Running title: Riparian arthropod responses to river regulation

Riparian arthropod responses to flow regulation and river channelisation

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Summary

1. Alterations of river flow and morphology represent a widespread impact to riverine habitats. Little is known about the consequences of such alterations on riparian arthropods although they contribute substantially to riverine biodiversity and play a critical role in linking aquatic and terrestrial food webs.

2. We investigated the interactive effects of flow regulation (hydropeaking) and river channelisation on habitat charactistics and riparian arthropod abundance and diversity of differently impacted gravel bars in seven Alpine rivers. Digital elevation models were developed to simulate inundation dynamics of each gravel bar.

3. Channelisation significantly increased inundation duration and frequency, and hydropeaking increased substrate embeddedness. Total abundance of riparian arthropods was significantly reduced only by hydropeaking, whereas arthropod species richness was reduced by both hydropeaking and channelisation. Sites that were affected by both hydrological and morphological modifications together were almost devoid of arthropods.

5. Sensitivity of riparian arthropods to alterations in flow and morphology differed among taxa. Spider abundance was significantly reduced by channelisation and hydropeaking, and spider diversity was reduced by channelisation only. Ground beetles showed no significant response. Rove beetle abundance was negatively affected by hydropeaking whereas rove beetle diversity was reduced by hydropeaking only in channelised rivers. Diversity of all arthropods, spiders and ground beetles was negatively correlated with inundation frequency and substrate embeddedness. Rove beetle diversity was negatively correlated with embeddedness and gravelbank area.

Synthesis and applications. Results indicate that the diversity and abundance of riparian arthropods were predominantly controlled by the availability of exposed gravel habitat above average high water level and substrate embeddedness. Restorations of river morphology are likely to benefit riparian arthropods and mitigate negative effects of hydropeaking. Riparian arthropods, particularly spiders and rove beetles, appear to be sensitive indicators to assess the ecological effects of hydro-morphological alterations in rivers.

Key-words: braided rivers; disturbance; exposed riverine sediments; flow regime; ground beetles; hydro-morphology; hydropower; river restoration; rove beetles; spiders.

Introduction

Natural rivers and their fringing riparian zones are pivotal centres for biodiversity (Naiman & Décamps 1997; Sabo *et al.* 2005). At the same time they are among the most threatened ecosystems worldwide (Malmqvist & Rundle 2002; Tockner & Stanford 2002). Riparian zones, in particular, have been severely modified by river engineering and alterations of the natural flow regime (Nilsson & Berggren 2000; Nilsson *et al.* 2005). Recently, elaborate attempts are underway to restore rivers and to balance river restoration efforts with continued use of dams for hydropower production (Robinson & Uehlinger 2003; Giller 2005; Palmer *et al.* 2005). To optimise such efforts, we particularly need to understand the interactive effects of flow regulation and channel modification on riverine ecosystems (Jansson *et al.* 2005; Revenga *et al.* 2005). However, most of our current understanding of the ecological consequences of river regulation is based on single impact studies and selected groups of organisms, particularly fish and riparian vegetation (Lillehammer & Saltveit 1984; Nilsson, Jansson & Zinko 1997; Leyer 2005). Little is known about the consequences of river regulations on riparian arthropods, although they contribute significantly to riparian biodiversity, and they are assumed to be particularly sensitive to hydrological and morphological river modifications (Ellis, Crawford & Molles Jr. 2001; Manderbach & Hering 2001; Sadler, Bell & Fowles 2004; Andersen & Hanssen 2005). Riparian arthropods also represent a functionally important component of riverine systems because they have a critical role in linking aquatic and terrestrial food webs (Baxter, Fausch & Saunders 2005; Paetzold, Schubert & Tockner 2005).

To assess the interactive effects of flow regulation and river channelisation on riparian arthropods, we conducted a large scale comparative field study in seven Alpine braided, or formerly braided, rivers. Natural braided rivers are characterised by extensive areas of exposed gravel which are inhabited by a specialized riparian arthropod fauna

(Tockner *et al.* 2006). Today, however, most braided rivers, which were once widespread in temperate mountain-valley areas, are channelised and impacted by flow regulation (Tockner & Stanford 2002; Tockner *et al.* 2006). As a consequence, a high proportion of the gravel bar associated arthropod fauna has conservation status (Eyre, Luff & Phillips 2001; Manderbach & Hering 2001; Andersen & Hanssen 2005). In the UK, for instance, almost 20% of beetles on exposed riverine sediments are listed as endangered and vulnerable (Sadler, Bell & Fowles 2004).

Hydrologically, we focused on the effects of hydropeaking, i.e. diel water level fluctuations caused by hydroelectric power generation at peak demand (Moog 1993). Hydropeaking represents the major type of hydrological alteration in mountainous regions (Petts 1984). In Switzerland, for example, 30% of all hydrologically surveyed rivers are impacted by hydropeaking (BUWAL 2003). Because complete restoration of the natural flow regime is often not an option in rivers that are exploited for hydropower production it is important to understand whether restoration of the river morphology can provide an alternative measure to mitigate potential negative effects of hydropeaking. We infer potential effects of morphological restorations on riparian arthropods by comparing channelised sites with sites of remaining natural morphology. Specifically, we addressed the following questions: (1) What are the quantitative effects of hydropeaking and river channelisation, separately and combined, on the density and diversity of riparian arthropods? (2) Do dominant taxonomic groups (spiders, rove beetles, and ground beetles) differ in their sensitivity to hydrological and morphological modifications? and (3) What are the principle underlying abiotic factors associated with hydropeaking and channelisation that explain the response of riparian arthropods to river regulation? Based on our results, we discuss implications for river restoration and assessment.

