 2007). However, these aims compete with that of the EU WFD, which states that the ecological integrity of surface waters must not deteriorate further. The EU Flood Directive itself is controversial in its recognition of the natural retention capacity of floodplains. Despite the various environmental directives, the Danube has been defined as a priority-axis of the TEN-T. In particular, the few remaining large floodplains along the Lower Danube River, as well as along the Sava, Drava and Tisza Rivers, are threatened by these navigation plans (Schneider 2002; WWF 2002). Although these floodplains provide invaluable ecosystem services (i.e. water storage, recharge of groundwater, nutrient retention, retention of suspended and dissolved materials, biodiversity 'hot spots', ecotourism), these services remain mostly neglected by politicians. Given the expected increase in economy and large infrastructure projects in the DRB, sustainable strategies are required (e.g. Brundic *et al.* 2001; for Middle Sava). The Joint Statement on Inland Navigation and Environmental Sustainability in the DRB aims to develop new navigation strategies (ICPDR 2007b). The feasible first steps to a more sustainable DRB inland navigation are to modernise the vessels and harbours along the Danube, and to harmonise the TEN-T guidelines with the WFD objectives (WWF 2005). Another step forward was the elaboration of the PLATINA-Manual for sustainable navigation where environmental aspects are respected and balanced with economic development (ICPDR 2010b).

Legal protection of endangered species remains a specific problem. For example, five out of six sturgeon species native to the DRB are critically threatened by extinction, and one species (*Acipenser sturio*) is already extirpated. The Sturgeon Action Plan, within the framework of the Bern Convention on the Conservation of European Wildlife and Natural Habitats, stipulates the re-opening of sturgeon migration routes by making the Iron Gate hydropower dams passable and by conserving key habitats for recruitment (Bloesch *et al.* 2006). Further, the Convention on International Trade in Endangered Species (CITES, http://www.cites.org) regulates the trade of sturgeons and their products.

Pollution remains an important issue in the DRB. Since 2007, industrial emissions have been regulated by the Integrated Pollution Prevention and Control (IPPC) Directive. The list of priority substances most dangerous for human and environmental health (http://ec.europa.eu/environment/air/pollutants/stationary/ippc/index.htm) is presently under revision. Various directives are in force, some under the WFD, which serve as legal guidelines and back up international conventions to support river and wetland protection, conservation and management (http://ec.europa.eu/environment/water/water-framework/index_en.html). All quoted conventions (Table 1) have been ratified by the majority of the DRB countries and are therefore legally binding, at least in theory. There is emerging mutual understanding among the Danube countries that the principles of 'polluter and user pays' (e.g. for pollution), 'solidarity' (e.g. for sturgeon protection), and 'precaution and prevention' (e.g. for flood protection or through preventing accidental spills) should be implemented. The application of economic instruments in water management is generally perceived as an effective tool to promote the protection of the environment (Speck 2006). For example, the 'polluter pays principle' forms the base of all European environment policies; it implies that people and private industries, but not the public and tax payers, should pay the damages and environmental impacts they cause through their activities. This principle is actually transferred to other sectors such as the ship-waste management sector (http://www.wandaproject.eu). However, in the downstream DRB countries, the alignment and harmonization of the legal frameworks with EU policies, as well as its enforcement, are far from being satisfactory (Speck 2006). The solidarity and precaution-principles are complementary and must be ensured because impacts of upstream pollutants may cause major damages to downstream communities. Additional pressure towards reductions in pollution was gained by the Protocol on Pollutant Release and Transfer Registers (Table 1). Internationally binding, it gives the statutory right to the public to have free access to emission data in national pollutant release and transfer registers.

Unfortunately, where economy meets ecology, the former is usually the winner (Tockner and Stanford 2002). Political compromises are inevitable, need to be based on scientific concepts for river basin management, and must include participatory methods to achieve win-win situations among the different user groups (Bloesch 2004).

Table 1: Principal multilateral agreements related to the management of water resources in the DRB (websites accessed 17 June 2009). Modified, extended, and updated from Bogdanovic (2005).

Treaty	Main Topic	Geographical scope	Status of ratification by Signatories and Parties[A]
Belgrade Convention (1948)	Danube Navigation Regime	Regional	1*S*, 9*R*
Ramsar Convention (1971)	Wetlands of International Importance Especially as Waterfowl Habitat	Global	14*R*
Bern Convention, Council of Europe (Bern, 1979)	Conservation of European Wildlife and Natural Habitats BConservation of European Wildlife and Natural Habitats[B]	Danube River Basin	1*S*, 10*R*, 4*A*
Espoo Convention (1991)	Environmental Impact Assessment in a Transboundary Context	Europe	9*R*, 4*A*
UN/ECE Water Convention (Helsinki, 1992)	Protection and Use of Transboundary Watercourses and International Lakes	Europe	12*R*
Helsinki Convention – industrial accidents (1992)	Transboundary Effects of Industrial Accidents	Europe	11*R*
Danube River Protection Convention, DRPC (Sofia, 1994)	Cooperation for the Protection and Sustainable Use of the Danube River	Danube River Basin	15*R*
New York Convention (1997)	Non-Navigational Uses of International Watercourses	Global	2*R*
Aarhus Convention (1998)	Access to Information, Public Participation in Decision-Making and Access to Justice in Environmental Matters	Europe	11*R*, 2*A*
Protocol on Water and Health (London, 1999)	Promotion and Protection of Human Health	Europe	2*S*, 8*R*
Framework Agreement on the Sava River Basin, FASRB (Kranjska Gora, 2002)	International Regime of Navigation, Sustainable Water Management, Prevention and Limitation of Hazards in the Sava River Basin	Sava River Basin	4*R*
Protocol on navigation to FASRB (Kranjska Gora, 2002)	Navigation on the Sava River from Sisak to the Danube Confluence, and on relevant sections of the Sava Tributaries	Sava River Basin	4*R*
SEA Protocol (Kiev, 2003)	Strategic Environmental Assessment for Large Infrastructure Projects	Regional	9*R*, 4*A*
Protocol on Civil Liability (Kiev, 2003)	Compensation for Damage Caused by Transboundary Effects of Industrial Accidents on Transboundary Waters	Regional	6*S*, 1*R*
Protocol on Pollutant Release and Transfer Registers PRTR (Kiev, 2003)	Enhance Public Access to Information through the Establishment of Coherent, Integrated, Nationwide Pollutant Release and Transfer Registers	Regional	14*S*, 1*A*
Carpathian Convention (Kiev, 2003)	Protection and sustainable Development of the Carpathians	Regional	6*R*

[A] Encompassing 14 DRB countries (Germany, Austria, Czech Republic, Slovak Republic, Hungary, Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Romania, Bulgaria, Moldova, Ukraine, Montenegro) and the European Community; the newest Signatory is Montenegro (since 3 June 2006), which will gradually adopt the treaties ratified by Serbia–Montenegro (in particular the Agreement on the Sava River Basin). *S*, signed; *R*, ratified; *A*, accession.

[B] The Action Plan for the conservation of sturgeons (Acipenseridae) is particularly relevant in the DRB. The goal is to secure viable populations of all endangered Danube sturgeons by sustainable management and by restoration of their natural habitats and migratory corridors. The Action Plan was adopted by the Standing Committee of the Bern Convention in December 2005 (Bloesch et al. 2006).

10 Proactive and reactive management strategies

10.1 Proactive management activities

The EU WFD considers the river basin as the key spatial unit to understand and sustainably manage water resources. The DRBM Plan is the instrument to ensure good status in all water bodies by 2015 and beyond (ICPDR 2009). The availability of high-quality monitoring data is crucial for the compilation of the DRBM Plan and allows for a cost-efficient implementation of the EU WFD. Building on existing national monitoring networks, the TransNational Monitoring Network (TNMN) was set up in 1996 (adapted in 2006 in order to comply with WFD requirements) under the umbrella of the ICPDR. The revised TNMN includes 81 monitoring stations that provide a basin-wide overview of the status and the long-term trends of surface and ground water quality (ICPDR 2009). The TNMN data are checked via an analytical quality control program by a network of 69 national laboratories quarterly, and the results are published annually ('QualcoDanube', VITUKI 2009).

