Zeitschrift: Bulletin of the Geobotanical Institute ETH

Herausgeber: Geobotanisches Institut, ETH Zürich, Stiftung Rübel

Band: 65 (1999)

Artikel: Research Project : the role of island dynamics in the maintenance of biodiversity in an Alpine river system

Autor: Edwards, Peter J. / Kollmann, Johannes / Tockner, Klement

DOI: https://doi.org/10.5169/seals-377827

RESEARCH PROJECT

The role of island dynamics in the maintenance of biodiversity in an Alpine river system

PETER J. EDWARDS[1], JOHANNES KOLLMANN[1*], KLEMENT TOCKNER[2] & JAMES V. WARD[2]

[1]Geobotanisches Institut ETH, Zürichbergstrasse 38, 8044 Zürich, Switzerland; [2]Department of Limnology, ETH/EAWAG, Überlandstrasse 133, 8600 Dübendorf, Switzerland; [*]corresponding author: kollmann@geobot.umnw.ethz.ch

Summary

1 The current concepts of large river systems have been advanced with limited empirical knowledge of natural systems, because most large rivers in Europe and USA have been more or less radically altered by engineering. For example virtually all large Alpine rivers were channelised during the 19th century. Without first hand knowledge of natural systems we lack baseline data to assess human impacts and to address restoration and conservation strategies.

2 In this project we are interested in the dynamics of vegetated islands on active floodplains and their role in maintaining biodiversity. The central hypothesis of the project is that these islands are a product of the interaction between the fluvial regime and the dominant plants, the Salicaceae. Through accumulation of sediments and woody debris which form islands these plants act as ecosystem engineers. These dynamic processes help to maintain a complex braided channel system which supports a high level of habitat diversity. From our preliminary studies we conclude that three aspects of the natural river system are particularly important for the maintenance of island dynamics: a natural disturbance regime, an unconstrained channel, and a sufficient supply of large woody debris. In addition sediment grain size and nutrient concentrations may have important effects as well.

3 The project investigates the following three overview hypotheses: (i) Five willow species (*Salix alba, S. daphnoides, S. elaeagnos, S. purpurea, S. triandra*) and *Populus nigra* are the key ecosystem engineers in the active zone of the River Tagliamento. We hypothesize differences in their habitat niches within the floodplain system, and a differential ability to influence island dynamics by vegetative (generative) regeneration and to withstand disturbance. (ii) Islands increase the diversity and heterogeneity of habitats at the reach scale and at the island/bar scale. Ecosystem expansion and contraction dictate the variability and connectivity of these habitats; islands create important refugia for aquatic invertebrates in dynamic natural systems. (iii) Islands, i.e. riparian ecotones within the active plain, function as sources, sinks and transformers of organic matter and nutrients. Ecosystem expansion and contraction facilitate the exchange of organic matter and nutrients across the floodplain.

Keywords: aquatic biodiversity, decomposition, ecosystem engineers, large woody debris, refugia and dispersal, Salicaceae

Bulletin of the Geobotanical Institute ETH (1999), **65**, 73–86

Introduction

The concepts that underpin current scientific knowledge of large river systems have been advanced with limited empirical knowledge of natural systems. In particular, virtually all large western European rivers which rise in the Alps were channelised during the 19th century (Whitton 1984; Petts *et al.* 1989); Vischer (1989) reported examples for Switzerland. Without first hand knowledge of natural systems we lack baseline data to assess human impacts and to address restoration and conservation strategies.

This project takes place on the Fiume Tagliamento in northern Italy, which can be regarded as the last morphologically intact Alpine river in Europe (Müller 1995; Ward *et al.* 1999b; Tockner *et al.*, in press). We are particularly interested in the dynamics of vegetated islands on the active floodplain and their role in maintaining biodiversity. Our central hypothesis is that these islands are a product of the interaction between the fluvial regime and the dominant plants, the Salicaceae. Through accumulating sediments and woody debris to form islands these plants act as "ecosystem engineers" *sensu* Jones *et al.* (1994). These dynamic processes help to maintain a complex braided channel system of the kind which tends to support a high level of habitat diversity. The effects of Salicaceae and large woody debris on sediment dynamics and island formation have received little attention in central Europe (see Ellenberg 1996), although these woody plants and related physical structures are recommended for engineering of river banks (Schiechtl 1992; Schiechtl & Stern 1994).

From our preliminary studies we conclude that three aspects of the natural river system are particularly important for the maintenance of island dynamics (Fig. 1): a natural disturbance regime, unconstrained channels, and a substantial supply of large woody debris. We review briefly the literature concerning each of these aspects before considering the central role of the Salicaceae as ecosystem engineers.

ROLE OF DISTURBANCE IN RIVER SYSTEMS

Disturbance theory is one of the unifying themes in contemporary ecology (Sousa 1984; Pickett & White 1985; Pahl-Wostl 1995). In river ecosystems, natural disturbances play major roles in structuring patterns and processes across a range of scales (Resh *et al.* 1988; Junk *et al.* 1989; Ward 1998). It is the lack of disturbance, engendered by a variety of flood control measures that regulate discharge and constrain channel migration, that accounts for the reduced habitat heterogeneity and the loss of functional integrity in many of the world's rivers (Amoros *et al.* 1987; Dynesius & Nilsson 1994; Stanford *et al.* 1996; Tockner *et al.* 1998).

