

Amphibian diversity and nestedness in a dynamic floodplain river (Tagliamento, NE-Italy)

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Abstract

Amphibian distribution and assemblage structure were investigated along the last morphologically intact river corridor in Central Europe (Tagliamento). Thirteen taxa were identified with *Rana latastei* and *Bufo bufo* being the predominant species. In the main study reach, a 2 km² dynamic island-braided floodplain in the middle section of the river, 130 water bodies were delineated that were situated either in the active floodplain (82 sites) or in the adjacent riparian forest (48 sites). Results demonstrated that the active floodplain increased appreciably the available habitat for amphibians, despite frequent disturbances by floods or droughts. Amphibian richness within a given habitat was significantly correlated with distance from vegetated islands, fish density, and water temperature. In the active floodplain, species distribution was highly predictable, exhibiting nearly perfect nestedness, suggesting that selective colonisation and extinction processes predominated. The degree of nestedness was much higher than in the adjacent riparian forest or in regulated floodplains in Central Europe. Results clearly emphasise that amphibians can exploit the entire hydrodynamic gradient, except the main channel. In the active floodplain, vegetated islands and large woody debris are important, directly and indirectly, in maintaining both habitat and amphibian diversity and density in this gravel-bed river.

Introduction

Globally, amphibian populations have declined over the past several decades and continue to do so (Houlahan et al., 2000; Stuart et al., 2004). Possible underlying causes of the decline are changes in climate, increased exposure to UV-B radiation, increased prevalence of diseases, acidification, water pollution, habitat fragmentation, and habitat loss (Leuven et al., 1986; Alford & Richards, 1999; Kiesecker et al., 2001). Therefore, many amphibian species are listed as threatened or endangered, regionally and globally (Beebee, 1996; Nöllert & Nöllert, 1992).

Natural floodplains are highly dynamic environments with floods as the primary agent of disturbance. Their high species diversity and

landscape-corridor function place floodplains high on the conservation agenda (Ward et al., 1999a; Hughes & Rood, 2001; Tockner & Stanford, 2002). However, today they are among the most endangered ecosystems worldwide. In Europe, for example, more than 90% of the former floodplains either disappeared or they are functionally extinct (Tockner et al., 2006). Amphibians are generally considered as ‘indicators’ of stable floodplain ponds with a low degree of hydrological connectivity, or as indicators of temporary waters lacking fish predators (e.g., Waringer-Löschenkohl & Waringer, 1990; Joly & Morand, 1994; Morand & Joly, 1995; Wellborn et al., 1996; Skelly, 1997; Tockner et al., 1999; Kuhn et al., 2001). Limited information is available, however, about amphibian populations in dynamic gravel-bed rivers, since

such rivers were never the main focus of amphibian research (e.g., Beebee, 1996). One reason was that nearly all formerly dynamic floodplain rivers in developed countries were regulated during the last two centuries (Petts et al., 1989; Nilsson et al., 2005; Tockner & Stanford, 2002). Further, flood prone gravel-bed rivers were not expected to provide hospitable habitats for amphibians. Kuhn (1993), however, demonstrated that species such as *Bufo bufo* exhibited a pronounced reproduction plasticity that allowed this species to exploit dynamic and ephemeral habitats in gravel-bed rivers.

Understanding patterns and processes in natural river corridors is a prerequisite for a sustainable conservation and management of their biodiversity (e.g., Ward & Tockner, 2001). The Tagliamento River in NE-Italy, the last morphologically intact river corridor in the Alps, offered the rare opportunity to investigate amphibian populations under natural environmental conditions. In the main investigation area, an island-braided floodplain, we compared amphibian population density, diversity and nestedness in the active floodplain (area that extends laterally to the lower limit of persistent vegetation and is frequently modified by floods) and the adjacent riparian forest (periodically inundated by the river). In the present paper, we link habitat heterogeneity with the composition and distribution of amphibians and identify indicator species for different floodplain habitats. In addition, we present an empirical example of nestedness in the dynamic floodplain system and compare it with more regulated riverine floodplains. Measure of nestedness provides a quantitative indicator of the degree of community 'order' in fragmented systems (e.g., Atmar & Patterson, 1993; Patterson & Atmar, 2000).

Materials and methods

The Fiume Tagliamento

The Fiume Tagliamento in NE-Italy (46° N, 12° 30' E; Fig. 1) is the last large gravel-bed river in the Alps that has escaped intensive river management (Müller, 1995; Ward et al., 1999b; Tockner et al., 2003). More than 70% of the catchment area (2580 km²) is located within the southern fringe of the Alps, with Mt. Coglians as the highest peak (2781 m a.s.l.). The Tagliamento

is a 7th order river, characterised by a flashy hydrological regime, with highest discharges during spring and autumn. The main-stem corridor covers about 150 km². The corridor is characterised by a high number of vegetated islands within the active zone (652 islands >0.01 ha), numerous gravel bars (952), a considerable habitat diversity and a continuous riparian woodland along the margins of the active channel (Tockner & Ward, 1999). For a complete description of the catchment and longitudinal geomorphic features see Ward et al. (1999b), Arscott et al. (2000, 2002), Gurnell et al. (2001), and Tockner et al. (2003).