Methods

STUDY SITES

We investigated 12 gravel bars (hereafter called sites) along seven mid-sized (5^{th} - 7^{th} stream order) Alpine rivers in Switzerland and Italy (Table 1). All study sites were characterized by a braided, or formerly braided (channelised), channel style. Sites were selected to study the ecological effects of flow regulation (hydropeaking) and morphological alteration (channelisation), separately and combined, using a full factorial design (Table 1). The Rivers Tagliamento, Sense, and Thur exhibited an essentially natural flow regime driven by snow melt and heavy rain events (Uehlinger 2000; Arscott *et al.* 2002). The Rivers Alpenrhein, Vorderrhein, Hinterrhein, and Upper Rhône were strongly affected by hydropower operation. Their natural flow regime was controlled by rain fall, snow and glacier melt. Hydroelectric power operation caused major diel flow variations (hydropeaking) and reduced seasonal and interannual flow extremes as a result of increased winter and decreased summer discharge (Loizeau & Dominik 2000).

The length of each study site was 5-10 times the channel width, corresponding to a pool-riffle sequence (Ferguson 1981). The lateral extent of each site was defined by the average annual low- and high-water mark. All sites were dominated by exposed gravel and cobble with sparse vegetation. Sites along the Tagliamento River were located in an 800 m wide island-braided section with a complex channel network and extensive areas of exposed gravel (van der Nat *et al.* 2002; Tockner *et al.* 2003). Tagliamento 1 was a 60 m wide gravel bar with a steep eroding bank and patchy woody vegetation in elevated areas. Tagliamento 2 was a 170 m wide shallow bank. Sense 1 was a 45 m wide gravel bar with steep and shallow banks in a natural-braided river section. Sense 2 was a 15 m wide, isolated gravel bar within a channelised reach. Both sites on the Thur River were shallow 20-30 wide gravel bars in two channelised reaches. Alpenrhein 1 was a 110 m wide gravel bar in a morphologically semi-natural river section. The site included steep and shallow banks with sparse woody vegetation. Alpenrhein 2 represented a relatively uniform, 40 m wide gravel bar in a channelised river section. Both Alpenrhein sites were affected by daily water level fluctuations of up to 1.5 m. The sites Hinterrhein and Vorderrhein were morphologically natural braided sections. Both sites contained shallow and steep banks with maximum widths of 120 m (Hinterrhein) and 90 m (Vorderrhein) and were affected by daily water level fluctuations of ~0.9 m. The two sites at the Upper Rhône River were isolated shallow gravel bars that were 9 m (Rhône 1) and 14 m (Rhône 2) wide. Their upper banks were stabilized by steep ripraps. Maximum diel water-level fluctuation was 0.8 m and 1.4 m at Rhône 1 and Rhône 2, respectively.

INUNDATION DYNAMICS AND SUBSTRATE MAPPING

All gravel bars were mapped during low water using a differential GPS (Trimble Pro XR/XRS) operated in carrier phase mode with a local base station <1 km apart. Data were collected in a 5×5 m grid. In addition, important breaks in slope were surveyed (Brasington, Rumbsy & McVey 2000). We obtained average accuracies (±95% confidence interval) of ±2 cm for plain and ±5 cm for elevation measurements.

For each gravel bar, a digital elevation model (DEM) was derived from triangular irregular networks based on 3-dimensional point data (Fig. 1). DEM's were corrected for the slope of the water level. Water level was measured repeatedly at each site. Inundation dynamics of each gravel bar were simulated using a linear regression between measured water levels at the site and at the nearest permanent gauging station (distance 3-35 km). Sites were revisited at high water to evaluate inundation models (Fig. 1). We included the year before sampling (2000-2001) in the analysis because inundation dynamics of the previous year can affect recruitment of ground-dwelling arthropods (Manderbach & Plachter 1997).

Percentage cover of substrate types (silt and sand, gravel, pebbles, cobbles and boulders) and classes of substrate embeddedness (<5%, 5-25%, 25-50%, 50-75%, and >75%) were visually estimated at each GPS point (5×5 m grid). Embeddedness describes the proportion of interstitial space of coarse substrates filled by sand and fines. Point estimates classified by their dominant substrate type (cover > 50%) were used to extrapolate substrate surface cover for each site. Point estimates of embeddedness of >50% were classified as embedded to calculate percentage cover of embedded substrate for each gravel bar. All sites were mapped by the same two persons. ArcInfo and ArcView GIS (ESRI) were used for spatial analysis of the data.

SAMPLING FOR TERRESTRIAL ARTHROPODS

In April/May, June/July, and September 2001 ground-dwelling arthropods were quantitatively sampled at all sites. Arthropods were sampled within quadrats (0.25 m^2) randomly positioned within 0-2 m of the water's edge ($N = 24$ per site and season). Quadrat sampling provides the most reliable estimate of density and richness of ground-dwelling arthropods (Andersen 1995). To justify the focus on the 0-2 m shoreline strip, we took an additional eight samples (per stratum and season) at 2-5 m and 5-30 m (when present) at each site. Analyses demonstrated that average seasonal abundance and species richness of all riparian arthropods was significantly higher along the shoreline than at more distant habitats (ANOVA: $F_{3, 103} = 24.44$, $P < 0.001$, $F_{3, 103} = 8,91$, $P < 0.001$, respectively). 75% of the average abundance of ground beetles and rove beetles and 48% of spiders occurred within the 0-2 m shoreline strip. 74% (83% after excluding rare species with ≤ 2 individuals per site) of all taxa occurred in the 0-2 m strip (see Appendix S1 and S2 in

Supplementary Material). Arthropod abundance within the narrow shoreline strip also provides the best indicator of potential trophic linkages between aquatic and terrestrial systems as trophic interactions occur predominantly close to the shoreline (Paetzold, Schubert & Tockner 2005).

