

# *The role of lateral connectivity in the maintenance of macrophyte diversity and production in large rivers*

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## ABSTRACT

1. Large European river floodplains have been intensively reduced through human activities over several millennia. Ecological assessments of natural large river systems remain rare and potentially flawed since they typically omit either the main channel of the river or, more commonly, aquatic habitats that occur naturally in the floodplain of dynamic systems.

2. Surveys were conducted over a longitudinal and lateral gradient to assess distribution, richness and production of macrophytes along two little-disturbed large upland rivers in Scotland.

3. Lateral dynamics, through the creation of backwaters, underpinned the occurrence, abundance and production of macrophytes in these rivers. Indeed, backwaters, despite representing only 5% of the total area of aquatic habitat, supported a significantly higher concentration of species (65% of species recorded at the riverscape scale were unique to backwaters) than the main channel.

4. The frequency with which backwaters were connected to the main channel during flood flows influenced their species richness. Highest species richness in backwaters was typically found at low connectivity. Standing crop in backwaters was 150 times higher per unit area than in the main channel, while at the riverscape scale backwaters accounted for an average 89% of aquatic plant biomass. The highest plant biomass was found at low and medium connectivity with the main channel.

5. Backwaters appear to be crucial habitats in maintaining macrophyte diversity and production in large river ecosystems. These results emphasize the importance of river hydrodynamics and lateral connectivity in maintaining macrophyte community diversity along large rivers. The results illustrate also the potentially very significant role of backwaters as source habitats supplying propagules and organic matter to downstream reaches.

6. It is argued that the entire riverscape (floodplain plus main channel) must be considered in the holistic assessment of such systems, while protection of this resource requires greater recognition of linkages within and across habitats, both aquatic and terrestrial, to be effective.

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## INTRODUCTION

Natural river floodplains are among the most biodiverse and productive ecosystems in the world (Tockner *et al.*, 2000). Nevertheless, floodplains have been heavily reduced by human activities. At present

in Europe at least 90% of the area of floodplains has disappeared through channel straightening and embankment (Tockner and Stanford, 2002). The main drivers for such reductions are flood control, navigation, hydropower and agricultural expansion

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(Scholten *et al.*, 2005). For instance, in Germany more than 76% of the Elbe floodplain has been converted into agriculture (Scholten *et al.*, 2005). In the UK no such figures exist but it is widely acknowledged that floodplains have been modified very extensively for agriculture (Bailey *et al.*, 1998). River flow regulation and reduction dictate that channel and flow dynamics are increasingly disconnected from floodplain ecosystems. Thus, near-natural examples of large ecologically intact rivers have become very rare (Bornette and Amoros, 1991; Nicolas and Pont, 1997; Yager *et al.*, 2011).

Natural river floodplains present a mosaic of habitats generated by fluvial deposition and lateral instability in planform associated with a dynamic flow regime. Such processes lead to the formation of a variety of water bodies or backwaters within the riverscape that are almost lentic in character. In this paper, the term 'backwater' refers to a former river channel that has lost its upstream connection with the main stem through alluvial or woody debris deposition, but retains a downstream connection to the river channel (Bornette *et al.*, 1998a). During flood flows the upstream connection between backwater and main stem is briefly restored thus creating full continuity with the river corridor.

The restricted connectivity of backwaters to the river is believed to play a key role in providing refuge, reproduction and nursery habitats for various aquatic biota (Boedeltje *et al.*, 2001; Amoros and Bornette, 2002; Nunn *et al.*, 2007). Backwaters may therefore be seen as reservoirs of diversity and to be a significant lateral component of river floodplains (Tockner *et al.*, 2000). Despite this, biological assessments of large rivers are typically confined to the main river channel only, or backwaters separately (Thorpe *et al.*, 2006). Thus, assessments commonly fail to consider the contribution of floodplain water bodies to the biodiversity, production and ecology of the overall riverscape or ignore the potential interactions between different aquatic habitat types. Even for some of the most studied large rivers in Europe, such as the Danube and Rhine, little comparative quantitative information exists (Tockner and Stanford, 2002; Sarbu *et al.*, 2011). Also, in many large lowland rivers the main channel is no longer free-flowing owing to impoundments for navigation or power generation which may reduce the contrast in physical character between the main channel and lateral aquatic habitats (Hohensinner *et al.*, 2004; Birk *et al.*, 2012). At a larger scale, synoptic surveys of aquatic vegetation, from which

criteria for conservation evaluation have been developed (e.g. in the UK, Palmer *et al.*, 1992; Holmes *et al.*, 1998), have ignored floodplain water bodies because they do not sit comfortably in conventional definitions of lake or river habitats.