The monitoring efforts through the TNMN have been supplemented by 'Danube expeditions'; two Joint Danube Surveys (JDS1 in 2001 and JDS2 in 2007) were carried out by multidisciplinary teams of scientific experts. These international expert teams collected hydromorphologic, physico-chemical, and biological data along the entire Danube main stem, as well as along selected tributaries, in a standardized way. In total, 280 environmental parameters were evaluated. Despite limitations owing to the snapshot character, the results of both JDS provide a useful scientific basis for the further improvement of DRB management strategies, and concurrently stimulate the dialogue with different stakeholder groups. Furthermore, the surveys provided the opportunity to check the comparability of the nationally applied WFD-compliant sampling and assessment methods, as well as to train field and laboratory staff.

The JDS are supported by the DRB governments, private and public-run laboratories, private companies, local authorities and NGOs. The 'Danube expeditions' received major attention by the media and therefore helped to enhance public awareness about the multiple threats in the DRB (http://www.icpdr.org/jds). It is planned to repeat the JDS at six-year intervals to detect long-term trends, at a high spatial resolution, and to assess the success of the DRB management strategies.

A comparative and consistent water quality classification and status evaluation is a legally binding requirement of the WFD. At the European and DRB level, this task of benchmarking is subsumed as 'intercalibration' (European Commission 2005). The purpose of the intercalibration exercise is not to harmonise assessment systems, but their results. The exercise aims to ensure that good ecological status represents the same level of ecological quality throughout Europe. For large and lowland rivers, near-natural reference sites are absent; therefore, intercalibration approaches for impacted conditions were developed (Heiskanen *et al.* 2004; Birk and Hering 2009). Owing to data gaps, and because national WFD-compliant assessment methods were not developed to a sufficient extent, not all biological quality elements in all water categories have been intercalibrated within the first phase of the intercalibration exercise between 2005 and 2007. The exercise should be finalised by the end of the second phase (2008–2011). Moreover, the assessment of the ecological status of large rivers, such as the Danube, has been recognised as a particular challenge, and is dealt with by specific working groups at the DRB and the European levels (ICPDR 2009).

10.2 Proactive management options for nutrient reduction

The model MONERIS (MOdelling Nutrient Emissions into RIver Systems) was used to quantify point and diffuse source emissions for seven emission pathways into surface waters as well as instream retention processes (Venohr *et al.* 2010). In addition, management options are implemented in the model that can be evaluated according to their potential to reduce nutrient emissions (Behrendt *et al.* 2002; Schreiber *et al.* 2005). Based on this model, a total of 650 kt (49% agricultural sources) of nitrogen (N) and 53.5 kt (62% urban sources) of phosphorus (P) are emitted into the DRB annually (2005 is used as a reference year); whereas geogenic background emissions only contribute ~7% for N and 12% for P to the current loads (Table 2). A major management goal for the DRB is to reduce the nutrient load to the level observed in the 1960s (MoU ICPDR-ICPBS 2001). This requires a 40% and 20% reduction for N and P loads, respectively. Of all the suggested measures, establishing efficient WWTPs has the greatest N-reduction potential (–5%). The reduction of atmospheric deposition of NO_x (–4%), altered N-surplus (–2%) and reduced soil loss (–1%) would also further reduce N emissions (Fig. 3; Venohr and Behrendt, unpubl. data).

Table 2: Emissions of total nitrogen (TN) and phosphorus (TP) at mean runoff condition into the Sava, Tisza, Upper, Middle (excluding Sava and Tisza sub-basins) and Lower Danube (106 t y^{-1}).

Source	Upper Danube		Middle Danube		Lower Danube		Sava		Tisza		Total DRB	
	TN	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN	TP
Total emissions	157.4	7.4	169.9	14	119.4	14.5	104.6	8.8	98.8	8.8	650.1	53.5
Background sources	11.1	1.9	12.3	1.3	8.9	0.9	7.9	1.4	7	0.8	47.1	6.2
Urban sources	19.6	2	55.9	9.3	44.5	9.5	31.3	6.1	31.6	6	183	33
Agricultural sources	99.3	2.1	76.5	3.1	51.7	3.8	43.8	1.3	46.2	1.9	317.5	12.2
Other sources	27.4	1.4	25.2	0.4	14.3	0.2	21.7	0.1	14	0.1	102.6	2.2

In all DRB countries, except Germany, Austria, Romania, and Slovenia, agricultural land use is predicted to increase until the year 2015 (Fig. 3). As a consequence, N emissions will most probably increase, which could counteract the reduction effects accomplished through other measures. Phosphate emission in the DRB via household detergents is also significant. Up to now, only Germany and Austria have imposed bans on phosphate in laundry detergents. However, this ban does not apply to

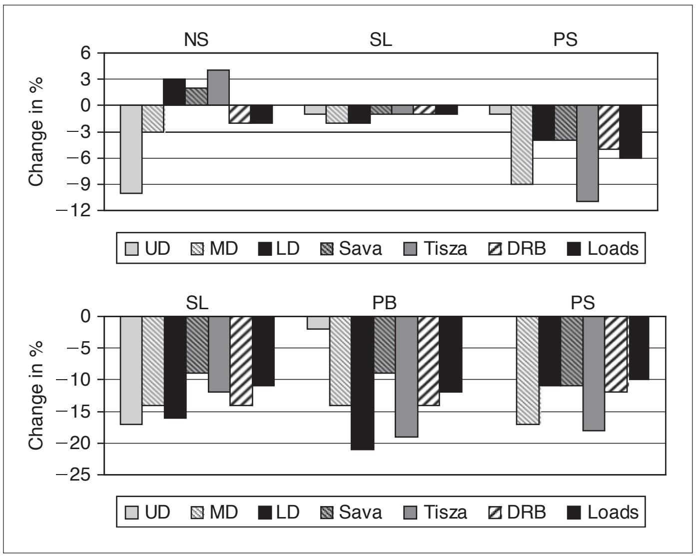

Fig. 3: The relative (% of total) emission reduction potential for N (upper panel) and P (lower panel) based on different measures in the Upper (UD), Middle (excluding Sava and Tisza sub-basins, MD) and Lower Danube (LD), as well as in the Sava and Tisza basins, the entire DRB, and the change in the resulting loads to the Black Sea basin (Loads). NS, nutrient surplus on agricultural land (assumes moderate development of the agricultural sector up to 2015, values are based on estimated N-surplus for the year 2015 as delivered by DRB countries). SL, soil loss (reduction of soil loss from all arable land by measures like mulch sawing, no-tillage or ploughing in parallel to the contours). PS, measures to reduce discharges from WWTPs and households connected to no or decentralised WWTPs (implementation of the legally binding EU Urban Waste Water Directive in the EU member states paralleled by the installation and expansion of waste water infra- structure in the non-EU member states). PB, total P-ban (basin-wide ban of phosphorus in laundry and dishwasher detergents).

dishwasher detergents, and these remain an emerging pollution pathway. Nevertheless, the reduction potential of a P ban in laundry detergents amounts to 14% and 21.2% in the Middle and Lower Danube, respectively (Fig. 3). In February 2010, DRB environmental ministers committed themselves to initiate a basin-wide P ban in laundry detergents by 2012 and to work towards a market launch of polyphosphate-free dishwasher detergents by 2015 (Danube Declaration 2010). This decision is a reaction to the cost-effectiveness of this measure, as indicated by scientific results, and thus a good example of effective science–policy interaction.