For arthropod collection, loose stones, gravel, and debris were carefully removed to a sediment depth of 20 cm and water was poured on the sampling plots to drive hidden organisms to the surface. Arthropods were stored in 70% ethanol, counted, and the dominant taxonomic groups including spiders (Araneida), ground beetles (Carabidae) and rove beetles (Staphylinidae) were identified to species. Ants were excluded from the analyses as they are not strictly associated with riparian habitats (Hammond 1998) and their clumped distribution (aggregation around their nests) complicates representative abundance estimates in a randomized sampling approach.

DATA ANALYSIS

To compare responses of environmental factors and riparian arthropods to river regulation, sites were grouped by flow regime (natural flow regime *versus* hydropeaking) and morphology (braided *versus* channelised). Three sites for each combination of altered morphology and flow regime were investigated (Table 1). Due to the limited availability of comparable sites on different rivers of similar size we had to select some sites within the same river for individual combinations of morphology and flow regime. However, sites could be considered as independent as they were >10 km apart.

Differences in environmental variables (gravelbank area, inundation frequency and duration, embeddedness, relative proportions of gravel-cobble and sand) in response to flow alteration (natural flow *versus* hydropeaking) and channelisation (braided *versus* channelised) were tested using two-way factorial ANOVAs. We focussed on variables describing inundation dynamics and sediment composition because they are assumed to be primary factors in controlling riparian arthropod abundance and diversity (Uetz *et al.* 1979; Hammond 1998).

Arthropod abundance at each site was expressed as the average of all samples in each season (24 quadrat samples per season and site). Species richness was expressed as the sum of all taxa found at each site over the entire study period (72 quadrat samples per site). For comparisons of sites, we excluded rare species (≤ 2 individuals per site) and species with restricted geographic distribution (a total of 55 species) to provide a robust comparison and to account for regional variability. Two-way factorial ANOVAs were performed to test for the effects of hydropeaking and channelisation on riparian arthropod abundance and species richness. ANOVAs were performed for the entire riparian arthropod assemblage as well as for spiders, ground beetles, and rove beetles separately. For abundance, we included season as a blocking factor.

Multiple regressions were performed to analyse how much of the variation in arthropod species richness and abundance was explained by the environmental variables. A stepwise backward procedure was used to determine the variables explaining most of the variation. All tolerance values were >0.3 and condition indices of the variables were <30, indicating that independent variables were not highly correlated (Belsley, Kuh & Welsch 1980; Weisberg 1980).

All data except gravelbar area were square-root transformed to standardize variances and improve normality. Area was $\log_{10}$-transfomed because species richness was expected to be linearly correlated with area on a logarithmic scale (Williamson 1981). For multiple comparisons we adjusted significance levels with Bonferroni corrections. Statistical analyses were performed with SYSTAT 10.0 (SPSS 2000). Unless indicated otherwise, values presented are mean ± standard error of the mean.

Results

EFFECTS ON ABIOTIC HABITAT CONDITIONS

Hydropeaking and channelisation significantly affected gravel bar inundation dynamics and substrate embeddedness. We found no significant effect on gravel bar area and on the relative proportion of gravel-cobble. In channelised reaches, the duration and frequency of inundation of the entire gravel bars were significantly higher than in braided reaches (Fig. 2, Table 2). Hydropeaking significantly increased the embeddedness of the gravel bars. Channelisation resulted in a reduced embeddedness in river reaches with a natural flow regime (Fig. 2, Table 2).

ARTHROPOD COMMUNITY COMPOSITION

A total of 1476 individuals from 87 taxa (spiders: 24 taxa; ground beetles: 27 taxa; rove beetles: 36 taxa) were collected in 864 samples from 12 gravel bars (see Appendix S1). Fifty-three taxa (61%) were considered rare (≤ 2 individuals per site). The spider *Pardosa wagleri,* Hahn (64±11% of total spider abundance, present at 8 sites), the rove beetle *Paederidus rubrothoracicus,* Goeze (36±9% of total rove beetle abundance, present at 8 sites) and the ground beetles *Nebria picicornis,* Fabricius (19±7% of total ground beetle abundance, present at 10 sites) and *Bembidion fasciolatum/ascendens* (15±4%, present at 8 sites) dominated the arthropod communities (Appendix S1). For all taxa, abundance was positively related to species richness ($R^2 = 0.93$, d.f. = 11, F = 151.43, P < 0.001) across the 12 sites suggesting weak density compensation.

EFFECTS ON RIPARIAN ARTHROPODS

Hydropeaking significantly reduced riparian arthropod density, and hydropeaking and channelisation had significant negative effects on riparian arthropod species richness (Fig. 3, Table 3). Mean arthropod density and richness were highest at natural sites (18.9 ± 3.4 individuals / m^2 and 11.0 ± 1.5 species, respectively) and lowest at channelised sites that were also affected by hydropeaking (3.6 ± 1.2 individuals / m^2 and 2.3 ± 0.9 species, respectively). Impacted sites contained primarily a subset of the species that occurred at natural sites (see Appendix S1).