The dynamic nature of rivers is a function of flow and sediment regimes interacting with the physiographic features and vegetation cover of the landscape (Amoros & Petts 1993; Ward & Stanford 1995; Décamps 1996; Ward *et al.* 1999a). The erosive action of seasonal flooding is responsible for the formation of habitat patches across riverine floodplains and for maintaining those patches in a diversity of successional stages. Natural distur-

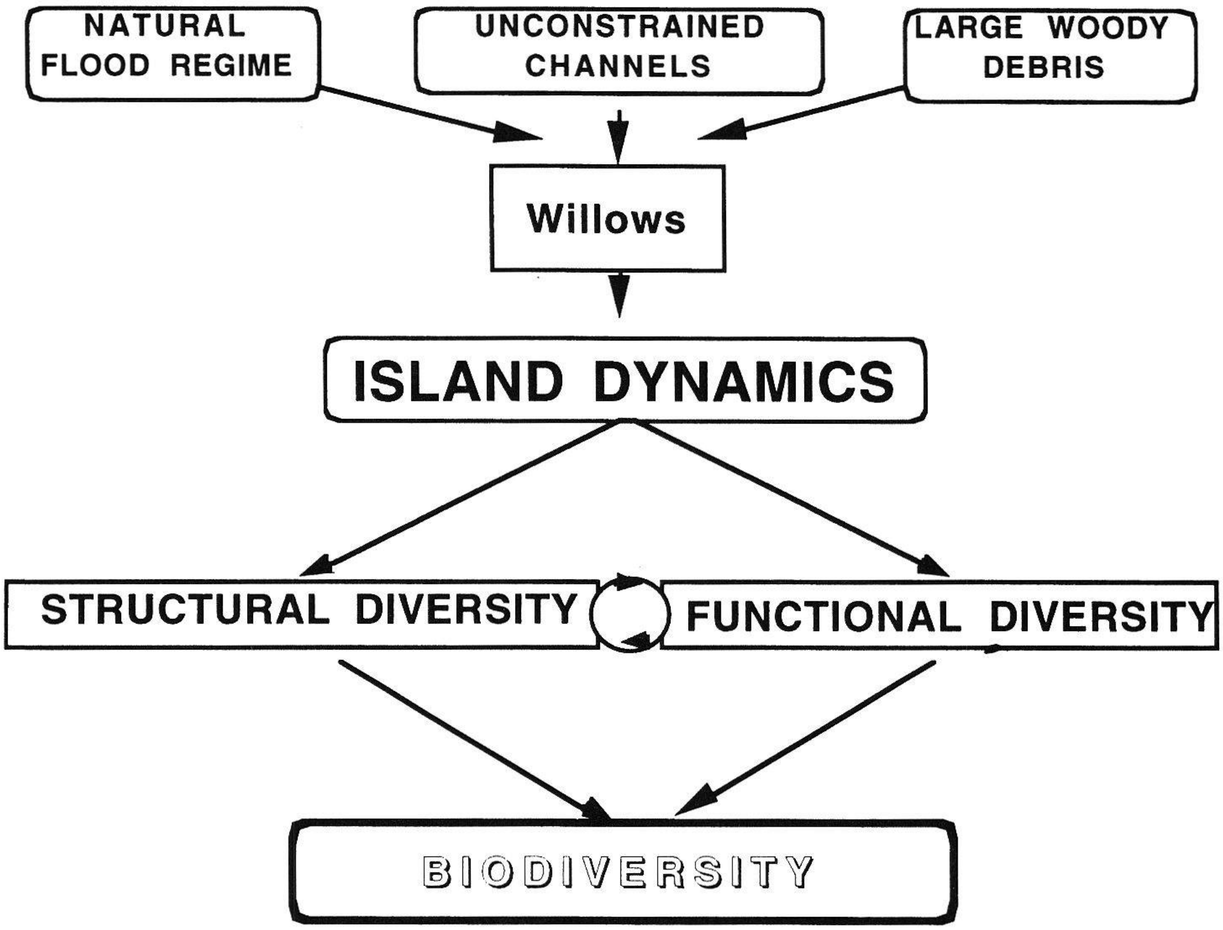

Fig. 1. *Postulated role of island dynamics in structuring biodiversity in Alpine rivers.*

bance forms a shifting mosaic of aquatic, semi-aquatic and riparian communities, collectively sustained by a balance between terrestrialization and rejuvenation processes.

UNCONSTRAINED CHANNELS

Rivers with unconstrained channels and a natural flow regime migrate across their floodplains by a process of cut and fill alluviation (Anderson *et al.* 1996). The erosive action of flooding regulates two distinct, though interrelated, types of succession on riverine floodplains. Hydrarch succession refers to the ontogeny of aquatic habitats. As an unconstrained river migrates laterally across its alluvial floodplain new water bodies are formed as channel segments are abandoned, whereas previously abandoned water bodies are rejuvenated as flood waters reconnect them to the channel. The biotic communities that characterize the different types floodplain water bodies reflect the degree of hydrological connectivity and associated rate of succession (Castella *et al.* 1984; Copp 1989). A diversity of aquatic habitats and biotic communities, therefore, typifies unconstrained alluvial river systems with natural flood regimes.

The role of natural disturbance in maintaining a successional mosaic of riparian plant communities is well documented in unconstrained river systems (e.g. Salo *et al.* 1986; Terborgh & Petren 1991; Naiman & Décamps 1997). A diversity of stand types of different age structure occur across the riverine landscape. The erosive action of flooding simultaneously deposits alluvium in some locations, thereby initiating primary succession, and undercuts mature stands in other locations. The interactions between riparian vegetation and island dynamics have, however, received little attention, no doubt partly because the disturbance regimes that form islands have been all but eliminated from managed rivers (Ward *et al.* 1999b).

LARGE WOODY DEBRIS

It is increasingly recognised that large woody debris (*LWD*) is an extremely important factor structuring the morphology and ecology of rivers (Harmon *et al.* 1986; Maser *et al.* 1988; Bilby & Ward 1991; Gregory & Davis 1992; Gurnell *et al.* 1995; Edwards *et al.*, in press; Kollmann *et al.*, in press). Particularly convincing are historical studies which demonstrate the effects of removing or reducing the supply of *LWD*. For example, in the Willamette River in Oregon, the large quantities of woody debris present in the 19th century helped to create and maintain shoals, multiple channels, oxbow lakes, and complex aquatic habitats at the outside bends of the rivers (Sedell & Froggatt 1984). After eighty years of snag removal, much of this diversity of habitat has been lost and there now exists one main channel, and the river shoreline is less than one quarter of the length that it was formerly.