We investigated the amphibian fauna in six geomorphic reaches along the entire corridor, with detailed studies in an island-braided reach in the middle section of the river. The six geomorphic reaches are: constrained headwater streams (Reach I, 1005–1200 m a.s.l.), headwater island-braided floodplain (Reach II, 705 m a.s.l.), bar-braided floodplain (Reach III, 200 m a.s.l.), island-braided lowland reach (Reach IV, 180 m a.s.l.), braided-to-meandering transitional floodplain (Reach V, 19 m a.s.l.) and meandering floodplain (Reach VI, 5 m a.s.l.).

The main investigation focused on a 2 km² island-braided floodplain in Reach IV (river-km 80; Figs 1 & 2). There, the floodplain was separated into the active area frequently inundated and reworked by floods and the adjacent riparian forest only inundated during annual floods. Along the left bank, hillslope forests of Monte Ragogna bordered the active floodplain. Along the right bank, the riparian forest extends laterally to a distance of about 0.5–1 km. Bare gravel, aquatic habitats and vegetated islands were the main landscape elements of the active floodplain. The Tagliamento is characterised by a dynamic flood regime, with turnover rates of aquatic habitats in Reach IV as high as 50 % during a single flood season (Arscott et al., 2002; Van der Nat et al., 2003).

Sampling methods and data analyses

Along the mainstem corridor, all water bodies in the six reaches were sampled in March, May, and July 2000, periods without severe floods. In the detailed investigation of the floodplain in Reach IV, the exact location and area of aquatic habitats

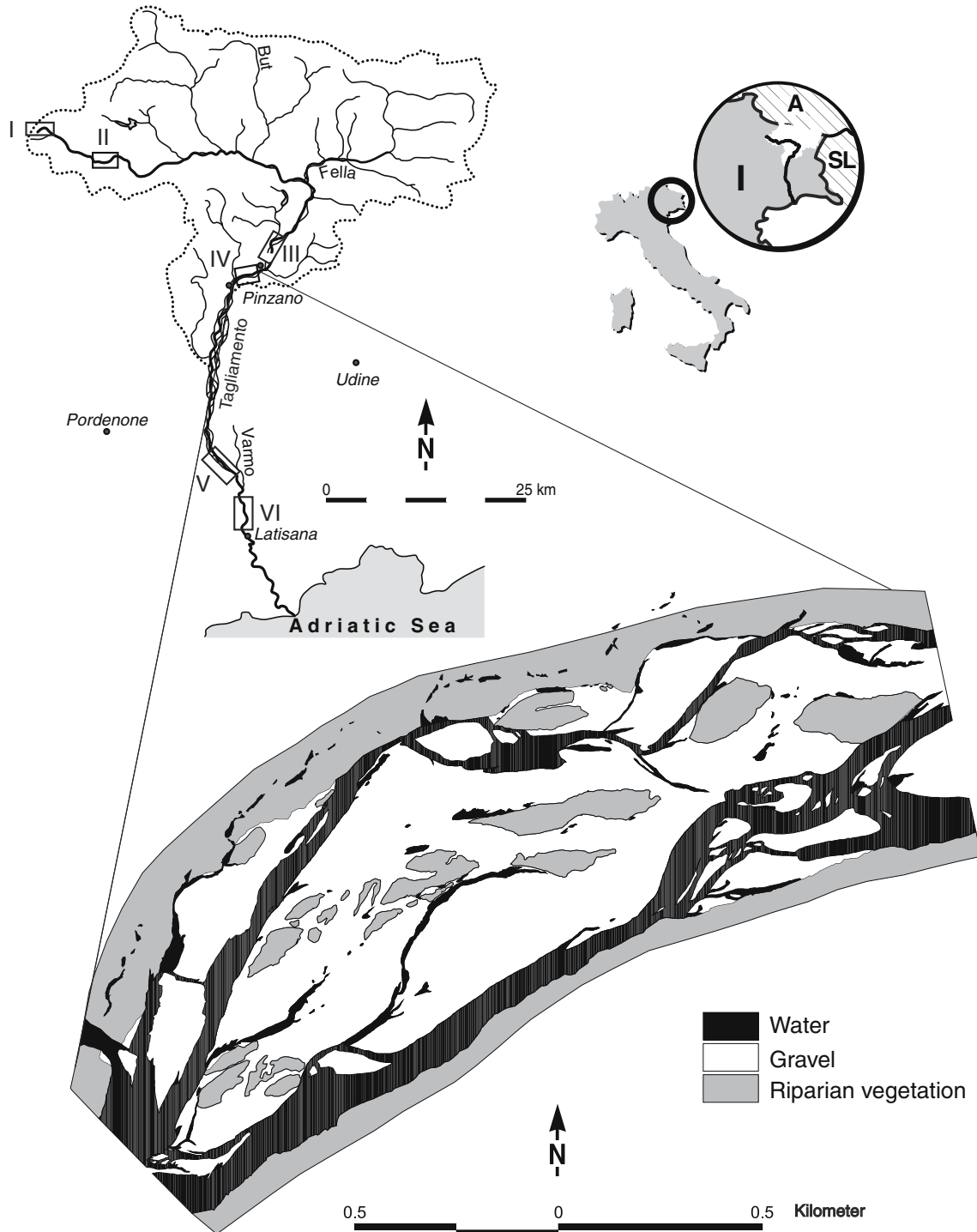


Figure 1. Tagliamento catchment, locations of study reaches I–VI, and map of the main study area (Reach IV; mapping date: May 2000). Most ponds investigated are too small to be shown at this scale. The river flows from right to left.