Measures to prevent soil loss from arable land could further reduce phosphorus emissions considerably (up to 14% reduction when applied to all arable land, Fig. 3). This is an important measure in the Upper Danube where other options are less effective. In combination, all measures can reduce N and P by 8 and 40%, respectively. However, for N, the management objective, as stated in the DRBM Plan, cannot be achieved by 2015 (ICPDR 2009).

10.3 Proactive management of protected areas

Within the DRB, 1071 freshwater protected areas (>500 ha) have been identified (ICPDR 2009). However, it is difficult to estimate the total area of protection sites within the DRB because various protection categories spatially overlap. For example, parts of the Danube Floodplain National Park east of Vienna (Austria) are concurrently designated as a NATURA2000 site, Ramsar area, UNESCO Biosphere Reserve, National Park, Nature Reserve, IBA (Important Bird Area) and Protected Landscape. Moreover, there is variation throughout the DRB countries whether aquatic ecosystems are the focus of protection, and categories like 'National Park' and 'Nature Reserve' are often not in accordance with the international categories of the IUCN (Dudley 2008). The different uses and protection categories of freshwater reserves can be attributed to the biogeographic setting, the uneven economic development of the DRB, and different stressors that act in the different regions. Although water abstraction for irrigation and chemical pollution are major stressors in SE Europe, hydropower generation, flood protection and navigation (i.e. hydromorphologic alterations) dominate in Central and Western Europe. Protected areas managed by an administrative authority usually belong to the highest conservation category. The Accessory Publication (Part A) lists these protected areas along the Danube River and its major tributaries.

The NATURA2000 concept constitutes the first uniform definition of habitat types to be protected in Europe. Special Protection Areas (SPAs) under the Birds Directive (Directive 2009/147/EC) as well as the protection of threatened (Red List) species protected by the Bern Convention, are integrated into the NATURA 2000 network. Along the main stem of the Danube River, 117 NATURA2000 sites, ranging from 30 ha to ~600 000 ha, have been designated for the protection of habitats and species (European Environment Agency, DG ENV E2). This number will most likely grow when non-EU Member States, after accession, designate their NATURA2000 sites. The standardised NATURA2000 rules allow EU citizens to have actions that might be destructive to the environment assessed via the European Commission, mostly independent of local or governmental interests. However, the implementation and adjustment of the NATURA2000 network is a longterm endeavour. Criticism has been made with regard to the: (i) doubtful representativeness of the nominated sites; (ii) often small areal coverage of the sites; (iii) insufficient update of the lists of protected species and habitats; and (iv) spatial isolation of the individual sites.

The NATURA2000, as well as other protection measures such as the Ramsar Convention and the WFD, should not be regarded as the end points of the EU conservation policy (Maiorano *et al.* 2007). There is urgent need to simplify and properly harmonise existing protection concepts and directives, as well as to incorporate them into a general nature conservation strategy. Additionally, advanced reserve network designs, such as the concept of 'Key Biodiversity Areas' (KBAs), are currently under development (Langhammer *et al.* 2007; http://www.freshwaterbiodiversity.eu). They are envisaged to allow for a more effective protection of species and prioritisation of sites for conservation. However, all protection categories outlined above focus on the preservation of the environmental status quo and consider the structure rather than the function of ecosystems as the main conservation target.

Currently, the remaining ecologically valuable river sections of the Danube are at high risk because of large-scale navigation and flood management plans. Therefore, in 2007 the representatives of the large protection areas within eight Danubian countries launched the initiative for a Danube River Network of Protected Areas ('Danubeparks'; funded by the EU SE Europe Transnational Cooperation Program, http://www.danubeparks.org). The main goals of this initiative are to: (i) exchange experiences in river restoration and invasive species control; (ii) propose management strategies for sustainable sedimen balances, nutrient control, inland navigation and hydromorphologic integrity; (iii) conserve flagship species such as sturgeons and the white-tailed eagle; (iv) act as an observer within the ICPDR and to advocate for large protected areas as part of basinwide management strategies; (v) promote the implementation of the NATURA 2000 concept and of transnational monitoring programs; (vi) implement a basin-wide public relation program for nature conservation; and (vii) stimulate eco-tourism.

10.4 Reactive management strategies: restoration

Nature restoration is a thriving enterprise worldwide. This is also true in the DRB. Some case studies are outlined in the Accessory Publication, Part B. In the Upper Danube Basin, channel widening, re-connection of side-arms, shoreline restoration, and re-establishing the continuum for migratory fish and benthos are the main activities (e.g. near Ingolstadt, Germany; in theWachau valley, Austria; Alluvial Zone National Park, Austria; the latter are pictured in Part C of the Accessory Publication). In the Middle Danube, restoration projects mostly focus on the reconnection of former side-arms (e.g. Ven-Duna in the Duna- Drava National Park, Hungary; Vemeljski Dunavac in Kopacki Rit, Croatia; Monoštorski rit restoration project in Gornje Podunavlje, Serbia). In the Lower Danube, large stretches have been embanked and restoration projects focus on the integration of former floodplains and wetlands into the river flow regime (e.g. Kalimok marshes, Bulgaria; opening of polders in the Danube Delta, Romania).

River restoration projects along the Danube are mostly designed and implemented locally. Usually, national river engineering administrations constitute the highest level of planning. Moreover, cultural diversity and political and language barriers hinder the exchange of experiences regarding the design and implementation of river restoration strategies. Proper monitoring (i.e. assessing success) is mostly lacking. The Danube River Network of Protected Areas aims to fill these gaps and to serve as an adequate future information platform (http://www.danubeparks.org).

The ICPDR initiated a spatially-explicit prioritization approach for restoration, with a focus on fish species migrating long and medium distances in the DRB. Barrier-free fish migration along key migration routes is envisaged by 2015 (ICPDR 2009). Barriers along the main stem and close to the mouth of major tributaries need to be re-opened first for achieving this high priority goal.

11 Public participation

Public participation is recognised as a legally important and politically efficient tool for the development and implementation of sustainable management strategies (Aarhus Convention, http://www.unece.org/env/pp). At present, 19 organisations, including non-governmental (NGO) and non-profitable organisations (NPO), as well as representatives of the private industry and intergovernmental organisations have observer status in the ICPDR (Part D of the Accessory Publication). The stakeholders represent interest groups on navigation (3 groups), hydropower generation (1 group), dredging (1 group), water management (5 groups), drinking water generation (1 group), tourism and angling (3 groups), and environmental protection (5 groups). Because of the often competing interests, interaction and cooperation among these groups mostly remain restricted to the joint ICPDR meetings, stakeholder conferences, and project meetings. The Danube Day, organised in all DRB countries by the ICPDR since 2004, fosters public awareness and participation.

Environmental NGOs can strengthen the political decision making process by provoking sound decisions based on the best available scientific knowledge. With regard to the implementation of the WFD and the elaboration of the DRBM Plan, NGOs support governmental bodies, disseminate information, and foster awareness within the NGO community as well as in the public. However, because the DRB has been a main 'political fault-line' within Europe for many centuries, societal differences and diverse attitudes make the development and implementation of a 'sustainable' RBM a challenging task (Sommerwerk *et al.* 2009). In the Upper DRB, environmental NGOs already have a long tradition, are well-established, and are embedded into an international network. In contrast, in the Middle and Lower DRB most NGOs do not yet have such a strong foundation in the civil society, and public awareness is less prevalent. Knowledge about international conventions or experience in acquiring funding is less pronounced. Nevertheless, the NGOs of the Middle and Lower DRB have gradually increased their membership and their political influence since the fall of the Iron Curtain.