Recent work has shown that *LWD* deposited in the active channel and floodplain creates conditions suitable for plant colonization in an otherwise inhospitable alluvial environment (Sedell *et al.* 1988; Fetherston *et al.* 1995; Hering & Reich 1997). Abbe & Montgomery (1996) showed how jams of *LWD* on gravel bars in the Queets River of the Olympic Peninsula in northwest Washington lead to the development of vegetation. For example, they describe bar apex jams which "are associated with a crescentic pool, an upstream arcuate bar and a downstream central bar that is the focus of forest patch development". Similarly, Fetherston *et al.* (1995) showed how *LWD* in montane rivers of the Pacific Northwest provides sites for vegetation colonization and forest island growth. Islands thus formed may grow in size through the accumulation of *LWD* and coalesce with other islands to form a larger forested floodplain mosaic.

Study area Fiume "Tagliamento"

The Fiume Tagliamento is considered the "last large natural alpine river in Europe" (Martinet & Dubost 1992; Müller 1995; Ward *et al.* 1999b) and can, therefore, serve as a model river ecosystem for the Alps. The river traverses a course of 172 km from its headwaters in the Italian Alps to the Adriatic Sea. Its headwaters are situated in the limestone Alps of northern Italy, from which it flows unimpeded by high dams to the Adriatic Sea, traversing an idealized sequence of constrained, braided, and meandering reaches. The Tagliamento has a flashy pluvio-nival regime (mean Q = 109 m^3s^{-1}, with flood flows up to 4000 m^3s^{-1}). Vegetated islands comprise 8.5%, surface water 17% (at mean water level), and exposed gravel devoid of woody plants 75% of the area of the active floodplain (Ward *et al.* 1999b). The river is not entirely without human impact however. Water is abstracted from some locations and in the last few kilometres near the sea the channel is constrained by embankments. Nonetheless, the Tagliamento retains an essentially pristine character, with a highly complex channel morphology structured by a dynamic hydrological regime. In addition, the Tagliamento provides an immense river corridor, covering an area of about 150 km^2, connecting the Mediterranean with the Alps; for more detailed information see Tockner *et al.* (in press).

Fig. 2. Main study area of the project at the Tagliamento near Pinzano (August 1997; photo: J. Kollmann).

Preliminary work on the Tagliamento led us to develop a six-reach model, islands being a prominent feature of three of the reach types. Island are most numerous in the area up- and downstream of Pinzano where the main study site of the present project is located (Fig. 2).

Salicaceae as ecosystem engineers

Following an exceptionally high flood on the River Tagliamento in autumn 1996, we observed the first stages of plant colonization and succession (Edwards *et al.*, in press). After the flood thousands of trees lay scattered over the floodplain. The larger of these trees had a very marked influence on the local deposition of sediments and smaller organic debris. They usually lay with their root plate facing in an upstream direction and the gravel of the bar was deeply scoured to form a crescent-shaped depression upstream and to the sides of the root mass. The root plates trapped large amounts of plant material and other debris. Plant material including smaller trees was also deposited along the sides of a large tree or became tangled in the branches. A ridge of sediment was deposited over the gravel bar in a long plume downstream of the root plate, and the trunk and branches were usually partially, and sometimes completely, buried. These trees deposited on the floodplain, together with the sediment and plant debris they trap, represent potential new vegetated islands.

As a result of field work during 1997 we developed a conceptual model to describe the vegetation dynamics as observed on the active floodplain of the Tagliamento (Edwards *et al.*, in press; A.M. Gurnell, unpubl. results). Vegetated islands are built up of *LWD,* other organic material and sediments transported from further upstream during flood events. Rapid regrowth from uprooted trees stranded on the floodplain is particularly important at the early stages of island development. Islands may also be eroded, particularly by lateral channel erosion, and the materials reincorporated into new islands downstream. Indeed, this cyclical process is influenced by the islands themselves, since the process of vegetation development leads to progressive channel narrowing (Friedman *et al.* 1996), and thus an increased intensity of erosion.

In the environment of the active floodplain, the Salicaceae show themselves uniquely equipped to flourish; they are "invaders", "endurers" and "resisters" *sensu* Naiman &

Décamps (1997). Thus the islands of the Tagliamento are dominated by five willow species (*Salix alba, S. daphnoides, S. elaeagnos, S. purpurea, S. triandra*) and by poplar (*Populus nigra*), and these species play a crucial role in island dynamics. In fact, the Salicaceae occur as the dominant pioneer trees on floodplains throughout the world (e.g. Nanson & Beach 1977; Dionigi *et al.* 1985; Schnitzler *et al.* 1992; Décamps 1996). More than any other group of temperate trees, they exhibit the capacity for rapid shoot growth, even from exposed logs (e.g. Houle & Babeux 1993). These shoots are very flexible and are not easily broken by flood waters or pieces of floating debris. Perhaps even more important, these species produce roots very rapidly from branches and trunks, and these roots can reach a considerable depth in coarse gravel substrates. Busch *et al.* (1992) demonstrated that *Populus* and *Salix* could take up groundwater even when this was at a depth of 3.5 m.

Jones *et al.* (1994) have defined ecosystem engineers as "organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In doing so they modify, maintain, and create habitats". The role of the Salicaceae in accumulating sediments and *LWD* to form islands is an example of ecosystem engineering. According to the classification of Jones *et al.* (1994) they act as autogenic engineers because the plant structures themselves alter the environmental conditions through trapping sediment and organic debris.

Island dynamics and biodiversity

An important effect of vegetation is to create habitats of much greater stability than would otherwise exist on the floodplain. Aerial photographs show that at the upstream end of a large island complex, the vegetation is often highly dissected, since the apex receives the full impact of flood waters and erosive forces are thus most intense (Kollmann *et al.*, in press). There is a high probability that developing vegetation in this part of the island complex will be washed away or covered by shingle, and much of the vegetation is successionally young. In contrast, the tail of an island complex is sheltered, and provides sites of greater stability. This is one way in which the islands help to provide a diversity of habitats.