Figure 2. The main investigation area in the mid-section of Reach IV. Active floodplain width is up to 900 m (Photo: D. Arscott, May 2000).

within the active floodplain and the adjacent riparian forest were measured using a differential-GPS (Global Positioning System). Individual water bodies were marked (130 in all) and numbered in the field. Between 7 March and 15 July 2000 all water bodies were repeatedly (totally eight times) visited throughout the amphibian breeding period. This sampling period included the larval period of all amphibians known to use Central European floodplains as spawning sites (Nöllert & Nöllert, 1992). Further, adjacent uplands were occasionally investigated for species not typical for floodplains. Species presence was based on eggs or larvae encountered in a specific water body. Egg masses of brown frogs (*Rana dalmatina*, *R. latastei*, and *R. temporaria*) and common toad (*Bufo bufo*) were quantified for each water body. Since it was difficult at the beginning to separate egg clutches of *R. dalmatina* and *R. latastei*, density data of brown frogs were lumped in the analyses. The number of egg strings of *B. bufo* has to be considered as an approximate value since egg strings from several females are sometimes inextricably entangled on the same spawning support or have been broken. Densities were standardised for both aquatic area and terrestrial habitat area (riparian forest and vegetated islands; egg masses per ha). The riparian forest extended laterally over a distance of ca. 500 m from the active floodplain to a main road and a railway that follow the course of the river. For brown frogs and the common toad a lateral terrestrial breeding migration distance of 500 m was considered as appropriate, although migration

distance can be up to 1500 m (C. Baumgartner, unpubl. data).

Because it was not possible to distinguish the forms of green frogs expected for the Tagliamento corridor (*Rana lessonae*, *R. klepton esculenta*; Günther & Plöttner, 1994, Lapini et al., 1999) from eggs or larvae, they were grouped as a single taxon in all analyses. Maximum water depth (m), specific conductance (μS ; portable meter), water temperature ($^{\circ}\text{C}$) and the presence of fish (four abundance classes based on visual examinations: absent, rare, abundant, dominant) were recorded during each field campaign. Oxygen (% saturation), sediment composition (relative proportion of silt, sand, fine and coarse gravel, coarse particulate organic matter), density of riparian vegetation (four cover classes: <10%, 10–25%, 25–75% and >75%), macrophyte cover (four classes as for riparian vegetation), accumulations of large woody debris (LWD) (four cover classes as for riparian vegetation), and actual surface area (m^2) were estimated every second visit (four times totally). Rank-correlation analyses (Spearman-rank test) were used to test the relationship between environmental factors (average values), taxa richness and egg mass density as a surrogate for adult female population size.

Two-Way INDicator SPecies ANalysis (TWINSPAN), a complex clustering method (Hill, 1979), was used to identify indicator species characterising individual sampling sites (based on presence/absence). Samples were ordinated using reciprocal averaging and clusters were arranged subsequently in a hierarchical procedure. The habitat association between species was also calculated. For each pair of species the contingency table of presence/absence was used to calculate a Chi-squared value.

The presence of nested distributions was estimated using the 'nestedness calculator' (Atmar & Patterson, 1995). Its metric, 'system temperature' (T), reflects the extent of order in a presence-absence species matrix. Perfectly nested communities have a $T=0$, and maximally disordered ones a $T=100$. Analyses were carried out on presence/absence matrices that have been packed into a state of minimum unexpectedness. The characteristic ' T ' of randomised matrices was calculated through Monte Carlo simulations (500 iterations per test) and compared with

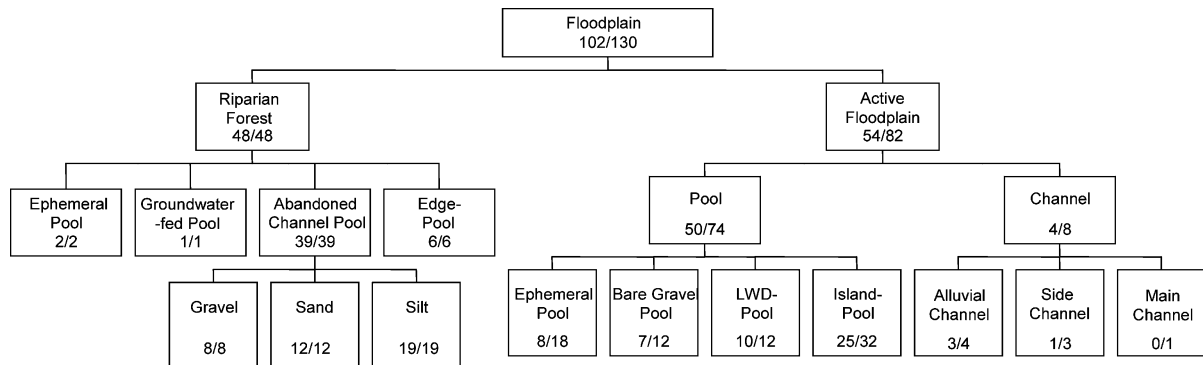


Figure 3. Floodplain water bodies separated into different types based on their position and morphology. Numbers indicate water bodies with brown frogs (*Rana latastei*, *R. temporaria*, *R. dalmatina*) and/or *Bufo bufo* (first value) and the total number of water bodies in each category (second value). LWD: Large woody debris.