Many NGOs in the eastern part of the basin are organised as platforms like the Danube Environmental Forum (DEF, http://def.distelverein.at). The DEF was founded in 1999 and encompasses ~85 NGOs from 14 Danubian countries. The DEF secretariat in Baja, Hungary, together with several national focal points, encourages cooperation among the organisations that are active in the DRB, supports the exchange of information, and promotes public participation in environmental decision making. The DEF gained assistance in the reinforcement of its NGO network via the Danube Regional Project 2002–2006 (DRP, http://www.undp-drp.org). The Regional Environmental Centre for Central and Eastern Europe (REC, http://www.rec.org) is another major player in supporting the public participation process in the DRB. In the frame of the Danube Regional Project, the DEF and the REC promote the capacity building for cleaning up DRB pollution hot spots.

The International Association for Danube Research (http://www.iad.gs) and the Worldwide Fund for Nature via its Danube-Carpathian Program, (http://www.panda.org/dcpo) are the oldest and largest NGOs in the DRB committed to science based decisions in environmental issues. They jointly established the Sturgeon Action Plan for the DRB (Bloesch *et al.* 2006), and they were key partners in the elaboration of the Joint Statement on Guiding Principles for the Development of Inland Navigation and Environmental Protection in the Danube River Basin (ICPDR 2007b).

12 Challenges and recommendations for the sustainable development of the Danube River Basin

'Sustainable management' of ecosystems is a buzzword that is highly popular among politicians and scientists. However, to properly define this concept and to implement it into a river basin management plan remains a major challenge that requires tight feedbacks between science and application (Bloesch 2005; Eberhard *et al.* 2009). Therefore, the European Union, along with national governments, has invested considerable financial resources in supporting the scientific community in the DRB during the past decades. However, the knowledge gained through supported projects is not yet efficiently implemented into management programs and legislative tools (Kramer and Schneider 2010). The science–policy integration is often hindered by inadequate communication and the lack of access of adequate scientific results. Therefore, the 'portal for science and technology transfer to policy making and implementation of integrated water resources management' was launched in 2007 as part of the Water Information System for Europe (WISE-RTD web portal, http://www.wise-rtd.info). Projects that are funded via the Seventh Framework Program of the European Community have to allocate a certain amount of the budget to involve 'communication with non-academic partners'. These dissemination efforts are expected to be part of the project evaluation (Holmes and Scott 2010). Despite the existence of these web portals and communication obligations, the transfer of scientific results into practice remains suboptimal (Kramer and Schneider 2010). It is therefore crucial that scientific experts actively participate and expose themselves in the public political discussion; for example, as members of the local and regional parliament. Unfortunately, scientific career-reviewing schemes rarely give credit to efforts for the integration of knowledge to fulfil policy objectives (Quevauviller 2006). In addition, the scientific community needs to come up with a clear concept of ecosystem services that can be integrated into management strategies. If this issue stays under dispute within the community, its persuasive power is weakened.

The identification of research needs and the setting of research agendas have to be an ongoing process and should not only start when an urgent problem emerges (Holmes and Scott 2010). Thus, effective science–policy integration requires joint framing and planning of fundamental and applied research, the presence of policy makers and stakeholders on research steering boards, and an agreement on clear environmental targets. Quantitative tools that allow the prediction of the effects of management options under rapidly changing environmental and political conditions are urgently needed. In addition, spatially-explicit priorities for conservation and restoration need to be developed. Further, synergies among the presently competing targets such as navigation, biodiversity conservation, and flood control need to be established. In this respect, the ecosystem service concept might be very promising for the management of ecosystems that are under multiple uses.

In Europe, but also globally, the establishment of catchment commissions for transboundary rivers is a major step forward in integrating science–policy activities. For example, the ICPDR, with its seven technical expert groups and network of observers, is an important platform for dialogue and debate. The members of the secretariat have a scientific background, and thus function as 'translators' of research outcomes into management practice. Moreover, the ICPDR initiates programs like the JDS, serves as a member in the advisory board for several initiatives such as the WISE-RTD portal, and presents the DRBM Plan on scientific conferences. A special website has also been launched that actively involves the public in the preparation of the DRBM Plan (http://www.icpdr.org/participate). This more holistic approach allows for the recognition of cause–effect chains and the formulation of measures to properly address them.

Despite progress, many obstacles undermine the implementation of the DRBM Plan. The distinct west–east (upstream–downstream) gradient matters with regard to economic wealth, and many large projects funded through international programs (e.g. EU-Phare, World Bank) did not meet their goals and were unsuitable for the long-term capacity building within the DRB. For example, installing modern chemical laboratories is useless if the necessary experts are not yet available. Hence, there is a need for step-by-step procedures that progressively introduce new skills and technologies in this region (Harremoës 2002).

Bureaucracy, corruption, and politicians ignoring the current best science can hinder the implementation of effective management strategies. This is particularly the case in the downstream DRB countries. For example, ongoing poaching of endangered sturgeons in the Danube Delta undermines the implementation of sturgeon protection strategies and CITES regulation. Although Romania banned commercial fishing and the trade of wild sturgeon products for a 10-year period, the enforcement, and therefore the efficacy of this ban, is doubtful.

The lack of political willingness at the national level can undermine the implementation of the WFD. A stronger involvement of the public and of the stakeholders, as required by the WFD and the Aarhus Convention, may support the implementation of management practices. However, participatory processes to finding agreed solutions need to be taught, are laborious, time consuming, and slow-particularly when conflicting stakeholders are involved.

A few decades ago, the construction of large dams at the Iron Gate and Gabíkovo, as well as the memorable occupation of the Hainburg floodplains in Austria, were subjects of great public debates. Present hot spots of controversy are large-scale river regulation projects for navigation and flood control. A major challenge is to produce sound environmental impact assessments based on published and 'grey literature' data, *in situ* investigations, a good monitoring strategy, and optimised measures of impact mitigation. In this respect, the Directives on Environmental Impact Assessment (EIA) and Strategic Environmental Assessment (SEA) are starting to be properly applied in the Lower DRB (Table 1). However, the great difficulties to implement western standards of EIA is demonstrated by the ongoing discussions about the ISPA 1 and 2 navigation projects (Instrument for Structural Policies for Pre-Accession, TEN-T Program) in the Green Corridor (wetland protection and restoration programme along the entire Lower Danube; http://www.wwf.de/fileadmin/fm-wwf/Publikationen-PDF/DanubeDeclaration2000.pdf).

Open discussions and the utilisation of innovative strategies may lead to a paradigm change that yields acceptable solutions to otherwise conflicting groups. For example, in recent restoration projects along the Danube River east of Vienna, navigation maintenance work was balanced with structural measures for improving hydrologic and geomorphic conditions (Reckendorfer *et al.* 2005). Moreover, the ecosystem services provided by near-natural and restored ecosystems are increasingly taken into consideration in management strategies (e.g. WWF 1995; Barbier *et al.* 1997; Schuyt 2005; Kettunen and ten Brink 2006). Croatia, for example, doubled the size of flood retention areas based on the economic use and non-use values of these floodplains (Brundic *et al.* 2001).

A major difficulty in the implementation of the DRBM Plan is the harmonisation of legal aspects, as well as the improvements of scientific concepts and methods to investigate large rivers. Most DRB countries have developed their own national standards, and ISO standards can only provide a general guideline. Hence, method harmonisation and intercalibration is an important issue of the ICPDR (European Commission 2000; Birk and Schmedtje 2005). Furthermore, mapping of the hydrogeomorphologic conditions according to CEN-Standards provides a powerful tool for decision making (Schwarz 2007).

In summary, the DRB is in a state of fast political and environmental transition. The political and cultural diversity within the DRB can either be considered as an obstacle or as an asset to develop novel and innovative management strategies. The EU WFD supports the protection and restoration of the DRB; however, it is a time-consuming process that requires continuous support from responsible scientists and politicians to foster public awareness and to search for sustainable solutions.

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Accessory Publication

A Protected areas along the Danube River and its major tributaries

Only areas that are managed by an administrative authority committed to nature protection are listed. *River ecosystems comprise only a small part of the total size (websites accessed 18 August 2009).