Macrophyte surveys of rivers generally focus on small wadeable channels because of the practical difficulty of surveying macrophytes in large rivers. The channel dimensions, water velocity, depth and turbidity of large rivers demands a fundamentally different survey approach to that used in small rivers. As a consequence, knowledge of macrophyte ecology in large rivers is still limited (Franklin *et al.*, 2008). A sensible and realistic approach to monitor macrophytes in large river systems is needed to encompass more accurately the ecological relationships between the main river channel and its backwaters.

The aim of this research was to determine the role of lateral connectivity in driving the distribution, diversity and production of macrophytes in large rivers using as a case study two of the largest rivers in the UK (Tummel and Tay). This study first compares the distribution of macrophytes in main channel and backwaters using richness, composition and biomass to characterize the aquatic vegetation. Second, it analyses the response of vegetation in backwaters to various environmental variables including connectivity to the main channel. We hypothesized that: (1) backwaters will concentrate macrophytes and will be highly productive compared with the river corridor; (2) macrophyte richness and production will vary between backwaters as a function of their connectivity to the hydrologically dynamic main stem, as well as other factors, such as their fertility. From a conservation and methodological aspect this study aims to quantify the importance of riverine backwaters as aquatic habitats for macrophytes at the riverscape scale, whether they merit specific protection, and how they can contribute to the ecological assessment of large rivers.

## METHODS

### Study sites

Assessment of macrophytes took place along the rivers Tummel and Tay between Pitlochry and Perth in Perthshire, Scotland (Figure 1). The rivers Tummel and Tay are among the largest rivers in the UK (Tummel catchment: 1670 km<sup>2</sup>, average discharge: 73 m<sup>3</sup> s<sup>-1</sup>, maximum discharge: 706 m<sup>3</sup> s<sup>-1</sup>; Tay catchment: 4991 km<sup>2</sup>, average discharge: 169 m<sup>3</sup> s<sup>-1</sup>,

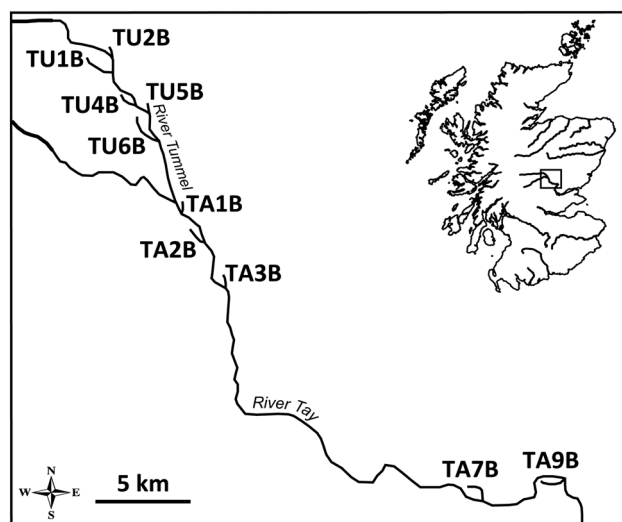


Figure 1. Map of the River Tummel and River Tay floodplain showing the position of these rivers in Scotland and the riverine backwaters that were assessed.

maximum discharge:  $1554 \text{ m}^3 \text{ s}^{-1}$ ). The reach assessed was 33 km long (5.2 km on the River Tummel and 27.8 km on the River Tay). Further details on this system can be found in Gilvear and Willby (2006). Five backwaters were monitored on each river. Backwaters were typically 200–500 m in length and, within the 33 km study reach, had a combined surface of  $0.15 \text{ km}^2$  compared with a main channel surface area of  $2.75 \text{ km}^2$ .

### Paired backwater and main channel macrophyte sampling

Backwaters and the main channel were surveyed on five occasions distributed over the growing season (May to September) of the years 2009–2011. Abundance of all aquatic macrophytes (subdivided into hydrophytes and helophytes) and their total above-ground biomass were recorded on each date. Backwaters and main channel were monitored using six transects established perpendicular to the channel. In backwaters these transects were equidistant in order to subdivide the site equally. Transects in the main channel were located adjacent to the relevant backwater by extending transects towards the river channel (Figure 2). Sampling effort was thus similar between backwaters and between backwaters and main channel. Presence of macrophytes was recorded in a 5 m wide zone centred on each transect. Plant taxa were classified as either hydrophyte (submerged + floating leaved taxa) or helophyte (emergent taxa). Macrophyte biomass was collected in a  $30 \times 30 \text{ cm}$  quadrat at three