observed 'temperatures'. The nestedness calculator also produces a measure of unexpected presence or absence of species. Species with many such deviations from perfect nestedness cause idiosyncratic patterns due to their 'species temperatures' that are much higher than the overall matrix temperature. Such patterns can be explained with respect to extinction and recolonisation, and may reflect exclusions or the presence of unique geomorphic features on some 'islands' (Atmar & Patterson, 1993). Nestedness values were compared with values calculated from more regulated floodplains along the Danube and the Rhône rivers. There, data were collected in an intensity comparable

to the present study (Joly & Morand, 1994; C. Baumgartner, unpubl. data).

Results

Habitat identification and spawning sites

In the main investigation area (Reach IV), 130 water bodies were identified, 1/3 of which were located in the riparian forest and 2/3 in the active corridor (Fig. 3). The average surface area of lentic water bodies (floodplain ponds) was 340 m², without a significant difference between those located in the two parts of the floodplain. Based on

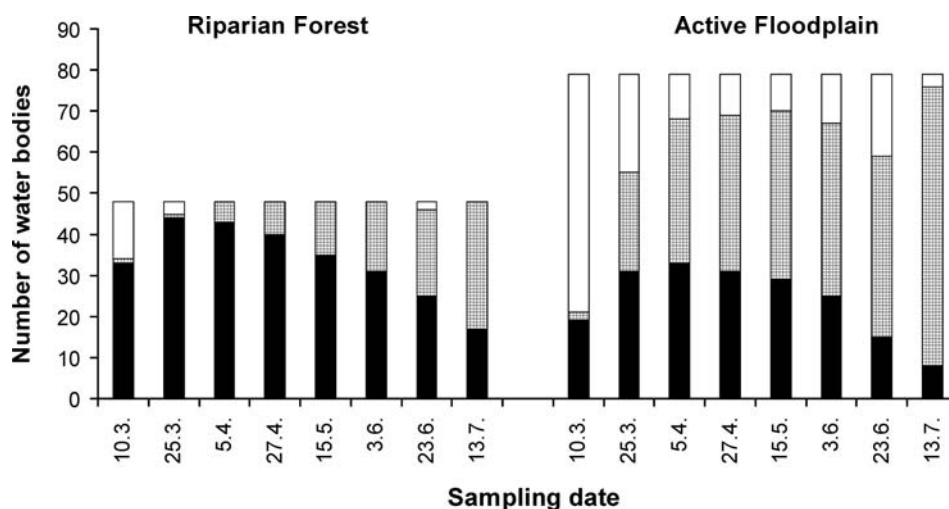


Figure 4. The total number of water bodies in the active floodplain and the adjacent riparian forest of Reach IV and their proportion with egg masses/larvae (black), without egg masses/larvae (hatched), and those that were dry (white) during each sampling date. Egg masses/larvae were from brown frogs (*Rana latastei*, *R. temporaria*, *R. dalmatina*) and/or the common toad (*Bufo bufo*).

their location and their formation, ponds were divided into several classes and subclasses. Within the active plain, more than 60% of all water bodies were associated with LWD or vegetated islands. Most ponds in the riparian forest were permanent; however, many water bodies in the active floodplain were temporary. In the active plain, many ponds were dry at the end of winter but were filled during high spring flow in mid-March and slowly contracted during subsequent months (Fig. 4). All riparian forest water bodies and two third of the water bodies within the active plain were used as spawning habitats by amphibians (eggs/larvae present). Within the active plain, ponds associated

with large wood (LWD) and vegetated islands were preferred as spawning sites (cf. Fig. 3). Main and side channel habitats were almost devoid of amphibians. During the investigation period the number of water bodies utilised by amphibians decreased (Fig. 4).

Species diversity and number of egg mass clutches

Ten taxa were identified along the corridor of the Tagliamento river. Three additional species (*Salamandra salamandra*, *Pelobates fuscus* and *Triturus alpestris*) were observed in adjacent uplands. Along the entire corridor, the number per

Table 1. Distribution of amphibians along the Tagliamento (reaches I–VI)

Reach	I	II	III	IV	V	VI	Adjacent upland
Altitude (m a.s.l.)	1050	705	165	140	20	5	
Average slope (%)	5.5–19.5	2.5	1	1	0.5	< 0.5	
Geomorphic type	Constrained	Island-braided	Bar-braided	Island-braided	Braided-anastomosed	Meandering	
Width of active floodplain (m)	30	260	830	1000	830	250	
<i>Triturus vulgaris</i> (Smooth Newt)				X			
<i>Triturus carnifex</i> (Alpine Warty Newt)				X			
<i>Triturus alpestris</i> (Alpine Newt)							X
<i>Salamandra salamandra</i> (Fire Salamander)							X
<i>Bombina variegata</i> (Yellow-bellied Toad)		X					
<i>Bufo bufo</i> (Common Toad)		X	X	X (A)	X		
<i>Bufo viridis</i> (Green Toad)			X	X (A)		X	
<i>Hyla intermedia</i> (Italian Tree Frog)				X (A)			
<i>Rana latastei</i> (Italian Agile Frog)			X	X (A)	X		
<i>Rana temporaria</i> (Common Frog)	X	X	X	X (A)	X		
<i>Rana dalmatina</i> (Agile Frog)			X	X (A)	X		
<i>Rana lessonae</i> and <i>R. kl. esculenta</i> (Green Frogs)				X (A)	X	X	
<i>Pelobates fuscus</i> (Common Spadefoot)							X