In temperate areas, 66% of the continental extinctions are aquatic taxa (Denny 1994). This emphasizes the exceptional sensitivity of freshwater and in particular riverine and wetland ecosystems to external pressures, for they behave like biogeographical islands (Allan & Flecker 1993; UNEP 1995; Ward 1998). In order to effectively manage and restore riverine floodplains it is essential to understand how patterns of diversity are generated and maintained across the alluvial landscape. A hierarchical approach has been applied to specific groups of aquatic organisms in the Danube River basin at the following levels: catchment, floodplain complex, floodplain, water body and habitat patch (Ward *et al.* 1999c). The Danube River is, however, highly regulated with only remnants of its previous structural complexity and functional integrity (Tockner *et al.* 1998). For example, from a total of over 2000 islands in the 350 km section of the Austrian Danube, only six islands remain.

In the natural state, riverine floodplains are disturbance-dominated ecosystems characterized by high levels of habitat diversity and highly diverse biota adapted to the spatiotemporal heterogeneity (Welcomme 1979; Salo *et al.* 1986; Junk *et al.* 1989; Mitsch &

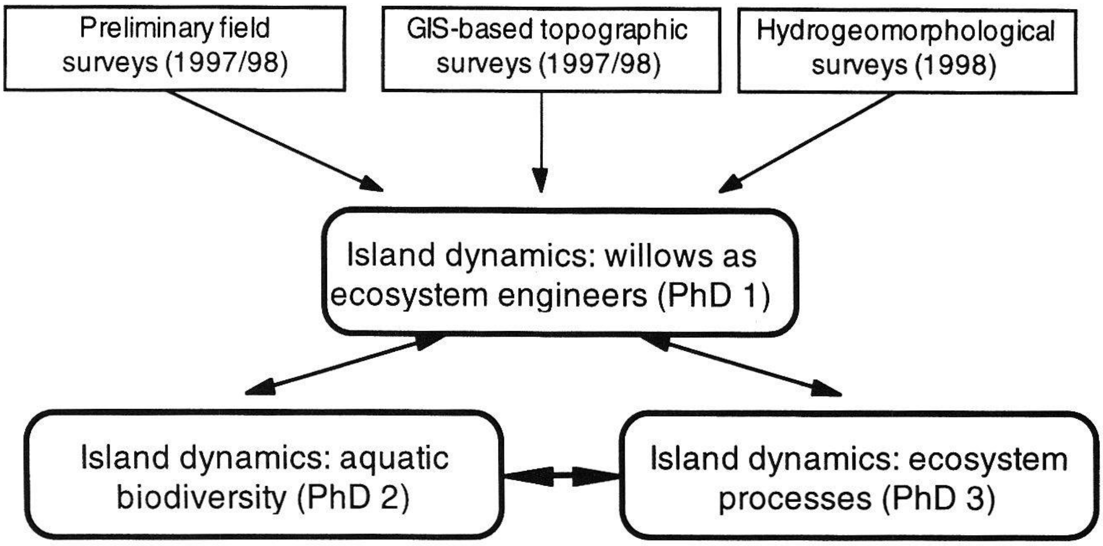

Fig. 3. *Structure of the research plan on island dynamics and its consequences for biodiversity in the River Tagliamento.*

Gosselink 1993; Décamps 1996). Ecotones, connectivity, and succession, all of which are sustained by disturbance, play major roles in structuring the heterogeneity of habitats leading to high biodiversity levels (Lachavanne & Juge 1997; Ward *et al.* 1999c). The contribution of island dynamics to the processes leading to high levels of biodiversity have been almost totally ignored by aquatic ecologists (Thorp 1992). Figure 1, based on our preliminary work on the Tagliamento (Ward *et al.* 1999b), is presented as a hypothesis of the interactions that form riverine islands, and thereby sustain biodiversity. Managed rivers typically lack all three attributes – a natural flood regime, an unconstrained channel, and a source of large woody debris – that we believe to be necessary for island formation.

Structure of the project

The structure of the proposed research is summarized in Fig. 3. It draws upon extensive preliminary data which were gathered during our field surveys (Ward *et al.* 1999a,b), on GIS analysis of aerial photographs and maps (Kollmann *et al.*, in press), and on the work of our collaborators in the UK who have concentrated on hydrogeomorphological aspects (Gurnell *et al.*, in press). The research consists of three independent but cooperating PhD projects. One PhD student, Sophie Karrenberg, will focus on the processes of island dynamics and in particular the role of Salicaceae as ecosystem engineers. The second study, by Luana Bottinelli, is concerned with the central role of islands in maintaining habitat heterogeneity and biodiversity across the riverine landscape. The third project, to be conducted by Dimitry van der Nat, will concentrate on ecosystem processes and in particular on the role of islands in producing, retaining and transforming organic matter.

ISLAND DYNAMICS: WILLOWS AS ECOSYSTEM ENGINEERS (PHD PROJECT SOPHIE KARRENBERG)

This project will investigate the effects of ecosystem engineering by Salicaceae (*Salix alba, S. daphnoides, S. elaeagnos, S. purpurea, S. triandra, Populus nigra*) on sedimentation and erosion, deposition of *LWD,* groundwater table, and microclimate, i.e. the creation of habitats.

The overall research hypotheses are the following:

1. The six Salicaceae occupy distinct niches in the active zone of the river (cf. Schnitzler *et al.* 1992) and therefore play different roles in maintaining island dynamics.
2. The six Salicaceae differ in their regeneration niches (cf. Krasny *et al.* 1988; Niiyama 1990; van Splunder *et al.* 1995, 1996). Vegetative propagation is much more effective than generative regeneration for establishment on coarse sediment in a braided river.
3. The Salicaceae play a crucial role in island development through accumulating sediment and *LWD*, and thus creating conditions of greater stability. The study species differ in their biophysical characteristics and their ability to withstand disturbance (cf. Speck 1994; Oplatka & Sutherland 1995), and these differences reflect the niches they occupy.

These questions will be investigated by descriptive surveys in the field, by experiments under field conditions and by experiments in controlled environments. Although the main focus will be on the comparative ecology of the various willow species, we are also interested in the range of variation that exists within species. Our sampling of plant material will be designed to investigate intra- as well as interspecific differences.