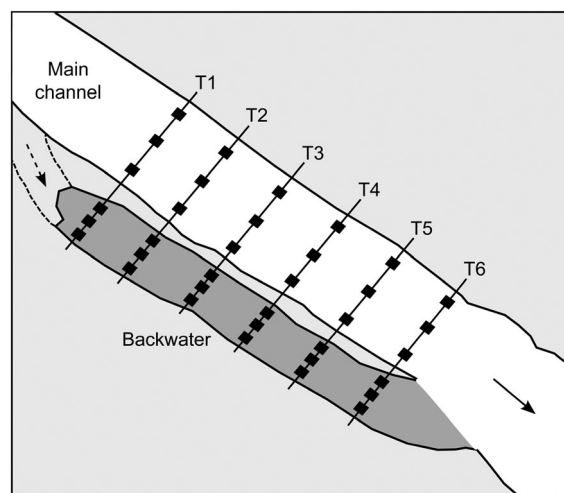


Figure 2. Macrophyte sampling method in backwaters and main channel. Lateral transects (T1 to T6) were equally distributed in backwaters and along the adjacent main channel sections. Dark grey colour represents the backwater area; white colour represents the main channel area. Species richness was surveyed along a 5 m wide strip centred on each transect (labelled T1 to T6) and biomass was measured at 18 sampling points (black squares) in main channel and backwater. Dashed section and arrow at the upstream part of the backwater represent connection between the main channel and backwater during flood flow.

equally spaced points along each transect by clipping at ground level or scraping hard substrate. Thus on each sampling occasion biomass was collected at 180 sampling points over all backwaters ( $10 \times 6 \times 3$ ). In total 1800 quadrats were sampled, divided equally between backwaters and main channel. Sampling was carried out by wading or snorkelling. For safety reasons (flow velocity  $> 1 \text{ m s}^{-1}$  and water depth  $> 3 \text{ m}$ ) some intended sampling sites in the main channel could not be sampled, but snorkelling and kayaking confirmed that these sites were very sparsely vegetated or lacked any vegetation at all.

### Laboratory processing

After collection samples were stored in a fridge at  $4^\circ\text{C}$  and processed within 5 days of collection. Each sample was separated into its component species. Samples were carefully washed to remove sediment and detritus, and then oven-dried at  $80^\circ\text{C}$  for 48 hours and weighed to determine the dry weight.

### Environmental parameters

For each backwater sinuosity, length, width, water depth and sediment size were recorded. For each sampling point in the main channel and backwaters water temperature, dissolved oxygen concentration (LDO HQ20 dissolved oxygen meter) and light intensity at the water surface and in the water

column were recorded. Light extinction profiles for the main channel and sample backwaters were constructed for PAR using a SKP 2200 light meter fitted with a SKP 210 PAR sensor. The extinction coefficient,  $k$ , was derived from these data in accordance with the Beer–Lambert Law. Also, once per month over the growing season, three water samples per backwater and one in the main channel upstream from each backwater were collected for analysis of major nutrients. Nitrate (cadmium reaction), nitrite (sulphanilamide/N-1-naphthylethylene reaction) and ammonium (Berthelot reaction) were determined with a Bran Luebbe autoanalyser 3. Total phosphorus (antimony/molybdate reaction), was read at 690 nm with a Cecil Aquarius 7000 spectrometer. Connection frequency of backwaters with the main channel during flood flows was calculated by coupling levelling data for each backwater transect with hydrological data supplied by the Scottish Environment Protection Agency from 1 January 2000 to 31 December 2010 (station 15012 at Pitlochry (Tummel) and station 15006 at Ballathie (Tay)). By comparing water level and the sill elevation at the upstream end of each backwater the increase of water level required to make an upstream connection during floods could be determined. The number of connections in the last 10 years was calculated for each backwater. In this study connection frequency refers to the average number of discrete connection events per year over the last 10 years.

### Data analysis

Analyses were performed using the R statistical package (R Development Core Team, 2011). A Wilcoxon test was used to compare species richness and standing crop between backwaters and main channel. Differences between backwaters, and the effect of timing of sampling were assessed using

the multiple comparisons Kruskal–Wallis test. Generalized Linear Models were used to test the significance of environmental variables in explaining variation in plant richness and biomass in backwaters. Biomass data were square root transformed before analysis. A log link function with Poisson distribution was used to model species richness. Environmental variables were treated as the fixed effect with site and transect as a nested random effect. Species composition in backwaters and main channel was compared using a non-metric multidimensional scaling (NMDS) ordination. Environmental determinants of vegetation composition in backwaters were tested using a canonical correspondence analysis (CCA).