Name	River-km	Country	Major landscape elements	Total area [ha]*	Website
Danube Delta Biosphere Reserve	115–Black Sea	Romania	delta	564,054	http://www.ddbra.ro/en/index.php
Danube Biosphere Reserve	53–Black Sea (Chilia Arm)	Ukraine	delta	49,676	http://www.dbr.org.ua
Srebarna Nature Reserve	393–391	Bulgaria	natural river banks, islands, lakes	902	http://whc.unesco.org/en/list/219
Kalimok-Brushlen Protected Site	463–434	Bulgaria	natural river banks, islands, marshes	6,000	http://www.kalimok.org
Persina Nature Park	600–560	Bulgaria	natural river banks, islands, marshes	21,762	http://www.persina.bg
National Park Djerdap	1041–940	Serbia	Iron Gate Gorge, hillslopes	63,608*	http://www.npdjerdap.org/en_aktuel.html
Iron Gate Nature Park	1075–935	Romania	Iron Gate Gorge, hillslopes	115,655*	http://www.portiledefierpn.ro/
Deliblatska Pescara	1091–1076	Serbia	natural river banks, various transition zones	29,352*	http://www.vojvodinasume.rs/indexni-vo_en.php?&nivo_1=8&nivo_2=34
Special Nature Reserve Koviljsko-Petrovaradinski Rit	1251–1231	Serbia	natural river banks, highly connected river section	4,840	http://www.vojvodinasume.rs/indexni-vo_en.php?&nivo_1=8&nivo_2=32
Kopacki Rit	1412–1382	Croatia	natural river banks, floodplains	17,700	http://www.kopacki-rit.hr/
Special Nature Reserve	1433–1366	Serbia	natural river banks, floodplains	19,648	http://www.vojvodinasume.rs/indexni-vo_en.php?&nivo_1=8&nivo_2=33
Duna-Drava National Park	1499–1433	Hungary	natural river banks, highly connected river section	49,479	http://www.ddnp.hu
Duna-Ipoly National Park	1713–1657 (several distinct areas)	Hungary	natural river banks, islands	60,314*	http://www.dinpi.hu
Szigetköz	1852–1806 (several distinct areas)	Hungary	highly connected river section	9,158	http://www.szigetkoz.info/galeriak/2007_conference/index_2.htm
Protected landscape area Danube Floodplains	1864–1780 (several distinct areas)	Slovakia	highly connected river section, islands	12,284	http://www.sopsr.sk
Danube Floodplain National Park	1917–1880	Austria	highly connected river section	9,300	http://www.donauauen.at
Protected landscape and World Heritage Site Wachau	2050–2020	Austria	riverine landscape, hillslopes	18,387	http://www.wachau.at/donau/WN/?id=31947
Naturpark Obere Donau	2750–2658	Germany	valley, karstic river bed	135,000	http://www.naturpark-obere-donau.de/
Lonjsko Polje	Sava River	Croatia	highly connected river section	50,600	http://www.pp-lonjsko-polje.hr/
Gajna (protected landscape, partly ornithological reserve)	Sava River	Croatia	floodplain, pastures	1,500	http://www.bed.hr/EN/Gajna.html
Obedska Bara	Sava River	Serbia	swamp forest and vegetation, ponds, meadows	20,000	http://www.vojvodinasume.rs/indexni-vo_en.php?&nivo_1=8&nivo_2=35
Zahorie	Morava River	Slovakia	floodplain forest, side-arms, meadows	27,522	http://www.sazp.sk/slovak/struktura/copk/chodniky/chkoza.html

B Restoration case studies

— UPPER DANUBE —

B.1 Morava River (Slovakia and Austria): reconnection of meanders

Situation before/after human impact Originally a meandering river, more than 90 % of the river course faced intensive river regulation during the 20th century, like dike construction, canalisation, and elimination of all major meanders.

Restoration project Within the project GEF-Biodiversity four cut-off meanders were partly reconnected to the river between 1993 and 1995 (Morava-Rkm 12, 19, 65). The aim was to increase the flow dynamics in the former anabranches. The bypass-canals stayed fully active, water inflow to the re-opened meanders was limited by rock dams.

Situation after restoration The expected washout of settled sediments did not occur, and the opened meanders suffered severe sedimentation after restoration. The morphology and the sediment layer did not develop towards an active meander. Biotic response showed an increase of fish taxa; mainly additional rheophylic species. Invertebrate and plant communities shifted towards the riverine set of species, but could not be considered equivalent to those observed in active meanders.

Another type of meander re-opening was tried on the Austrian side of Morava River at river-km 18, where the meander was reconnected at the downstream part to the river which lead to severe sedimentation in the outflow area of the meander.

Lessons learnt The results provide evidence that reconnected meanders might be unsustainable if a parallel shortcutting is not blocked. It is one of the only projects where full meander bends of lowland rivers have been reconnected and the resulting hydromorphologic changes were well-documented (Phare Project Report 1999).

— MIDDLE DANUBE —

B.2 Wachau (Austria): side arm restoration

http://www.life-wachau.at

Situation before/after human impact The Danube has an alpine character in that region, with coarse gravel as bed sediment. Mean water flow velocity is 1.5 to 2.0 m s^{-1}, mean water discharge is 1.950 $m^3 s^{-1}$. Due to regulation works in the 20th century the river banks are fixed by embankments, and side arms are cut-off by rocky dams.

Restoration project A silted side arm has been reconstructed by dredging near Rossatz-Rührsdorf (Rkm 2013.5–2010.0) at a total length of 3.5 km in winter 2005/2006 to create habitat for rheophilc fish species. Implementation by Austrian Waterway Agency via donau and local partners; subsidised by the EU LIFE-Programme.

Situation after restoration The side arm has been active since dredging, with flow velocities similar to those in the main river and no aggradation of the river bed in the side arm. The density of rheophilic fish and number of fish species has increased considerably, and the side arm obviously became important for fish reproduction. Shelter from ship waves may be one of the major reasons.

Lessons learnt Endangered rheophilic fish communities can be supported efficiently by restoration of side arms, if a flowing water regime is guaranteed throughout most of the year.

B.3 National Park Donau-Auen (Austria): side arm restoration and river bank restoration

http://www.donauauen.at

Situation before/after human impact Danube characteristics see case study 2, Wachau.

Restoration project To enhance riverine morphodynamics, several side arms have been reconnected since 1995 (Rkm 1905.0 – 1895.5; 1905.2 – 1902.0; 1910.1 – 1906.5) and since 2005 river embankments and groynes have been removed from 2.85 kilometres (Danube Rkm1885.75 – 1882.9) and from 1.2 km (Danube Rkm 1883.1 – 1881.9) (Accessory Publication, Part C). The long-term goal of the project is to come as close as possible to the pre-regulation status of this Danube section. Implementation is by the Austrian Waterway Agency (via donau) and Danube Floodplain National Park; subsidised by the EU LIFEProgramme.

Situation after restoration Reconnected sidearms show considerable erosion of lateral fine sediment layers and meandering is starting to take place. However, morphodynamics are not yet sufficient for adequate bedload gravel transportation. Sidearms have not increased water depth by incision.

Along the Danube natural river banks were restored within half a year with lateral erosion rates of up to 10m, though the erosion rate is currently declining (Accessory Publication, Part C).

Lessons learnt Revitalisation of floodplains, flood control and inland navigation are compatible, when win-win situations are created. In these cases it is even possible to obtain or to proactively protect riverine landscapes with steep river banks several meters high, to have gravel relocation rates that allow for the formation of gravel banks and to have river banks structured with large woody debris.

B.4 Lobau (Austria): reconnection of floodplains

http://www.magwien.gv.at/umwelt/wasserbau/hydrologie/dotationlobau.html

Situation before/after human impact The floodplain area "Lobau" is situated along the left bank of the Danube River at the eastern border of the city of Vienna (Rkm 1924 – 1907). During the 19th century, this former braided-anabranching floodplain complex was disconnected from the main channel by the construction of lateral embankments and a flood protection dyke. Land use change has led to a

74% decrease in surface water area and has dramatically altered habitat composition and related ecosystem functions.