X: species recorded. Reach IV: A: Species found in the active floodplain. For comparison, we included for reach IV data from three sampling dates (March, May, July) as for all other reaches.

reach ranged from 1 species (Reach I) to 9 taxa (Reach IV) (Table 1).

In the main study area (Reach IV), eight taxa were identified in the riparian forest and seven taxa in the active plain. *Bufo bufo* and *Rana latastei* were the most common species in active and riparian floodplain habitats. *Bufo viridis* was restricted to the active corridor; *Triturus vulgaris* and *T. carnifex* were only observed in the riparian forest. Average species richness was higher in riparian forest water bodies (maximum of six species per water body, mostly 2–3 species per pond) compared to the active floodplain (mostly 1–2 species per pond, with a maximum of five taxa; Fig. 5). The only parameters tested that were significantly correlated with species richness were surface water temperature (active floodplain and riparian forest, positive correlation), distances to vegetated islands (active floodplain, negative correlation), and fish density (active floodplain, positive correlation; Table 2).

In the riparian forest, total number of egg mass clutches (as a surrogate for adult female population density) of brown frogs combined (*R. latastei*, *R. dalmatina*, *R. temporaria*) and common toad (*B. bufo*) were as high as 1850 and 700, respectively (Fig. 6). In the active plain, the total number of egg clutches was 350 for brown frogs and 65 for the common toad, respectively. The maximum number of egg masses per individual water body in the floodplain (active plain and riparian forest) was 150 for brown frogs and 200 for *B. bufo*. Total and average (per hectare surface water) egg mass density of *B. bufo* and brown frogs was between six and

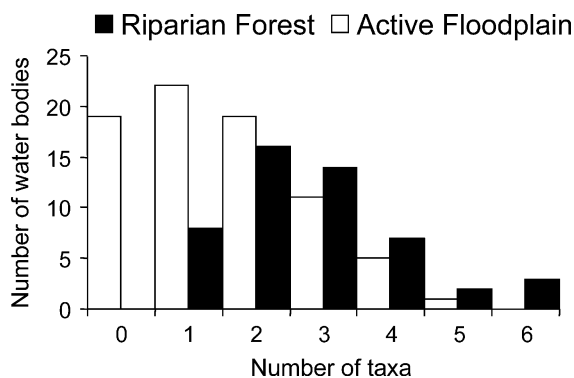


Figure 5. Frequency distribution of floodplain waters (active and riparian forest habitats) with different taxa richness.

ten times lower in the active floodplain compared to the riparian forest. Egg mass density of brown frogs was correlated with pond size (positive correlation) in the riparian forest, and to temperature (positive), fish density (positive) and distance to islands (negative) in the active plain. Density of *B. bufo* was correlated with pond size (riparian forest), vegetation cover and fish density (active plain; Table 2). Based on the area of surrounding vegetated terrestrial habitats (vegetated islands and riparian forest), within a certain distance to ponds (see methods), egg mass density measured 23 egg masses per hectare and was very similar in the active plain and the adjacent riparian forest.

Indicator species and species association

Based on TWINSPLAN analyses of amphibian species, active floodplain and riparian forest habitats were clearly distinct (Fig. 7). *Bufo viridis* was an indicator species of bare gravel ponds, *R. temporaria* and *B. bufo* characterised island- and LWD-associated waters in the active floodplain; however, *T. vulgaris* and *R. dalmatina* primarily occurred in isolated ponds in the riparian forest dominated by fine sediments and a dense vegetation cover. Ponds along the margin of the active corridor were colonised by species characteristic of both the active plain and the riparian forest (mainly *B. bufo* and *R. latastei*; Fig. 7). No positive spatial species associations were observed;

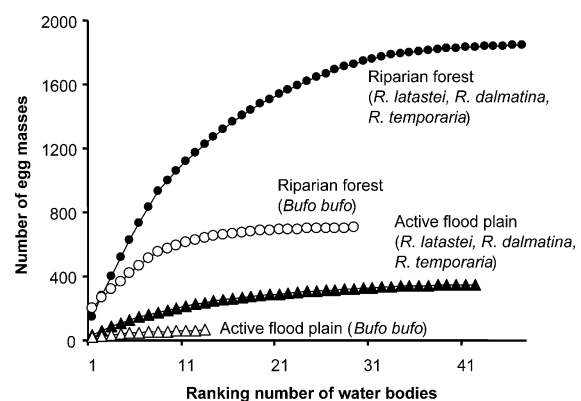


Figure 6. Cumulative number of egg-masses of brown frogs (*Rana latastei*, *R. temporaria*, *R. dalmatina*) and common toad (*Bufo bufo*) versus number of water bodies sampled from the active floodplain and the adjacent riparian forest. Ponds are arranged according to densities of egg masses, from the highest to the lowest.