Arthropod groups differed in their sensitivity to hydropeaking and channelisation. Spider abundance was negatively affected by both hydropeaking and channelisation. Spider richness was significantly lower at channelised sites but was not significantly affected by hydropeaking. The dominant spider *Pardosa wagleri* occurred at all sites with a natural morphology but only at two out of the six channelised sites. Hydropeaking and channelisation had no significant effects on ground beetle abundance and richness (Fig. 3, Table 3). However, their average species richness was highest at natural sites and lowest at sites that were affected by both hydropeaking and channelisation. Rove beetle abundance was significantly reduced only by hydropeaking. Rove beetle richness was significantly affected by hydropeaking and channelisation, whereas channelised sites with a natural flow regime had highest richness and channelised sites affected by hydropeaking had lowest richness. The dominant rove beetle *Paederidus rubrothoracicus* was absent at all channelised sites that were also affected by hydropeaking.

Pair-wise comparisons within individual rivers showed lower species richness and abundance of all arthropod groups combined at channelised compared to braided sections. At the River Sense (natural flow regime), abundance and species richness of all arthropods were reduced by 63% and 57%, respectively, at the channelised site (braided site: 14 species; channelised site: 6 species). At the River Alpenrhein (affected by hydropeaking), abundance and species richness were reduced by 21% and 33%, respectively, at the channelised site (braided site: 6 species, channelised site: 4 species).

ABIOTIC HABITAT CONDITIONS VERSUS SPECIES RICHNESS AND ABUNDANCE

Abundance and species richness of all riparian arthropods combined and of spiders were negatively correlated with frequency of total gravelbar inundation and the relative proportion (%) of embedded substrate (Table 4). Ground beetle abundance was negatively correlated with inundation duration, and their richness was negatively correlated with inundation frequency and embeddedness. Rove beetle abundance was negatively correlated with embeddedness. Their richness was negatively correlated with embeddedness and positively correlated with gravelbar area.

Discussion

Our results demonstrated that riparian arthropods are sensitive to changes in flow regime and river morphology. The significant effects of hydropeaking and channelisation on riparian arthropod abundance and diversity indicated that these impacts superimpose river-specific natural variation in environmental conditions, such as differences in the natural flow regime and stream order, among the studied rivers.

EFFECTS ON ABIOTIC HABITAT CONDITIONS

In channelised reaches small floods already caused inundations of entire gravel bars because there only shallow gravel bars have developed and water levels rose faster due to reduced channel cross-section areas. This explains the higher inundation duration and frequency of entire gravel bars in channelised sites compared to sites with a natural morphology. Hydropeaking did not significantly alter the inundation dynamics of the entire gravel bars because diel water-level fluctuations associated with hydropeaking affected only the shoreline parts of the gravel bars.

Hydropeaking increased the proportion of embedded sediments of the gravel bars, particularly along the ecologically important channel margins. The daily rapid increases in flow associated with hydropeaking remobilise fine sediments which become deposited in areas of low shear stress, i.e. channel margins and lees of obstacles (Sear 1995). Hydropeaking during higher flow conditions (snow-melt) might have been responsible for the accumulations of fines at higher areas of the gravel bars. Additionally, hydropower operations generally reduce the number of smaller flood events that can flush out fines from the gravel bars (Loizeau & Dominik 2000). In rivers with a natural flow regime, frequent flow pulses (*sensu* Tockner, Malard & Ward 2000) resulted in a low embeddedness of the gravel bars, particularly at channelised sites where already smaller floods flushed a large proportion of the shallow gravel bars.

EFFECTS OF RIPARIAN ARTHROPODS

Both river channelisation and hydropeaking had negative effects on riparian arthropods. The combination of both impacts resulted in a highly impoverished riparian arthropod fauna of low abundance.

The reduced abundance and diversity of riparian arthropods at channelised rivers was likely the result of the altered inundation dynamics of the gravel bars. Natural braided rivers represent harsh environments located at the decreasing limb of the humped-shaped harshness-diversity curve (Tockner *et al*. 2006). In line with the intermediate disturbance hypothesis (Connell 1978), the further increase in inundation frequency as a result of channelisation resulted in a decrease in species richness. Inverse relationships of inundation frequency with species richness and abundance of ground-dwelling arthropods were also found in a Midwestern forest floodplain, USA (Uetz *et al.* 1979). Gravelbar area, another factor that might potentially affect riparian arthropod abundance and richness, was not significantly affected by channelisation. Further, abundance and diversity of riparian arthropods were not significantly correlated with gravelbar area. By confining our sampling to a narrow shoreline strip, we deliberately reduced potential area-related increases in arthropod diversity resulting from the addition of xerothermic or ubiquitous taxa that generally occur in dry, sparsely vegetated higher parts of the gravel bars. Gravelbar area was also not a good predictor of species richness of riparian spiders and beetles in gravel-bed rivers in the European Alps and the UK, respectively (Manderbach & Framenau 2001; Sadler, Bell & Fowles 2004).

The negative effects of hydropeaking on riparian arthropod abundance and diversity likely resulted from the associated increased substrate embeddedness. High embeddedness reduced substrate heterogeneity and availability of open interstitial habitats; both are important habitat factors for many ground-dwelling riparian arthropods (see below). The reduced abundance and diversity of riparian arthropods in rivers impacted by hydropeaking might have also been caused by the frequent disturbances associated with the daily lateral movement of the shoreline. However, most riparian arthropods are highly mobile, and frequent sampling of riparian arthropods over a diel cycle indicated that riparian arthropods rapidly follow the moving shoreline in hydropeaking-impacted rivers (A. Paetzold, unpublished data). Hydropeaking generally results in a reduction in densities and biomass of aquatic insects (Petts 1984; Moog 1993). Such reductions in the productivity of aquatic insects associated with the hydromorphological alterations might have potentially affected the densities of riparian arthropods because aquatic insects can provide an important food source for many gravelbar inhabiting arthropods (Hering &

Plachter 1997; Paetzold, Schubert & Tockner 2005; Paetzold, Bernet & Tockner 2006). Further research is needed to understand the relative importance of such aquatic subsidy effects on the abundance and diversity of riparian arthropods.