Floodplain plant species richness was estimated using a sample-based rarefaction analysis to allow richness in different aquatic habitat types (main channel, backwaters, main channel + backwaters) to be compared when sampling effort was standardized (R package Vegan). Floodplain standing crop was estimated using the paired measurements of the standing crop in backwaters and main channel over the 3-year survey period. These figures were then applied to the water surface areas of both habitat types obtained from a GIS analysis to estimate the proportional contribution of different habitats to production at the riverscape scale.

## RESULTS

### Environmental characteristics of backwaters

Environmental characteristics (physical and chemical data) of the 10 backwaters and adjacent main channel sections surveyed in this study are summarized in Tables 1 and 2. These tables were compiled using data collected from June 2009 to September 2011 ( $n = 5$ ) and can be considered to represent growing season means. In the main

Table 1. General physical characteristics among surveyed main channel sections and paired backwaters

|              | Sinuosity | Width (m) | Depth (m) | Velocity (m s <sup>-1</sup> ) | Sediment (% cover) |      |        |        |
|--------------|-----------|-----------|-----------|-------------------------------|--------------------|------|--------|--------|
|              |           |           |           |                               | Silt               | Sand | Gravel | Cobble |
| Main channel |           |           |           |                               |                    |      |        |        |
| Average      | 1.1       | 71        | 2.1       | 1.6                           | 0.0                | 1    | 8      | 91     |
| Min.         | 1         | 51        | 0.6       | 0.6                           | 0.0                | 0.0  | 3      | 88     |
| Max.         | 1.2       | 105       | 9         | 3.5                           | 0.0                | 1.5  | 12     | 100    |
| Backwaters   |           |           |           |                               |                    |      |        |        |
| Average      | 1.2       | 17        | 0.75      | 0.0                           | 21                 | 17   | 11     | 51     |
| Min.         | 1.1       | 5         | 0.36      | 0.0                           | 0.0                | 0.05 | 6      | 0.0    |
| Max.         | 1.6       | 32        | 1.1       | 0.01                          | 88                 | 90   | 35     | 99.9   |



Table 2. General chemical characteristics among surveyed main channel sections and paired backwaters

| Site | NO <sub>3</sub> (mg L <sup>-1</sup> ) |               | NH <sub>4</sub> <sup>+</sup> (mg L <sup>-1</sup> ) |               | Total P (mg L <sup>-1</sup> ) |               | pH           |           | Conductivity (µS cm <sup>-1</sup> ) |               |
|------|---------------------------------------|---------------|--|---------------|-------------------------------|---------------|--------------|-----------|-------------------------------------|---------------|
|      | Main channel                          | Backwater     | Main channel                                       | Backwater     | Main channel                  | Backwater     | Main channel | Backwater | Main channel                        | Backwater     |
| TU1  | 0.148 ± 0.081                         | 0.119 ± 0.099 | 0.009 ± 0.005                                      | 0.030 ± 0.045 | 0.011 ± 0.005                 | 0.008 ± 0.003 | 7.3 ± 3.3    | 6.7 ± 0.1 | 39.0 ± 18.0                         | 51.2 ± 8.9    |
| TU2  | 0.153 ± 0.088                         | 0.475 ± 0.318 | 0.012 ± 0.006                                      | 0.014 ± 0.010 | 0.009 ± 0.005                 | 0.003 ± 0.008 | 7.4 ± 3.8    | 7.1 ± 0.2 | 42.3 ± 22.5                         | 184.7 ± 106.5 |
| TU4  | 0.156 ± 0.087                         | 0.597 ± 0.299 | 0.013 ± 0.004                                      | 0.012 ± 0.008 | 0.007 ± 0.003                 | 0.008 ± 0.012 | 7.4 ± 3.8    | 7.2 ± 2.0 | 41.2 ± 21.3                         | 98.1 ± 26.2   |
| TU5  | 0.168 ± 0.099                         | 0.154 ± 0.097 | 0.007 ± 0.004                                      | 0.012 ± 0.008 | 0.011 ± 0.006                 | 0.008 ± 0.004 | 7.5 ± 3.9    | 7.2 ± 3.3 | 41.4 ± 22.1                         | 40.3 ± 19.7   |
| TU6  | 0.137 ± 0.074                         | 0.306 ± 0.225 | 0.011 ± 0.004                                      | 0.042 ± 0.024 | 0.009 ± 0.004                 | 0.022 ± 0.008 | 7.6 ± 3.9    | 6.9 ± 0.3 | 40.6 ± 21.4                         | 142.7 ± 17.8  |
| TA1  | 0.157 ± 0.092                         | 0.316 ± 0.240 | 0.006 ± 0.003                                      | 0.020 ± 0.025 | 0.009 ± 0.004                 | 0.014 ± 0.006 | 7.4 ± 3.8    | 6.9 ± 0.2 | 40.7 ± 21.1                         | 108.2 ± 79.4  |
| TA2  | 0.204 ± 0.116                         | 0.180 ± 0.135 | 0.004 ± 0.003                                      | 0.004 ± 0.003 | 0.010 ± 0.005                 | 0.006 ± 0.002 | 7.3 ± 3.7    | 7.1 ± 0.2 | 43.2 ± 22.2                         | 58.8 ± 18.2   |
| TA3  | 0.190 ± 0.112                         | 0.268 ± 0.165 | 0.009 ± 0.005                                      | 0.007 ± 0.005 | 0.008 ± 0.004                 | 0.007 ± 0.003 | 7.4 ± 3.8    | 7.3 ± 0.1 | 42.5 ± 22.4                         | 83.8 ± 41.9   |
| TA7  | 0.150 ± 0.164                         | 0.188 ± 0.169 | 0.014 ± 0.007                                      | 0.031 ± 0.014 | 0.011 ± 0.006                 | 0.028 ± 0.015 | 7.5 ± 3.7    | 7.5 ± 0.4 | 45.8 ± 22.9                         | 133.3 ± 61.9  |
| TA9  | 0.241 ± 0.139                         | 0.555 ± 0.319 | 0.017 ± 0.008                                      | 0.023 ± 0.013 | 0.010 ± 0.006                 | 0.008 ± 0.004 | 7.5 ± 3.4    | 7.0 ± 2.9 | 41.5 ± 19.4                         | 87.7 ± 43.8   |