ISLAND DYNAMICS: AQUATIC BIODIVERSITY (PHD PROJECT LUANA BOTTINELLI)

This project is concerned with the diversity of aquatic habitat conditions generated through island dynamics, and the species diversity thereby supported. Aquatic biodiversity patterns will be studied at two different spatial scales: (i) reach-scale, which includes a direct comparison between island- and bar-braided segments; (ii) island-scale, which directly compares vegetated islands and gravel bars.

The overall research hypotheses are the following:

1. Islands increase habitat heterogeneity both at the reach and at the island/bar scales.
2. Islands play a key role in sustaining biodiversity of aquatic invertebrates.
3. Islands create refugia for aquatic invertebrates that enhance the persistence of species in an expanding and contracting environment.

Habitat heterogeneity (structural diversity), connectivity and fluvial dynamics are the key factors determining biodiversity patterns and ecosystem processes (e.g. organic matter dynamics) in the river-floodplain complex. Therefore, the investigation of habitat diversity is an integral part of the research of the projects 2 and 3.

The multiplicity of species diversity curves at different hierarchical levels (different groups peak in different habitats) make floodplains important foci of biodiversity (Ward 1998). Therefore, we will use the framework proposed by Ward *et al.* (1999c) to examine diversity patterns across scales. Species turnover between habitats (beta diversity) has largely been ignored in the analyses of biodiversity patterns (Harrison *et al.* 1992; Blackburn & Gaston 1996), especially in freshwater ecosystems (Ward *et al.* 1999c). However, Blackburn & Gaston (1996) propose beta diversity as a useful indicator of ecological integrity.

Macrocrustaceans (Amphipoda, Isopoda) and aquatic insects (Ephemeroptera, Trichoptera, Chironomidae) are taken as indicator taxa for estimating species diversity and ecological integrity. These are the dominant benthic groups in the Tagliamento River (Provincia di Udine 1997) and each of these assemblages provides distinctive information about ecosystem structure and function (Schiemer 1994; Dahm *et al.* 1995; van den Brink *et al.* 1996). Because of the major role played by temperature in structuring aquatic macroinvertebrate assemblages (e.g. Ward & Stanford 1982; Ward 1985; Sweeney *et al.* 1992; Hawkins *et al.* 1997), special attention will be given to the relationship between habitat-specific differences in the temperature regime and biodiversity patterns.

Townsend *et al.* (1997) state that the preservation and restoration of natural and diverse riverine communities depend on protecting refugia. Refugia, which lessen the effects of disturbance, have been postulated to exist at various spatial scales (Sedell *et al.* 1990; Lancaster & Hildrew 1993; Townsend & Hildrew 1994), but their availability and use by aquatic invertebrates of floodplain rivers have received little attention. The presence of a range of refugia, each likely to be used by different sets of species, is thought to be responsible for the high resilience of natural riverine ecosystems and are fundamental for maintaining biodiversity. Most experimental work has examined refugia at the scale of individual patches within the main channel (within-habitat refugia, e.g. Winterbottom *et al.* 1997). In floodplains, dispersal-mediated exchange between different channel types are thought to be the key processes in determining metapopulation structure (*sensu* Hanski & Gilpin 1997) and species diversity. We propose that at the reach-scale refugia from high and low flows may be provided by island-created habitats.

ISLAND DYNAMICS: ECOSYSTEM PROCESSES (PHD PROJECT **DIMITRY VAN DER NAT**)

This project is concerned with the influence of islands upon ecosystem level processes, and in particular the supply and processing of organic matter for the aquatic community. In the island-braided section of the Tagliamento River up to 38% of the active floodplain is covered by vegetated islands. A high perimeter-to-area ratio enhances interactions between the riparian zone and the floodplain (Polis *et al.* 1997) and thus islands represent an important source of organic matter for aquatic organisms which process this material.

The overall research hypotheses are the following:

1. Islands serve as riparian ecotones within the active plain and are important sources, sinks and transformers of organic matter.

Islands are postulated to supply large quantities of bioavailable organic matter in alluvial ecosystems. They are seen as natural "diffusers" that release labile organic matter and nutrients, supplying high-quality food for terrestrial, benthic and groundwater communities and thus enhancing instream primary productivity (cf. Naiman & Décamps 1997).

2. Islands enhance the retention of particulate organic matter at the reach scale and at the island scale. Island-formed habitats (backwaters, bays, scour pools) are important instream retention zones (Thorp & Delong 1994).

Retention of particulate and dissolved organic matter and nutrients is a major determinant of food availability to stream biota (Lamberti *et al.* 1989). Floodplains and floodplain waters are thought to be highly retentive systems, but the role of islands in retention of organic matter has not been investigated. Temporary retention of litter on the floodplain may promote a more efficient recycling of organic matter within the river system (Mayack *et al.* 1989).

3. The diversity of willow species of different ages resulting from island dynamics provide a wide range of decomposition rates of leaf litter. Decomposition of leaf litter reflects position along the inundation gradient.

Islands and bars are frequently associated with backwaters. The aggregate effect of these transient storage zones or "dead zones" is to delay the downstream passage of solutes and suspensoids (Reynolds & Carling 1991). The water exchange rate between these dead zones and the main flow, although thought to be a key functional process, is virtually uninvestigated (Bencala & Waters 1983; Tipping *et al.* 1993).

Decomposition rates of willow leaves are species-specific and depend on the age of the plant. Leaves of young willow shrubs contain higher nitrogen and phosphorus contents and, therefore, decomposition might be faster. There is also evidence that the change between terrestrial and aquatic phases accelerates the decomposition of organic material (Polunin 1984; Chauvet 1988; Junk *et al.* 1989; Xiong & Nilsson 1997). We suggest that island dynamics promote functional diversity.