DIFFERENTIAL EFFECTS ON RIPARIAN ARTHROPOD TAXA

We demonstrated that individual taxonomic groups responded differently to channelisation and hydropeaking, with spiders being particularly sensitive to alterations of the riverbank morphology and rove beetles being more sensitive to hydropeaking. The differential responses of the dominant arthropods can be attributed to specific differences in their life history strategies and environmental requirements.

The negative correlations of spider richness and abundance with inundation frequency demonstrate that spiders are particularly sensitive to frequent flooding. Unlike most riparian beetles that can survive floods in interstititial habitats or escape by flying, spiders depend on flood refugia above high-water level (Plachter & Reich 1998; Adis & Junk 2002). Along lowland rivers in Germany and Midwestern USA, spider richness also decreased with increasing flood duration and frequency (Uetz 1976; Bonn 2000). In Australian forested floodplains spider abundance and diversity were not significantly affected by inundation duration (Ballinger, Mac Nally & Lake 2005). However, comparisons among different types of rivers are problematic because flow regime, riparian vegetation, and arthropod community composition can differ considerably among river types. In lowland flood plains, long-term inundation dynamics determine the vegetation structure which in turn influences spider community composition (Bell, Petts & Sadler 1999; Ballinger, Mac Nally & Lake 2005). Many spiders of temperate lowland flood plains are opportunistic species from surrounding uplands that can escape floods by lateral migration to adjacent upland habitats or by climbing tree trunks (Adis & Junk 2002).

However, the spider fauna of the gravel bars was dominated by habitat specialists, such as *Pardosa wagleri*. We know very little about their ability to survive floods in adjacent vegetated habitats higher in the flood plain where they are exposed to different environmental conditions (e.g. microclimate, habitat structure) and biotic interactions (e.g. competition, predation). Further, access to terrestrial habitats higher in the flood plain was often limited during higher water levels because most gravel bars became surrounded by water with increasing water level (Fig. 1). Consequently, inundations of entire gravel bars might have resulted in a high mortality for ground-dwelling spiders. This indicates that the increase in flooding were the main reason for the negative effects of channelisation on spiders.

The negative correlation of spider richness and abundance with embeddedness can be explained by loss in structural complexity and hollows with increasing embeddeness. Hollows provide important daytime shelter for lycosid spiders (Framenau *et al.* 1996) and structural complexity appears to be a generally important determinant for the density and diversity of ground-dwelling spiders (Uetz 1979).

Ground beetles appear to be less sensitive to hydropeaking and channelisation than spiders and rove beetles. However, their abundance and species richness were reduced by the combined impact of hydropeaking and channelisation. Increased embeddedness associated with hydropeaking reduces the availability of air-filled interstitial habitats which appear to be important as flood refugia for ground beetles (Andersen 1985; Dietrich 1996). As duration and frequency of inundation increases the availability of flood refugia is likely to become more important. This can explain the negative correlation of ground beetles richness with both inundation frequency and embeddedness and the reduction in ground beetles abundance and richness only at sites characterized by the combined impact of channelisation and hydropeaking.

Many gravelbar inhabiting rove beetles require open interstitial spaces as habitats and flood refugia (Schatz, Steinberger & Kopf 2003). This can explain their high abundance and species richness at channelised sites in rivers with a natural flow regime because there, channelisation further reduced the proportion of embedded substrate of the gravel bars. The high dependency of specialist rove beetles on interstitial habitats can also explain their reduction in abundance at hydropeaking sites. Similar to the ground beetles, the combined effects of hydropeaking and channelisation created extremely hostile habitat conditions for the rove beetles. This might be explained by the additional loss in the absolute area of interstitial habitats and flood refugia together with an increase in the frequency and duration of inundation.

IMPLICATIONS FOR RIVER MANAGEMENT

Riverine gravel bars are threatened habitats and their associated arthropod fauna is of high conservation value (Sadler, Bell & Fowles 2004; Andersen & Hanssen 2005). Our results indicate that the diversity of the gravelbar inhabiting arthropod fauna can be conserved in its entirety only in reaches with both a natural morphology and a natural flow regime. Full restoration of the natural flow regime, however, conflicts with the continued use of rivers for hydropower production and, therefore, alternative river rehabilitation strategies are required that balance between ecological requirements and hydropower production (Baron *et al.* 2002; Bratrich *et al.* 2004). Our findings suggest that the increase in substrate embeddedness represents the most important impact of hydropeaking for the riparian arthropod fauna. Alternative dam operation schemes including artificial flood releases that flush fines out of the gravel could therefore provide a potential mitigation strategy in hydropeaking rivers (Schmidt *et al.* 2001; Mürle, Ortlepp & Zahner 2003). Reduced embeddedness of the river bottom substrate would also potentially benefit macroinvertebrate and fish production (Osmundson *et al.* 2002). However, we know little about the efficiency of artificial floods to reduce embeddedness of gravel bars and their potential impacts on both aquatic and riparian biota (but see Stevens *et al.* 2001; Robinson, Uehlinger & Monaghan 2003). Consequently, artificial flood management should be carefully applied using an adaptive management approach (Richter *et al.* 2003; Robinson & Uehlinger 2003).