Table 2. Rank-correlations of species diversity and egg mass density (egg masses of brown frogs, *Rana temporaria*, *R. latastei* & *R. dalmatina*, and the common toad, *Bufo bufo*) with various extrinsic factors

	Active floodplain (n = 82)	Riparian forest (n = 48)
Taxa richness (S = 10)		
Temperature (°C)	R = 0.41 (p < 0.001)	R = 0.29 (p = 0.02)
Fish density (1–4)	R = 0.40 (p < 0.001)	R = 0.05 (p = 0.71)
Distance from vegetated islands (m)	R = -0.34 (p = 0.02)	N. A.
Egg mass density: Brown frogs (<i>Rana latastei</i> , <i>R. temporaria</i> , <i>R. dalmatina</i>)		
Area (ha)	R = 0.12 (p = 0.30)	R = 0.59 (p < 0.001)
Temperature (°C)	R = 0.36 (p < 0.001)	R = 0.27 (p = 0.05)
Fish density (1–4)	R = 0.40 (p < 0.001)	R = 0.19 (p = 0.18)
Distance from vegetated islands (m)	R = -0.38 (p < 0.01)	N. A.
Egg mass density: <i>Bufo bufo</i>		
Area (ha)	R = 0.05 (p = 0.65)	R = 0.36 (p = 0.01)
Fish density (1–4)	R = 0.30 (p = 0.007)	R = 0.12 (p = 0.39)
Vegetation cover (1–4)	R = 0.42 (p = 0.002)	R = -0.16 (p = 0.26)

N.A. not applicable. Only significant correlations are shown.

however, significant negative spatial associations occurred between *R. dalmatina*, *R. latastei*, *R. temporaria* and *B. bufo* (data not shown).

Nestedness

Nestedness-analyses indicated that amphibians were distributed as non-random assemblages (Table 3). Observed 'system temperatures' ranged from 5.0 (active floodplain) to 11.7 (riparian forest) and were significantly lower than estimated values produced by Monte Carlo simulations ($p < 0.001$). A few species showed unexpected presence and absence patterns (idiosyncratic species). In the riparian forest, *R. latastei* and *T. vulgaris* had 'temperatures' that were higher compared to the average. In the active floodplain, *B. viridis* had slightly higher temperatures compared to the average of all other taxa, demonstrating that these species tended to be absent from species-rich sites. 'System temperature' in the active floodplain of the Tagliamento was much lower compared to regulated floodplains along the Danube and Rhône rivers (Table 3).

Discussion

Floodplains along the Tagliamento are characterised by a very high density and diversity of aquatic

habitats, including ephemeral, lentic and lotic water bodies (Fig. 2; Arscott et al., 2000; Karaus et al., 2005). In gravel-bed rivers, lentic water bodies represent only a small proportion of total aquatic area; however, based on their number and variety, ponds are key features for maintaining aquatic invertebrate diversity in many floodplain systems (Homes et al., 1999; Ward et al., 1999a; Arscott et al., 2005; Karaus et al., 2005). Arscott et al. (2000), who compared aquatic habitat diversity in the six geomorphic reaches along the Tagliamento, found the highest habitat diversity in the island-braided floodplain (Reach IV). This is also the reach with the highest amphibian diversity (Table 1). Total species richness of amphibians along the Tagliamento was similar to values reported for the largest Central European rivers such as the Rhône and Danube (Ward et al., 1999a; Table 3). This suggests that dynamic gravel-bed rivers, such as the Tagliamento, are focal areas for amphibians. Moreover, endangered species such as *R. latastei* (endemic to northern Italy) developed large populations in the Tagliamento floodplain (based on egg mass density). *Bufo bufo*, the most frequent species in the active plain, exhibits a pronounced reproduction plasticity that allows this species to explore dynamic and ephemeral habitats (Kuhn, 1993). This includes spawning synchronisation with the hydrology, a fast metamorphosis, and the formation of small spawning aggregations.