Final remarks

Losses of biodiversity in Swiss riverine ecosystems have been severe (Gallandat *et al.* 1993), since more than 90% of the Alpine rivers are regulated. Recently, the aim of nature conservation authorities has been to restore riverine ecosystems (see Brülisauer & Klötzli 1998). However, a review of the current literature shows that many restoration measures in European rivers have failed because of the limited knowledge about natural systems. Since in Switzerland virtually no undisturbed large Alpine river is left (with exception of some fragments), we decided to investigate the River Tagliamento in NE-Italy, the last "undisturbed" large river in the Alps, and one of the last unregulated rivers in Europe. The results of this study will help to understand the mechanisms and the importance of island dynamics in river systems. This knowledge should be incorporated in future management plans.

Funding of the project

The project is funded by the ETH Zürich (no. 0-20572-98)

References

Abbe, T.B. & Montgomery, D.R. (1996) Large woody debris jams, channel hydraulics and habitat formation in large rivers. *Regulated Rivers: Research & Management,* **12**, 201–221.

Allan, J.D. & Flecker, A.S. (1993) Biodiversity conservation in running waters. *BioScience,* **43**, 32–43.

Amoros, C. & Petts, G.E. (1993) *Hydrosystemes Fluviaux.* Masson, Paris.

Amoros, C., Rostan, J.-C., Pautou, G. & Bravard, J.-P. (1987) The reversible process concept applied to the environmental management of large rivers. *Environmental Management,* **11**, 607–617.

Anderson, M.G., Walling, D.E. & Bates, P.D. (1996) *Floodplain Processes.* Wiley, Chichester.

Bencala, K.E. & Waters, R.A. (1983) Simulation of solute transport in a mountain pool-and-riffle stream: a transient storage model. *Water Resources Research,* **19**, 718–724.

Bilby, R.E. & Ward, J.W. (1991) Characteristics and function of large woody debris in streams draining old-growth, clear-cut and second-growth forests in southwestern Washington. *Canadian Journal of Fisheries and Aquatic Science,* **48**, 2499–2508.

Blackburn, T.M. & Gaston, K.J. (1996) The distribution of bird species in the New World: patterns in species turnover. *Oikos,* **77**, 146–152.

Brülisauer, A. & Klötzli, F. (1998) Notes on ecological restoration of fen meadows, ombrogenous bogs and rivers: definitions, techniques, problems. *Bulletin Geobotanical Institute ETH,* **64**, 47–61.

Busch, D.E., Ingraham, N. & Smith, S.D. (1992) Water uptake in woody riparian phreatophytes of the Southwestern United States: a stable isotope study. *Ecological Applications,* **2**, 450–459.

Castella, E., Richardot-Coulet, M., Roux, C. & Richoux, P. (1984) Macroinvertebrates as 'describers' of morphological and hydrological types of aquatic ecosystems abandoned by the Rhône River. *Hydrobiologia,* **119**, 219–225.

Chauvet, E. (1988) Influence of the environment on willow leaf litter decomposition in the alluvial corridor of the Garonne. *Archiv Hydrobiologie,* **112**, 371–338.

Copp, G.H. (1989) The habitat diversity and fish reproductive function of floodplain ecosystems. *Environmental Biology of Fishes,* **26**, 1–27.

Dahm, C.N., Cummins, K.W., Valett, H.M. and Coleman, R.L. (1995) An ecosystem view of the restoration of the Kissimmee river. *Restoration Ecology,* **3**, 225–238.

Décamps, H. (1996) The renewal of floodplain forest along rivers: a landscape perspective. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie,* **26**, 35–59.

Denny, P. (1994) Biodiversity and wetlands. *Wetlands Ecology and Management,* **3**, 55–61.

Dionigi, C.P., Mendelssohn, I.A. & Sullivan, V.I. (1985) Effects of soil waterlogging on the energy status and distribution of *Salix nigra* and *S. exigua* (Salicaceae) in the Atchafalaya River basin of Louisiana. *American Journal of Botany,* **72**, 109–119.

Dynesius, M. & Nilsson, C. (1994) Fragmentation and flow regulation in the northern third of the world, *Science,* **266**, 753–762.

Edwards, P.J., Kollmann, J., Gurnell, A.M., Petts, G.E., Tockner, K. & Ward, J.V. (in press) A conceptual model of vegetation dynamics on gravel bars of a large Alpine river. *Wetlands Ecology and Management.*

Ellenberg, H. (1996) *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht.* Ulmer, Stuttgart.

Fetherston, K.L., Naiman, R.J. & Bilby, R.E. (1995) Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. *Geomorphology,* **13**, 133–144.

Friedman, J.M., Osterkamp, W.R. & Lewis, W.M. (1996) Channel narrowing and vegetation development following a Great Plains flood. *Ecology,* **77**, 2167–2181.

Gallandat, J.-D., Gobat, J.-M. & Roulier, C. (1993) *Kartierung der Auengebiete von nationaler Bedeutung: Bericht und Beilagen.* Bundesamtes für Umwelt, Wald und Landschaft, Bern.

Gregory, K.J. & Davis, R.J. (1992) Coarse woody debris in stream channels in relation to river channel management in woodland areas. *Regulated Rivers: Research & Management,* **7**, 117–136.

Gurnell, A.M., Gregory, K.J. & Petts, G.E. (1995) The role of coarse woody debris in forest aquatic habitats: implications for management. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **5**, 143–166.

Gurnell, A.M., Petts, G.E., Harris, N., Ward, J.V., Tockner, K., Edwards, P.J. & Kollmann, J. (in press) Large wood retention in river channels: the case of the Fiume Tagliamento. *Earth Surface Processes and Landforms.*

Hanski, I. & Gilpin, M.E. (1997) *Metapopulation Biology: Ecology, Genetics and Evolution.* Academic Press, San Diego, CA.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. Jr. & Cummins, K.W. (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research,* **15**, 133–302.

Harrison, S., Ross, S.J. & Lawton, J.H. (1992) Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology,* **61**, 151–158.

Hawkins, C.P., Hogue, J.N., Decker, L.M. & Feminella, J.W. (1997) Channel morphology, water temperature, and assemblage structure of stream insects. *Journal of the North American Benthological Society,* **16**, 728–749.