The positive effects of a natural morphology on the riparian arthropod fauna indicate that morphological river rehabilitation can benefit riparian arthropods, particularly in rivers that are affected by hydropeaking. The success of morphological rehabilitations, however, is likely to be dependent on the formation of exposed gravel bars above average high water level as the availability of flood refugia appears to be crucial for the persistence of riparian arthropods. The development of such gravel bars requires both a sufficient supply of sediments and enough space for the river to redevelop a more natural river morphology. Sufficient sediment supply can be particularly problematic in dammed rivers where reservoirs can trap large amounts of sediments (Schmidt *et al.* 2001; Stanley & Doyle 2003). In the Grand Canyon, for instance, more than 90% of incoming sediment is trapped behind the dam in Lake Powell (Powell 2002).

The success of river restorations for riparian arthropods will also depend on the potential for colonization (Andersen & Hanssen 2005). As a consequence, the spatial distribution and configuration of individual gravel bars along river corridors need to be considered in restoration planning. Upstream gravel bars might be particularly important sources of colonization by flightless arthropods that are primarily dispersed via floating organic matter (Tenzer 2003; Tockner *et al.* 2006). However, further knowledge on the potential dispersal pathways by riparian arthropods is required to strategically place restoration measurements in a river corridor framework. Therefore, it is important to use future restorations as ecosystem-level experiments (*sensu* Jansson *et al.* 2005) to improve our understanding of the habitat requirements of many riparian arthropods and their ability to colonize new habitats.

We suggest that riparian arthropods should be integrated in future river assessments because they are (1) particularly sensitive to hydrological and morphological alterations, (2) they contribute significantly to overall riverine biodiversity (Hammond 1998), and (3) they play an important role in linking aquatic with terrestrial food webs (Paetzold, Schubert & Tockner 2005). In addition to the assessment of instream biota, riparian arthropods can provide complementary information on the ecological integrity of the riparian zone. While aquatic invertebrates and fish are controlled by a wide range of in-stream habitat conditions including water quality and temperature, riparian arthropods appear to be particularly suited to separate the effects of hydro-morphological river alterations.

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Table 1. Characteristics of the 12 study sites; Fl+: natural flow regime, HP: flow regime altered by hydropeaking, M+: natural morphology, M-: channelised sites.

Site	Area (m^2)	Catchment area (km^2)	Mean annual discharge (m^3/s)	Flow regime	Morphology	Area affected by hydropeaking (%)[†]
Tagliamento 1	10629	2580	90	Fl+	M+	-
Tagliamento 2	40587	2580	90	Fl+	M+	-
Sense 1	6118	132	9	Fl+	M+	-
Sense 2	1300	408	9	Fl+	M-	-
Thur 1	3593	1678	47	Fl+	M-	-
Thur 2	3654	1665	47	Fl+	M-	-
Alpenrhein 1	22990	3969	156	Hp	M+	25-30
Vorderrhein	24389	1235	32	Hp	M+	15-35
Hinterrhein	13487	1695	42	Hp	M+	15-50
Alpenrhein 2	29762	4018	156	Hp	M-	25-55
Rhône 1	397	3368	104	Hp	M-	40-60
Rhône 2	1491	3841	130	Hp	M-	45-60

[†] Relative proportion of the gravelbar area that is inundated daily due to hydropeaking.

Table 2. Values of *F* from two-way fixed-effects ANOVAs on the effects of morphology (natural *versus* channelised) and flow regime (natural *versus* hydropeaking) on maximum inundation duration and frequency and relative area of embedded substrates (embeddedness of gravel / pebble > 50%) of gravelbank sites.

Effect	Inundation		Substrate
	duration	frequency	embeddedness
Morphology (1,8)	7.90*	71.37***	4.07
Flow regime (1,8)	0.91	3.67	42.85***
Morphology × Flow regime (1,8)	1.86	3.67	8.54*

Notes: Each column summarizes results from a single ANOVA. Degrees of freedom for each effect and the corresponding error term are given in parentheses.

* P < 0.05; ** P < 0.01; ** P < 0.001

Table 3. Values of *F* from two-way fixed-effects ANOVAs on the effects of morphology (natural versus channelised) and flow regime (natural versus hydropeaking) on species richness and abundance of riparian arthropods.

Effect	All taxa	Spiders	Ground beetles	Rove beetles
	Species richness			
Morphology (1,8)	8.93*	9.38*	3.61	9.28*
Flow regime (1,8)	7.35*	0.86	1.78	24.83***
Morphology × Flow regime (1,8)	1.73	0.06	0.04	24.83***
	Abundance			
Morphology (1,8)	2.92	11.45**	2.10	0.32
Flow regime (1,8)	14.20***	8.67**	2.40	15.04***
Season (2,30)	2.32	1.52	2.62	1.99
Morphology × Flow regime (1,8)	1.65	1.44	1.07	0.59

Notes: For abundance, season was added to the model as a blocking factor. Each column summarizes results from a single ANOVA. Degrees of freedom for each effect and the corresponding error term are given in parentheses.

* $P < 0.05$; ** $P < 0.01$; ** $P < 0.001$

Table 4. Results of multiple regressions of species richness and abundance of riparian arthropods in relation to environmental characteristics of gravel bars. Standardized partial regression coefficients for each environmental variable and *F*-values from ANOVAs for the full and selected regressions are given.