Restoration project Lobau floodplains have been reconnected to an artificial flood relief channel of the Danube since 2001 (flow input: up to 1.5 $m^3 s^{-1}$ during the vegetation period, mean discharge during 2001-2008: 0.25 $m^3 s^{-1}$).

Situation after restoration The improved connectivity between water bodies at higher mean water levels in the floodplain has decreased the risk of massive eutrophication events, improved the water levels in small oxbows and some semi-aquatic areas, and conserved the existing species diversity in aquatic habitats (e.g. Bondar-Kunze *et al.* 2009, Funk *et al.* 2009).

Lessons learnt Increased connectivity has led to more diversified aquatic and semi-aquatic habitats and more intense biogeochemical cycling. However, due its vicinity to Vienna, societal demands, like flood protection, drinking water supply (20% of the drinking water for Vienna), and recreation (~650,000 visitors per year – census 2006) challenge floodplain management of the Lobau. A multi-criteria decision support system that integrates ecological and societal demands has been developed in order to identify future measures able to serve multiple uses and rehabilitate the hydrological connectivity in certain parts of the floodplain area (Hein *et al.* 2006b).

B.5 Krapje Djol (Croatia): reflooding of oxbow

Situation before/after human impact The spoonbill colony Krapje Dol is the heart of the Nature Park Lonjsko Polje. In 1963 the oxbows became the first Ornithological Reserve of Croatia. In 1988, 180 pairs of spoonbills and 210 pairs of herons nested there. During the implementation of the UN – World Bank SAVA 2000 program the site suffered as its surroundings were drained in a polder, large flooded pastures were transferred to arable land and herbicides delivered by airplane directly over the colony. A ditch drained the water from the oxbow and the site dried out in 1989 (Dezelic and Schneider-Jacoby 1999).

Restoration project Two important steps led to the recovery of the site. In 1989, a rehabilitation project was planned by the Croatian Institute for Nature Protection and EuroNatur to restore the water level in the oxbow. Moreover, a pipe was built to re-flood the area. It is in use when the water level in the Sava is above 620 cm. Funding was provided by the Zoological Society Frankfurt.

Situation after restoration In 1991, the first spoonbills returned. In 2004, the colony has reached 80 pairs of spoonbills and 370 herons. In 1997 the plant *Stratiotes aloides* was spotted again in Krapje Dol.

Lessons learnt Flooding without a pump and depending on the natural water regime of the Sava was the best solution. Water quality improves after the first flood wave. Today, the site is once again one of the key attractions of the Nature Park Lonjsko Polje and the mixed heron and spoonbill colony Krapje Dol offers a great insight in the biodiversity of alluvial wetlands (see: http://www.zoo.ch/xml_1/internet/de/application/d1/d90/f1541.cfm).

— DELTA —

B.6 Danube Delta (Romania): opening of agricultural polders

Situation before/after human impact Until the 20th century vast areas of the Danube Delta faced only minimal human impacts through extensive fishery and reed harvesting. Since then the Danube Delta has undergone multiple human impacts like embankment, channelization and drainage. Moreover, large areas were diked and the polders used for agriculture.

Restoration project The Babina polder (2.100 ha) was reconnected to the river in 1994, Cernovca polder (1.580 ha) followed in 1996, and recovery has been monitored by the Danube Delta National Institute (www.indd.tim.ro).

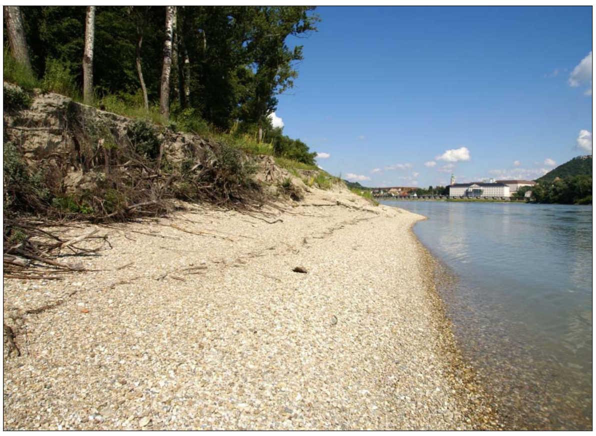
Situation after restoration Within a few years a redevelopment of the site-specific biodiversity occurred and ecosystem services like nutrient retention and fish recruitment became obvious. Additionally, the reconnected polders enable reed harvesting, grazing, fishing and ecotourism (Schneider *et al.* 2008).

Lessons learnt Already small scale measures to open large polder areas can lead to the restoration of natural wetlands. These cost-effective and thus realisable measures could serve as an example for the revitalisation of comparable areas in the Danube Delta. In order to keep polders active, the location of the in- and outflow has to be chosen appropriately.

C The Danube river bank (Rkm 1885.75 – 1882.9) before (A) and after (B) restoration.

The largest restoration project along the Danube is actually carried out between Vienna and Bratislava. About 50% of the riprap will be removed to allow natural bank processes (Photos C. Baumgartner).

A. before restoration



B. after restoration

D Observer organizations within the ICPDR

(Source: www.icpdr.org and respective websites of the organizations, accessed 18 August 2009)

Organization	Main objectives	Entrance date	Website
World Wildlife Fund for Nature WWF International & Danube Carpathian Programme DCPO	NGO that promotes the development of solutions to the challenges the DRB region is facing	19.07.1999	http://www.panda.org/what_we_do/where_we_work/danube_carpathian/
International Association for Danube Research IAD (SIL)	Scientific NGO that links basic with applied sciences	27.09.1999	http://www.iad.gs
Danube Commission CD	Implementation of Belgrade Convention (1948)	10.11.1999	http://www.danubecom-intern.org
Danube Environmental Forum DEF	DRB-wide platform of environmental NGOs	23.11.1999	http://www.def.org.hu
Regional Environmental Center for Central and Eastern Europe REC	Facilitating environmental dialogue, networking and regional cooperation	10.02.2000	http://www.rec.org
Ramsar Convention on Wetlands RAMSAR	Intergovernmental treaty; conservation of wetlands and their resources	31.05.2000	http://www.ramsar.org
Commission on the Protection of the Black Sea against Pollution BSC / ICPDR Black Sea Program Coordination Unit	Intergovernmental body to implement the environmental protection and rehabilitation of the Black Sea	13.11.2000	http://www.blacksea-commission.org/main.htm
Global Water Partnership GWP-CEETAC	Network that supports sustainable development and integrated water resource management	11.07.2001	(http://www.gwpforum.org/servlet/PSP?iNodeID=125)
UNESCO/IHP International Hydrological Programme	International scientific cooperative programme in water issues, capacity building, education in hydrology	11.07.2001	http://typo38.unesco.org/index.php?id=240
International Working Association of Water Works in the Danube Basin IAWD	Independent technical organization for the improvement and assurance of water quality in the Danube and its tributaries	30.11.2001	http://www.iawd.at/IAWD/Start.html
Die Donau - Danube Tourist Commission	Tourism marketing association among seven Danubian countries	13.12.2004	http://www.danube-river.org/en_home.html
VGB PowerTech e.V. (European technical association for power and heat generation, Essen, Germany)	Voluntary association of power plant companies dealing with power and heat generation	12.12.2005	http://www.vgb.org/en/startpage.html
Via donau - Österreichische Wasserstrassen-Gesellschaft	Association promoting waterways and inland navigation infrastructures	11.12.2006	http://www.via-donau.org
European Barge Union EBU	Representation of inland navigation interests at a pan-European level	11.12.2006	http://www.ebu-uenf.org
International Commission for the Sava River Basin ISRBC	Implementation of the Framework Agreement on the Sava River Basin (FASRB)	11.12.2006	http://www.savacommission.org
European Water Association EWA	Independent NGO/NPO for management and improvement of water environment	05.12.2007	http://www.ewaonline.de/portale/ewa/ewa.nsf/home?readform
Friends of Nature International	NGO for nature protection, cultural heritage, promotion of "sustainable" mobility and "soft" tourism	05.12.2007	http://www.nfi.at
Central Dredging Association CEDA	Independent NPO/NGO and professional society for dredging related issues	05.12.2007	http://www.dredging.org
European Angler Alliance EAA	NGO promoting conservation of fish species and their habitats	05.12.2007	http://www.eaa-europe.org