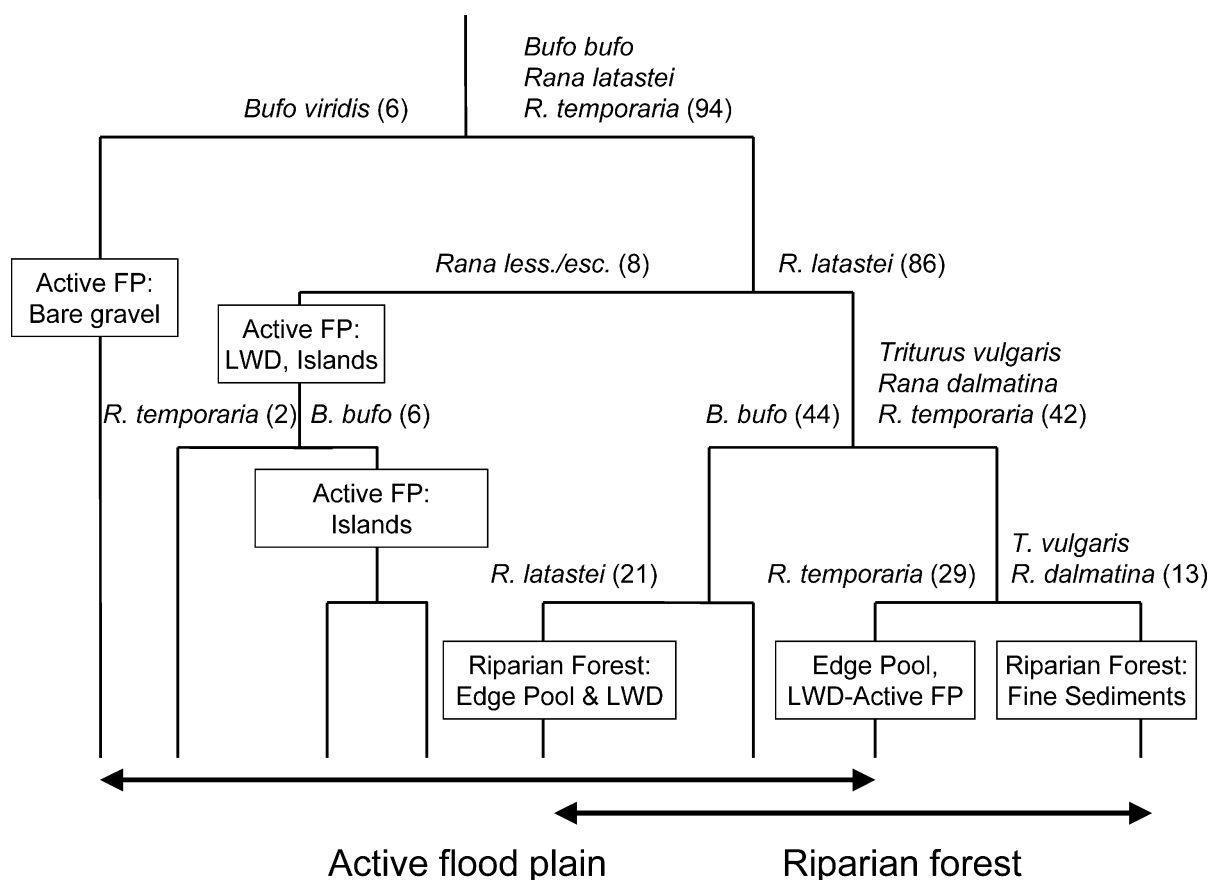


Figure 7. TWINSpan separation of floodplain waters and the indicator species responsible for the separation. LWD: Large woody debris.

The present results demonstrate that most species were able to utilise active floodplain habitats as spawning sites, although frequency of species occurrence, egg mass density, and the average number of species per water body were lower than in the adjacent riparian forest. None of the measured parameters, except water temperature, influenced amphibian diversity in both parts of the floodplain. For example, a significant positive relationship between egg mass density and pond size was found for the riparian forest but not for the active plain. This finding corresponds to data from many other wetlands, such as depression wetlands in the southern United States (Snodgrass et al., 2000) and ponds in Switzerland (Oertli et al., 2002) where no relationship between amphibian species richness and habitat size were observed. Pond size matters, not for species richness but for egg mass density, at least in the

riparian forest. This implies that species distribution patterns are determined by other characteristics of water bodies, such as hydrological connectivity (Morand & Joly, 1995), pond age (Merovich & Howard, 2000), presence of predators (Werner & McPeck, 1994), vegetation structure and cover (Healy et al., 1997), or the presence of vegetated islands and large woody debris (LWD; this study).

During their life cycle most amphibian species depend on both aquatic and terrestrial habitats. In the active floodplain, most water bodies colonised by amphibians were associated with vegetated islands and LWD. Hence, vegetated islands and large accumulations of woody debris were expected to control species numbers and egg mass density as demonstrated by the significant correlation between species richness and the distance to vegetated islands (so called 'wood benefit' *sensu*

Table 3. Nestedness analysis for the Tagliamento (active floodplain, riparian forest; Reach IV) compared with data for floodplains along the Danube (Austria) and the Rhône (France). Regelsbrunn (Danube) is the most dynamic of these additional floodplains, Obere Lobau (Danube) the most isolated one

	<i>N</i> sites	<i>N</i> taxa	Fill (%)	System <i>T</i>	Generated <i>T</i> (mean ± SD)	Significance
Tagliamento (Reach IV)						
Riparian Forest	50	9	30.4	11.7	53.2 ± 6.1	< 0.001
Active Floodplain	58	7	29.0	5.0	49.9 ± 6.9	< 0.001
Rhône (Jons, Upper Rhône)	17	10	28.7	12.9	45.1 ± 8.7	< 0.001
Danube (Regelsbrunn)	56	10	28.2	16.1	52.9 ± 5.0	< 0.001
Danube (Orth)	28	7	37.7	17.4	50.5 ± 7.2	< 0.001
Danube (Untere Lobau)	73	9	29.3	10.5	55.5 ± 5.3	< 0.001
Danube (Obere Lobau)	68	9	30.3	18.3	56.6 ± 5.6	< 0.001
Danube (Obere Lobau, only isolated sites)	29	9	36.0	31.5	50.9 ± 6.6	< 0.001

'Fill' represents the presences (%) in the site-taxon matrix, 'System *T*' is the system temperatures observed, and 'Generated *T*' is the system temperatures generated by Monte Carlo randomisations (500 iterations each). Data from the Rhône: Morand & Joly (1995). Danube: C. Baumgartner (unpubl. data).