Variables	All taxa	Spiders	Ground beetles	Rove beetles
	Species richness			
Full regression	$R^2 = 0.85$	$R^2 = 0.63$	$R^2 = 0.54$	$R^2 = 0.54$
	F = 16.35***	F = 5.18*	F = 4.17*	F = 3.02
Area	0.26	-0.11	0.22	0.39
Inundation duration	-0.09	0.26	-0.16	-0.20
Inundation frequency	-0.69**	-1.21**	-0.64	0.05
Embeddedness	-0.93***	-0.88*	-0.67*	-0.63
Selected regression	$R^2 = 0.81$	$R^2 = 0.60$	$R^2 = 0.56$	$R^2 = 0.52$
	F = 24.83***	F = 9.14**	F = 7.88*	F = 7.02*
Area	--	--	--	0.49*
Inundation frequency	-0.94***	-0.98**	-0.90**	--
Embeddedness	-1.04***	-0.71*	-0.81**	-0.73**
	Abundance			
Full regression	$R^2 = 0.77$	$R^2 = 0.67$	$R^2 = 0.42$	$R^2 = 0.51$
	F = 10.01**	F = 6.48*	F = 3.00	F = 3.83
Area	0.14	-0.30	0.19	0.37
Inundation duration	-0.25	0.09	-0.40	-0.07
Inundation frequency	-0.55	-1.25**	-0.30	0.04
Embeddness	-0.88**	-0.96**	-0.50	-0.78*
Selected regression	$R^2 = 0.72$	$R^2 = 0.65$	$R^2 = 0.43$	$R^2 = 0.49$
	F = 15.32***	F = 11.26**	F = 9.14*	F = 11.70*
Inundation duration	--	--	-0.69*	--
Inundation frequency	-0.79**	-0.97**	--	--
Embeddness	-1.05***	-0.85**	--	-0.73**

Notes: Tolerance values of environmental variables are > 0.3 and condition indices of the variables were < 30, indicating that environmental variables were not highly correlated.

* $P < 0.05$; ** $P < 0.01$; ** $P < 0.001$

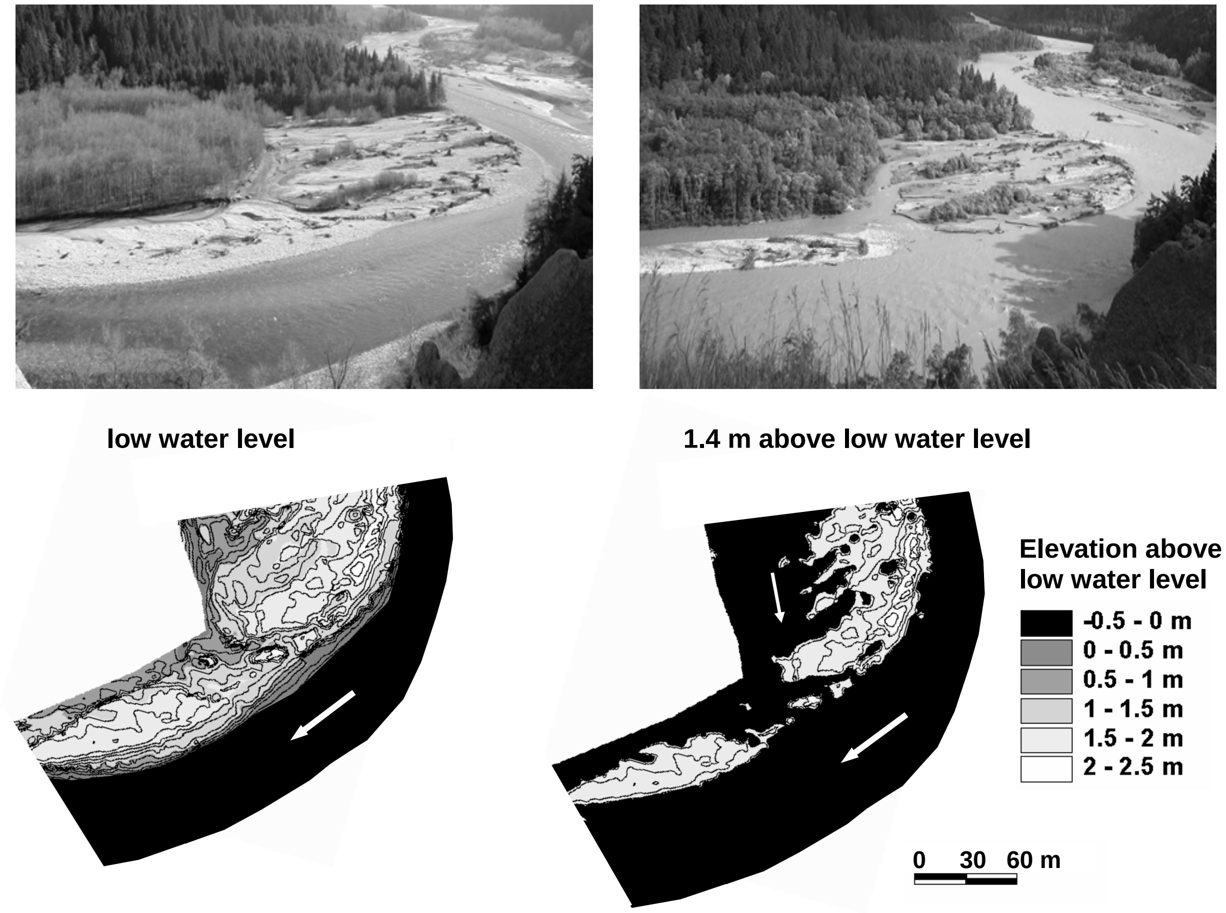

Fig. 1. Gravel bar in a river reach with a natural morphology (Hinterrhein) at low water level (left) and high water level (right) with respective inundation model based on a digital elevation model.