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Conclusions and future perspectives

Fresh water is essential for life. During the past decades, research has provided clear evidence that despite the unique importance of fresh water, of freshwater ecosystems and their rich biodiversity, humans have fundamentally – and in many cases – irreversibly altered these systems, their morphology, hydrology, and ecology. At the same time, land cover change, urbanization, industrialization, introduction of invasive species, and building of reservoirs and other infrastructure directly impact freshwater as a resource and freshwaters as unique ecosystems alike. Hence, there are growing interests and needs to restore and manage freshwater ecosystems more sustainably. In order to be successful, however, these attempts require a well-founded understanding of freshwater biodiversity patterns and dynamics as well as of the underlying natural and human drivers. Solid diagnoses of the often broad scale syndromes are needed based on adequate scientific studies, especially at large geographical scales. The communication of research results forms a prerequisite for the development of science-based solutions and consistent policy objectives. Science-based solutions are particularly critical because the resources available for conservation are scarce.

The first objective of this thesis was to examine large-scale freshwater biodiversity patterns in geographic Europe and to evaluate the multifaceted processes that cause biodiversity change. Moreover, to quantify the effects of anthropogenic stressors and natural, geo-climatic drivers on the contemporary patterns of European freshwater biodiversity and to evaluate the generality in biodiversity response (Chapters 1 and 2). The second part of the thesis focused on the analyses of current management strategies of the Danube River basin, the most international and transboundary river globally, in order to support the development and implementation of effective future conservation and management strategies (Chapters 3 and 4).

Major findings

In my first study (Chapter 1), I assessed how, and to what extent, the European freshwater fish fauna (total N=515 species) has changed between the mid-19th century and today (Chapter 1). The changes detected are profound: today, all 251 primary river catchments, which were used as study units, contain on average 5.7 more species than in the past because each catchment hosts exotic fish species (i.e. species originating from outside Europe, N=26) and 76% of the catchments contain translocated fish species (i.e. non-native species originating from Europe, but not native to the respective catchment, N=77). Moreover, the species composition of the individual catchments has changed due to species introductions and extirpations. Quantification of the relative species turnover using a newly developed Reshuffling Index (RI) revealed that, on average, 20% of the historic assemblages became reshuffled. Concurrently, the level of similarity of species assemblages increased by 3.1% among the catchments. The detected changes confirm the general findings of previous studies; still their prevalence across the continent and their presentation in an aggregated form was novel. I conceptualized and defined the "catchment range threshold" at which a species starts to increase taxonomic similarity (~47 catchments). The results demonstrated that the native range size of a species (i.e. the number of catchments a species occurs in as a native species) mainly determines the impact a species has on the change of species assemblage similarity. The larger the native range, the more likely a species causes taxonomic homogenization when it is introduced to a new catchment. The common understanding that taxonomic homogenization is attributed to translocated species remains true, but based on the results of this study it became evident that this statement has to be treated with caution, because the primary driver of taxonomic homogenization is different than previously proposed. Therefore, these findings have major management implications. Translocated species with a large native range contribute immediately to taxonomic homogenization when introduced elsewhere, even if they are introduced to only a single new catchment. In contrast, exotic species, which lack a native European range, as well as many translocated species, remain beneath the calculated catchment range threshold that leads to homogenization and cause taxonomic differentiation. As a consequence, they are attenuating the detected taxonomic homogenization levels. These findings are important because they allow a more differentiated understanding of the components and drivers of taxonomic homogenization and also an appraisal of the opportunities and limits of the calculation of taxonomic similarity change. It became evident that prevention of intended or unintended species introduction will not lower the rate of taxonomic homogenization *per se*: many species actually cause taxonomic differentiation despite their range gain, but still considerably contribute to taxonomic change with potential negative effects on ecosystem functions and services.

Overall, the results support the notion that human activities fundamentally altered the freshwater fish assemblages across Europe. Humans have clearly "reshuffled the deck".

For my second study (Chapter 2) I analyzed the European-wide data of five faunal groups of native freshwater species (fish, odonates, amphibians, molluscs, wetland birds; total N=1518 species). I quantified the effects of anthropogenic stressors and natural, geo-climatic conditions, single and in combination, on the contemporary patterns of freshwater biodiversity and evaluated the generality in biodiversity response using a variance partitioning scheme based on boosted regression tree analysis (BRT) and generalized linear regression modelling (GLM). The variation in biodiversity attributable to purely anthropogenic effects was consistently low (mean: 0.3%) across all faunal groups and biodiversity metrics. In contrast, purely geo-climatic effects, but also joint effects of geo-climatic, socio-economic and land use variables were much more influential on the variation in biodiversity (mean: 9.9 and 30.9%, respectively). This suggests that natural gradients inherent in the data were stronger than gradients of anthropogenic stressors, but also that, in Europe, anthropogenic and natural gradients are strongly linked. This finding was to a certain extent expected, but more importantly it implies that effects of anthropogenic stressors on (freshwater) biodiversity must be studied in the context of its natural, geo-climatic setting. It was surprising and contrary to the original hypothesis that purely geo-climatic drivers had minor effects on faunal groups with rather limited dispersal capacities such as amphibians or molluscs. This is most likely because the species assemblages of the faunal groups were comprised of species with heterogeneous dispersal capacities. This finding was supported by the fact that for all five faunal groups considered in this study the biodiversity metric "endemicity" showed the highest proportion of variance explained by pure geo-climatic effects. This suggests that geo-climatic conditions had minor effects on species with high dispersal capacities, but were the most important drivers for rare species with a restricted range of occurrence, independent of the faunal group. It was unexpected that there was no consistent decline in biodiversity response with increasing anthropogenic stressors.

Interestingly, the biodiversity metrics "species richness" and "endemicity" of several faunal groups showed a positive relationship (i.e., an increase) with an increased proportion of agricultural land use in the catchments. Since agricultural land use was moderate in most catchments (median 7.3%) this might mean that this form of land use caused only intermediate disturbance, maintaining high overall species richness and endemism. On the other hand, the metric "taxonomic distinctness" increased with increasing socio-economic activity in the catchments in all faunal groups. Taxonomic distinctness was only weakly correlated to species richness and endemicity and has been identified as a very useful response indicator, in addition to species richness and endemicity, as it responded coherently to anthropogenic stressors, and across all faunal groups studied.

However, to better understand the functioning of communities which are exposed to anthropogenic stress, it seems promising to include species identities and especially species traits in future studies on freshwater biodiversity and its response to anthropogenic stressors at large spatial scales (e.g. Poff 1997, Vandewalle *et al.* 2010).