Gurnell & Petts, 2002). Further, egg mass density of brown frogs per ha vegetated island was similar to densities in the riparian forest and was much higher than in regulated floodplains. The average density of egg masses of brown frogs in regulated floodplains along the Danube was about 3.5 per ha floodplain forest (Pintar et al., 1997; Baumgartner et al., 1997); this was one-order-of magnitude lower than in the present study. We may expect that LWD and vegetated islands play a pivotal role for (i) providing potential terrestrial habitats for adults (e.g., hibernation), (ii) creating aquatic habitats, and (iii) facilitating the subsequent colonisation by amphibians (Gurnell et al., 2005). LWD increases the permanency of water bodies (deep scour ponds at the apex of wood accumulations; e.g., Abbe & Montgomery, 1996), provides shelter during flood events, reduces predation by fish and birds, increases food availability by providing surfaces for biofilm development, and serves as a stable structure to attach egg masses (e.g., by brown frogs, *B. bufo*). The unexpected positive relationship between fish density and amphibian diversity in the active floodplain demonstrated that LWD may facilitate the coexistence of otherwise mutually exclusive groups. We did not investigate fish in more detail, but we observed that ponds were primarily colonised by fish larvae and young fish which most probably do not feed extensively on amphibian larvae. In addition, large wood and extensive shallow areas provide shelter for amphibians against predation.

Amphibians showed highly ordered distributional patterns (low 'system temperature'), especially in the active floodplain. This high degree of nestedness implies that a few common species tended to be ubiquitous and rare species tended to occur only at species-rich sites. As in many other systems (e.g., Patterson & Brown, 1991; Hecnar & Mc'Closkey, 1997), both extinction and selective colonisation may have contributed to structuring the nested assemblages of floodplain amphibians. The high turnover rate of aquatic water bodies ('selective' extinction of amphibians caused by flood fill/scour or drying) and the species preference of ponds associated with LWD and islands (selective colonisation) can explain the very high degree of nestedness in the active floodplain. Indeed, nestedness in the active plain was considerably higher than that reported in most investigations of aquatic and terrestrial areas (e.g., 294 examples listed in Atmar & Patterson, 1995; Table 3). Similar high degrees of nestedness have only been described for fish communities in Australian desert springs (Kodric-Brown & Brown, 1993). Those authors concluded that a common biogeographic history, similar contemporary environments and hierarchical ecological relationships among species were necessary to create such a deterministic assembly structure. In Swedish streams, however, Malmqvist & Hoffsten (2000) calculated 'system temperatures' that ranged from 12.6 for Simuliidae to 29.2 for Plecoptera. This lower degree of nestedness in streams

(higher 'system temperature') was expected to result from a higher probability of exchange rates between sampling sites (high degree of connectivity) and/or by high dispersal properties of species (e.g. drifting invertebrates, wind-dispersed plants; e.g. Kadmon, 1995). The much higher 'system temperature' calculated for regulated floodplains (Table 3) may result from a stable degree of connectivity, either between individual water bodies or by the presence of a closed floodplain forest matrix that may facilitate the exchange of larval and adult amphibians.

Nestedness has also major implications for the development of conservation strategies since a high degree of nestedness (low 'system temperature') means that the protection of the most diverse habitats is required in order to also conserve rare species. Hecnar & Mc'Closkey (1997), for example, concluded from their investigation of the amphibian fauna in 118 ponds in SW Ontario (Canada) that single large reserves were preferable to several small reserves for the conservation of temperate pond-dwelling amphibian assemblages. Alford & Richards (1999) concluded from their extensive review that most amphibians exhibited a metapopulation structure (Marsh & Trenham, 2001). Since in the active channel along the Tagliamento the exact location of sink and source habitats considerably changes with floods (half-life expectancy of ponds is less than 7 months, Van der Nat et al., 2003), the preservation of an entire floodplain complex is required for maintaining intact amphibian populations (De Nooij et al., 2006). Our results also demonstrate that amphibians in the active floodplain are differently organised than in the riparian forest (based on degree of nestedness), and that most likely different variables control the distribution and density in the active and passive floodplain sections (Table 2).

Natural floodplains are distinctive landscapes with respect to their natural richness and their bioproduction. River canalisation has restricted the active part of floodplains to a narrow ribbon of riparian vegetation along the main river channel. Elimination of islands and the reduced diversity of floodplain ponds have detrimental effects on both aquatic and terrestrial organisms (e.g. Stanford et al., 1996; Karaus et al., 2005). In regulated rivers, amphibians were eliminated from the active corridor and restricted in their occurrence to the

isolated parts of the floodplain. Re-establishing hydrological connectivity between the river and its floodplain has been generally regarded as having negative effects on amphibian species. The present investigation, however, demonstrates that even one of the most dynamic river corridors in Europe (Tagliamento) provides extensive habitats for diverse amphibian communities. Consequently, there is no general conflict between maintaining/creating high fluvial dynamics and high amphibian diversity and density. This is supported by recent studies along the Danube (Austria), where the reconnection of formerly isolated floodplains did not affect amphibian diversity and density in a negative way (C. Baumgartner, unpubl. data).

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