Hering, D. & Reich, M. (1997) Bedeutung von Totholz für Morphologie, Besiedlung und Renaturierung mitteleuropäischer Fliessgewässer. *Natur und Landschaft,* **77**, 383–389.

Houle, G. & Babeux, P. (1993) Temporal variations in the rooting ability of cuttings of *Populus* *balsamifera* and *Salix planifolia* from natural clones-populations in subarctic Quebec. *Canadian Journal of Forest Research,* **23,** 2603–2608.

Jones, C.J., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos,* **69,** 373–386.

Junk, W.J., Bayley, P.B. & Sparks, R.E. (1989) The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences,* **106,** 110–127.

Kollmann, J., Vieli, M., Edwards, P.J., Tockner, K. & Ward, J.V. (in press) Interactions between vegetation development and island formation in the Alpine river Tagliamento. *Applied Vegetation Science.*

Krasny, M.E., Vogt, K.A. & Zasada, J. C. (1988) Establishment of four Salicaceae species on river bars in interior Alaska. *Holarctic Ecology,* **11,** 210–219.

Lachavanne, J.-B. & Juge, R. (1997) *Biodiversity in Land–Inland Water Ecotones.* Parthenon Publications, New York.

Lamberti, G.A., Gregory, S.V., Ashkenas, L.R., Wildman, R.C. & Steinman, A.D. (1989) Influence of channel geomorphology on retention of dissolved and particulate matter in a cascade mountain stream. *USDA Forest Service General Technical Report,* PSW-**110,** 33–39.

Lancaster, J. & Hildrew, A.G. (1993) Characterisation instream flow refugia. *Canadian Special Publication of Fisheries and Aquatic Sciences,* **50,** 1663–1675.

Martinet, F. & Dubost, M. (1992) *Die letzen naturnahen Alpenflüsse.* CIPRA. *Kleine Schriften,* **11/92,** 6–60.

Maser, C., Tarrant, R.F., Trappe, J.M. & Franklin, J.F. (1988) From the forest to the sea: the story of fallen trees. *USDA Forest Service General Technical Report,* PNW-GTR-229, Pacific Northwest Forest and Range Experimental Station, Portland, Oregon.

Mayack, D.T., Thorp, J.H. & Cothran, M. (1989) Effects of burial and floodplain retention on stream processing of allochthonous litter. *Oikos,* **54,** 378–388.

Mitsch, W.J. & Gosselink, J.G. (1993) *Wetlands.* Van Nostrand Reinhold, New York.

Müller, N. (1995) River dynamics and floodplain vegetation and their alterations due to human impact. *Archiv für Hydrobiologie, Suppl.,* **101,** 477–512.

Naiman, R.J. & Décamps, H. (1997) The ecology of interfaces: riparian zones. *Annual Review Ecology and Systematics,* **28,** 621–658.

Nanson, G.C. & Beach, H. (1977) Forest succession and sedimentation on a meandering-river floodplain, northeast British Columbia, Canada. *Journal of Biogeography,* **4,** 229–251.

Niiyama, K. (1990) The role of seed dispersal and seedling traits in colonization and coexistence of *Salix* spp. in a seasonally flooded habitat. *Ecological Research,* **5,** 317–332.

Oplatka, M.S. & Sutherland, A. (1995) Tests of willow poles used for river bank protection. *Journal of Hydrology,* **33,** 35–58.

Pahl-Wostl, C. (1995) *The Dynamic Nature of Ecosystems: Chaos and Order Entwined.* Wiley, Chichester.

Petts, G.E., Moller, H. & Roux, A.L. (1989) *Historical Changes of Large Alluvial Rivers.* Wiley, Chichester.

Pickett, S.T.A. & White, P.S. (1985) *The Ecology of Natural Disturbance as Patch Dynamics.* Academic Press, New York.

Polis, G.A., Anderson, W.B. & Holt, R.D. (1997) Toward an integration of landscape and foodweb ecology: the dynamics of spatially subsidized food webs. *Annual Review Ecology and Systematics,* **28,** 289–316.

Polunin, N.V.C. (1984) The decomposition of emergent macrophytes in fresh water. *Advanced Ecological Monographs,* **42,** 71–92.

Provincia di Udine (1997) *Mappagio Biologico di Qualità dei Corsi d'Aqua della Provincia di Udine.* Udine.

Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B. & Wissmar, R. (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society,* **7,** 433–455.

Reynolds, C.S. & Carling P.A. (1991) Flow in river channels: new insights into hydraulic retention, *Archiv für Hydrobiologie,* **121,** 171–179.

Salo, J., Kalliola, R., Häkkinen, I., Mäkinen, Y., Niemelä, P., Puhakka, M. & Coley, P.D. (1986) River dynamics and the diversity of Amazon lowland forests. *Nature,* **322,** 254–258.

Schiechtl, H.M. (1992) *Weiden in der Praxis: die Weiden Mitteleuropas, ihre Verwendung und ihre Bestimmung.* Patzer, Berlin.

Schiechtl, H.M. & Stern, R (1994) *Handbuch für naturnahen Wasserbau: eine Anleitung für ingenieurbiologische Bauweisen.* Österreichischer Agrarverlag, Wien.

Schiemer, F. (1994) Monitoring of floodplains: limnological indicators. *Monitoring of Ecological Change in Wetlands of Middle Europe* (eds. G. Aubrecht, G. Dick & C. Pentrice), *Stapfia,* **31**, 95–107.

Schnitzler, A., Carbiener, R. & Trémolières, M. (1992) Ecological segregation between closely related species in the flooded forests of the upper Rhine plain. *New Phytologist,* **121**, 293–301.

Sedell, J.R. & Froggatt, J.L. (1984) Importance of streamside forests to large rivers: the isolation of the Willamette River, Oregon, U.S.A., from its floodplain by snagging and streamside forest removal. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie,* **22**, 1828–1834.