For the second part of my work, I focused on the Danube River Basin, one of the most complex and diverse basins in Europe in respect to climate and environmental conditions, topography, land use and water demand, as well as to past and contemporary socio-economic and political aspects. Collecting and synthesizing information on the main river corridor, its major tributaries and the delta (Chapter 3), I found that pollution is still a major issue in large parts of the catchment. Many tributaries, as well as sections along the main stem, exhibit high levels of BOD and COD; cyanide concentrations are often far above EU limits, and nitrogen and phosphorus loads are about 10 times higher than baseline values. Moreover, 'priority substances' such as persistent organic compounds (PAHs and PCBs) and hormone active substances (endocrine disruptors) are of increasing concern. Only 15% of the Upper Danube (upstream of the Gabčíkovo hydro-power station) remain free flowing and, across the entire basin, many floodplains got lost or are functionally extinct. One out of six sturgeon species native to the Danube went extinct, a second species is critically endangered, and the other four sturgeon species are threatened. These are only some examples of large-scale alterations that may cause major consequences for the functioning of river ecosystems within the Danube River Basin, albeit the potential consequences are not yet well understood.

Six percent of the total human population in the Danube basin lives in flood-prone areas and an even higher share of national assets and infrastructure are exposed to severe flood risks. Floods need plains; however, the required space is often used for agricultural and urban development. The analyses of the Danube basin clearly illustrate how complex the conflicts among economic and environmental issues are; and it is evident that the management of a basin such as the Danube requires the combined efforts of engineers, hydrologists, ecologists, chemists, geomorphologists, economists and social scientists.

Building on the information and insights of Chapter 3, I examined current Danube River basin management strategies (Chapter 4). In the suggestions for future strategies, the focus was particularly on the complex interactions between science and policy. The large size of the basin, the high number of riparian states and cultural diversity pose major challenges for transboundary management and cross-national cooperation in the Danube basin. While "sustainable management" – at least in theory – provides a balance between use and protection, many objectives remain disparate, asking for better harmonization and improved synergy. For example, joining the European Union stimulated the economic development of Middle and Lower Danube countries, which again caused severe impacts on the near-natural sections along the Danube corridor (e.g., supporting navigation, changing floodplain land use, increasing pollution). At the same time, the restoration of riparian areas throughout the basin requires space. While narrow riparian strips and small-scale rehabilitation measures might be aesthetically appealing, they are in most cases insufficient to support dynamic hydrogeomorphic and related ecological processes. The definition of "sustainable management" is still vague, as is the actual implementation into river management plans. This suggests that tight links and feedbacks between science and application are required. However, the science-policy integration is often hindered by inadequate communication and insufficient transfer of scientific results into practice. Joint framing and planning of science and research agendas, involvement of various stakeholders such as national and local governments, farmers and the power supply industry on research steering boards and the setting of transparent and agreed environmental targets would be required to strengthen science-society-policy integration. River basin authorities such as the International Commission for the Protection of the Danube River (ICPDR) can serve as important and useful platforms for dialogue and debate of appropriate goals and their implementation, involvement of stakeholders and the public but also as "translators" of scientific results.

Overall, it became obvious that there is, on the one hand, a principal lack of basic information on ecosystem processes, biodiversity and general environmental descriptors; on the other hand, available information remains scattered among different institutional levels, scientific institutions and individual scientists. The resulting information gap hinders a proper assessment of the environmental status and complicates decision making towards sustainable management.

Areas of future research and management implications

Additional research is needed to understand human-environment interactions in more detail, specifically, to identify key mechanisms and effects, such as natural drivers and multiple anthropogenic stressors to which freshwater biodiversity responds, but also to predict effects of rapidly changing environmental conditions on the long-term dynamics of freshwater biodiversity. Species data form the indispensable basis of the first part of the present work (Chapters 1 and 2), and biodiversity studies in general. Continuing efforts are required to assemble knowledge about the autecology of species, their native, contemporary and expected occurrence, their traits, as well as of their genetic diversity.

The results of this thesis confirm that most freshwater ecosystems in Europe are far from pristine. Altered nutrient regimes (Chapter 2), simplified hydromorphology (Chapters 3 and 4), and modified species assemblages (Chapter 1) however affect ecosystem processes and related services (EEA 2012, Hering *et al.* 2015). Additional fundamental but also applied/strategic studies of these highly modified, "novel" ecosystems, are therefore needed; especially when compared to the many studies of less impacted systems (Hildrew and Statzner 2009).

Nevertheless, well-founded advice to managers of freshwater ecosystems up to entire river basins can be made based on the available scientific knowledge and mechanistic understanding. Nowadays ecological studies and scientific programs increasingly emphasize solutions for effective management and improve the knowledge base for decision-making beyond mere problem identification (Pahl-Wostl *et al.* 2013). Surely, there is still a demand to improve the transfer of results of such studies and other policy-relevant scientific investigations to stakeholders and policy makers and, moreover, to develop tools which allow quantifying and predicting the effects of management actions. But ultimately, we will be only able to i) avoid further loss of freshwater species and their ecosystem services and ii) align aspirations of human well-being with environmental objectives, if tighter synergies among the presently competing targets of agriculture, food processing, mining industry, navigation, hydro-/thermal power production, flood control and biodiversity conservation will be established. There is the need for decision making concepts and processes, which allow balancing competing institutional cultures, perceptions and targets of water dependent sectors, including freshwater ecosystems as a tantamount "sector" (Pahl-Wostl *et al.* 2010, Davis *et al.* 2013). Such decision-making concepts and processes could for example restrict development in protected sites, but allocate developments elsewhere, and could address why it is sometimes "worth" paying the price of a lost economic opportunity (Hildrew and Statzner, 2009). Much of what is outlined above, however, can neither be solved by freshwater ecosystem research nor by trans- and interdisciplinary studies; ultimately, societal decisions are required – based on scientific evidence.

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Statement of academic integrity

I hereby certify that the submitted thesis “Patterns, determinants, and management of freshwater biodiversity in Europe” is my own work, and that all published or other sources of material consulted in its preparation have been indicated. Where any collaboration has taken place with other researchers, I have clearly stated my own personal share in the investigation. I confirm that this work, in the same or a similar form, has not been submitted to any other university or examining body for a comparable academic award.

Berlin, 25 October 2015

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Nike Sommerwerk

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Publications and Presentations

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Presentations (selection):

2015
Water quality challenge. Panellist at the roundtable "Water Quality Assessment" at the conference "Sustainable Development Goals – A Water Perspective", Bonn, Germany.

2013
IWQGES – International Water Quality Guidelines for Ecosystems: concept and implementation. Presentation at the World Water Week, Stockholm, Sweden.

2013
Development of International Water Quality Guidelines for Ecosystems – IWQGES. Presentation at the conference „Water Scarcity and Global Change", Berlin, Germany.

2012
European freshwater biodiversity: patterns, stressors and conservation priorities at the catchment scale. Presentation at the 2012 ASLO (Association for the Sciences of Limnology and Oceanography) Aquatic Sciences Meeting, Lake Biwa, Japan.

2012
European freshwater biodiversity. Panellist in the session "Conservation of freshwater ecosystems: towards sustainable management for future Generations" at the "Planet under Pressure Conference", London, UK.

2011
Homogenization of the European fish fauna. Invited lecture at the conference "Status and Future of the World's Large Rivers", Vienna, Austria.

2010
Same, same or different? Changes of the European freshwater fish fauna. Presentation at the conference „Large River Basins – Danube meets Elbe" of the International Association for Danube Research (IAD), Dresden, Germany.

2009
The European Catchment Database on Freshwater Biodiversity. Poster presentation at the Diversitas 2nd Open Science Conference, Cape Town, South Africa.

2006
Efficiency of hydromorphological river restoration measures. Invited lecture at the workshop „EU-WFD implementation in Baden-Württemberg: Definition of environmental objectives towards a programme of measures." Ministry of the Environment, Baden-Württemberg, Germany.

2005
PHARE Twinning and other EU financing instruments in south-eastern Europe, focus on Hungary. Invited lecture at the workshop "IWRM in economically marginal zones." University of Kassel, Germany.

2004
Water Framework Directive (EU-WFD) – Summary of the River Basin District Analysis 2004 in Germany. Invited lecture at the training course "Design of Water Quality Monitoring Networks." Danish Hydraulic Institute (DHI), Copenhagen, Denmark.