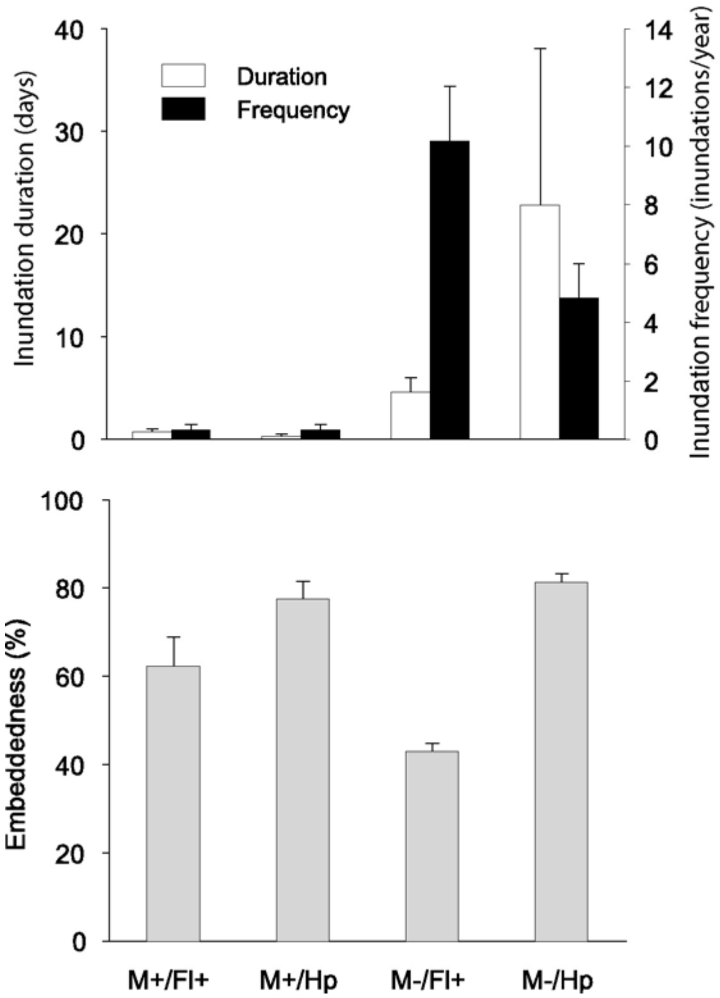

Fig. 2. Combined effects of gravelbar morphology (M+: natural morphology, M-: channelised river section) and flow regime (Fl+: natural flow regime, Hp: hydropeaking) on maximum inundation duration and inundation frequency of entire gravel bars (top panel) and on the relative area of embedded substrate (embeddedness of gravel / pebble > 50%) (bottom panel, see Table 2 for statistics). N = 3 gravel bars for each pair of morphology and flow regime. Values presented are means ± SE.

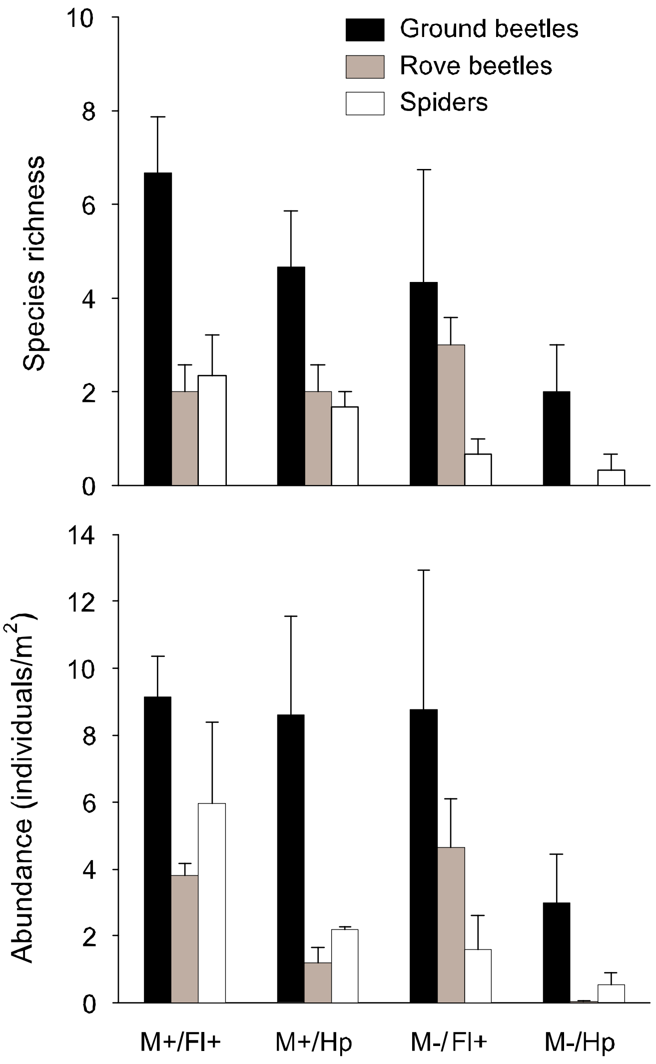

Fig. 3. Combined effects of gravelbar morphology (M+: natural morphology, M-: channelised river section) and flow regime (Fl+: natural flow regime, Hp: hydropeaking) on species richness (mean ± SE) (top panel) and abundance (mean ± SE) (bottom panel) of ground-dwelling terrestrial arthropods (see Table 3 for statistics). N = 3 gravel bars for each pair of morphology and flow regime.

Supplementary Material and Appendices

Appendix S1. Species list and abundances of riparian arthropods (0-2 m from river's edge) at all sites.

Appendix S2. Species list and abundances of riparian arthropods (> 2 m from river's edge) at all sites.