Sedell, J.R., Bisson, P.A., Swanson, F.T. & Gregory, S.V. (1988) What we know about trees that fall into streams and rivers. *From the Forest to the Sea: the Story of Fallen Trees* (eds. C. Maser, R.F. Tarrant, J.M. Trappe & J.F. Franklin). USDA Forest Service General Technical Report, PNW-GTR-229, Pacific Northwest Forest and Range Experimental Station, Portland, Oregon.

Sedell, J.R., Reeves, G.H., Hauer, F.R., Stanford, J.A. & Hawkins, C.P. (1990) Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems. *Environmental Management,* **14**, 711–724.

Sousa, W.P. (1984) The role of disturbance in natural communities. *Annual Review Ecology and Systematics,* **15**, 353–391.

Speck, T. (1994) Bending stability of plant stems: ontogenetical, ecological, and phylogenetical aspects. *Biomimetics,* **2**, 109–128.

Stanford, J.A., Ward, J.V., Liss, W.J., Frissell, C.A., Williams, R.N., Lichatowich, J.A. & Coutant, C.C. (1996) A general protocol for restoration of regulated rivers. *Regulated Rivers: Research & Management,* **12**, 391–413.

Sweeney, B.W., Jackson, J.K., Newbold, J.D. & Funk, D.H. (1992) Climate change and the life histories and biogeography of aquatic insects in eastern North America. *Global Climate Change and Freshwater Ecosystem* (eds. P. Firth & S.G. Fisher), pp. 143–176. Springer, New York.

Terborgh, J. & Petren, K. (1991) Development of habitat structure through succession in an Amazonian floodplain forest. *Habitat Structure* (eds. S.S. Bell, E.D. McCoy & A. Mushinsky), pp. 28–46. Chapman and Hall, London.

Thorp, J.H. (1992) Linkage between islands and benthos in the Ohio River, with implications for riverine management. *Canadian Journal of Fisheries and Aquatic Sciences,* **49**, 1872–1882.

Thorp, J.H. & Delong, M.D. (1994) The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos,* **70**, 305–308.

Tipping, E., Woof, C. & Clarke, K. (1993) Deposition and resuspension of fine particles in a riverine 'dead zone'. *Hydrological Processes,* **7**, 263–277.

Tockner, K., Schiemer, F. & Ward, J.V. (1998) Conservation by restoration: the management concept for a river-floodplain system on the Danube River in Austria. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **8**, 71–86.

Tockner, K., Ward, J.V., Arscott, D.B., Edwards, P.J., Kollmann, J., Gurnell, A.M., Petts, P.E. & Maiolini, B. (in press) The Tagliamento river: a model ecosystem for Alpine gravel-bed rivers the Alps. *Ecology and Conservation of Gravel Bed Rivers and Alluvial Floodplains in the Alps* (eds. H. Plachter & M. Reich). Junk, Dordrecht.

Townsend, C.R. & Hildrew, A.G. (1994) Species traits in relation to a habitat templet for river systems. *Freshwater Biology,* **31**, 265–275.

Townsend, C.R., Scarsbrook, M.R. & Dolédec, S. (1997) The intermediate disturbance hypothesis, refugia and biodiversity in streams. *Limnology and Oceanography,* **42**, 938–949.

UNEP (1995) *Global Biodiversity Assessement.* Cambridge University Press, New York.

Van den Brink, F.W.B., van der Velde, G., Buijse, A.D. & Klink, A.G. (1996) Biodiversity of the Lower Rhine and Meuse river-floodplains: its significance for ecological management. *Netherlands Journal of Ecology,* **30**, 129–149.

Van Splunder, I., Coops, H., Voesenek, L.A.C.J. & Blom, C.W.P.M. (1995) Establishment of alluvial forest species in floodplains: The role of dispersal timing, germination characteristics and water level fluctuations. *Acta Botanica Neerlandica,* **44**, 269–278.

Van Splunder, I., Voesenek, L.A.C.J., Coops, H., De Vries, X.J.A. & Blom, C.W.P.M. (1996) Morphological responses of seedlings of four species of Salicaceae to drought. *Canadian Journal of Botany,* **74**, 1988–1995.

Vischer, D. (1989) Impact of 18th and 19th century river training works: three case studies from Switzerland. *Historical Change of Large Alluvial Rivers: Western Europe* (eds. G.E. Petts, H. Moeller & A.L. Roux), pp. 105–132. Wiley, Chichester.

Ward, J.V. (1985) Thermal characteristics of running waters. *Hydrobiologia,* **125**, 31–46.

Ward, J.V. (1998) Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation,* **83**, 269–278.

Ward, J.V. & Stanford, J.A. (1982) Thermal responses in the evolutionary ecology of aquatic insects, *Annual Review of Entomology,* **27**, 97–117.

Ward, J.V. & Stanford, J.A. (1995) Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers: Research & Management,* **11**, 105–119.

Ward, J. V., Malard, F., Tockner, K. & Uehlinger, U. (1999a) Influence of ground water on surface water conditions in a glacial floodplain of the Swiss Alps. *Hydrological Processes,* **13**, 277–293.

Ward, J.V., Tockner, K., Edwards, P.J., Kollmann, J., Bretschko, G., Gurnell, A.M., Petts, G.E. & Rossaro, B. (1999b). A reference river system in the Alps: the "Fiume Tagliamento". *Regulated Rivers: Research & Management,* **15**, 63–75.

Ward, J.V, Tockner, K. & Schiemer, F. (1999c) Biodiversity of floodplain river ecosystems: Ecotones and connectivity. *Regulated Rivers: Research & Management,* **15**, 125–139.

Welcomme, R.L. (1979) *Fisheries Ecology of Floodplain Rivers.* Longman, London.

Whitton, B.A. (1984) *Ecology of European Rivers.* Blackwells Scientific Publications, Oxford.

Winterbottom, J.H., Orton, S.E. & Hildrew, A.G. (1997) Field experiments on the mobility of benthic invertebrates in southern English streams. *Freshwater Biology,* **38**, 37–47.

Xiong, S. & Nilsson, C. (1997) Dynamics of leaf litter accumulation and its effects on riparian vegetation. *The Botanical Review,* **63**, 240–264.

Received 19 April 1999
revised version accepted 2 June 1999