channel the vertically integrated light extinction coefficient,  $k$ , was typically 1.4 to 1.6 m<sup>-1</sup> under base-flow conditions during the growing season owing to the high humic content of river water. By contrast, backwaters exhibited high clarity and low humic content with  $k$  of 0.15–0.25 m<sup>-1</sup>. The value of  $k$  for the main channel suggests a euphotic depth of 2–3 m, although in practice biomass was negligible below 1 m presumably due to the combined effect of short accrual time and low bed stability.

### Species richness

#### Comparison between river channel and backwaters

During 2 years of macrophyte surveys 65 species were recorded (30 hydrophyte taxa; 35 helophyte taxa). Many fewer species were recorded in the main channel (all taxa: 21 spp.; 4 hydrophytes, 17 helophytes) than in backwaters over the same reach (all taxa: 63 spp.; 28 hydrophytes; 35 helophytes) (Figure 3).

At the floodplain scale 5% of species (3 spp.) were recorded only in the main channel, 30% (20 spp.) were found in both main channel and backwaters and 65% (42 spp.) were unique to backwaters. Two of the hydrophyte taxa found in the main channel (*Ranunculus fluitans* and *Fontinalis antipyretica*) were also found in backwaters, whereas *Racomitrium aciculare* and *Lemanea fluviatilis* were found only in the main channel. Nine per cent of main channel species (3 spp.) were found only there whereas 91% (20 spp.) were also common to backwaters. In backwater habitats 34% of species (20 spp.) were also recorded in the main channel whereas 66% of species (42 spp.) were

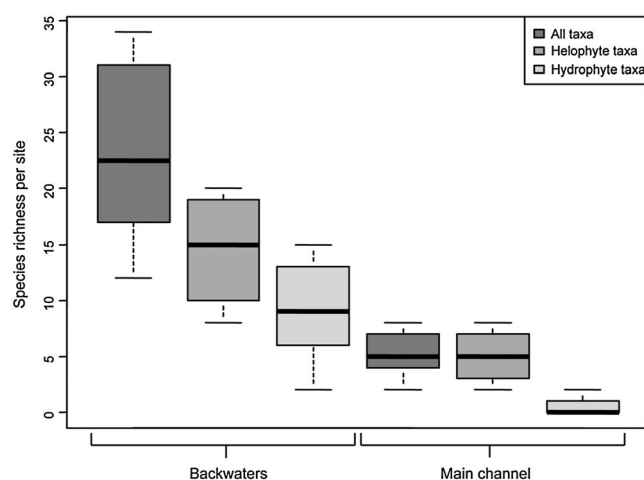


Figure 3. Species richness (all, helophyte, and hydrophyte taxa) per site between and among surveyed main channel sections and paired backwaters.

recorded only in backwaters. A full list of recorded taxa in backwater and main channel habitats is given in Appendices 1 and 2. No relationship was found between richness and distance downstream along the 33 km study reach for either main channel ( $R^2 = 0.017$ ;  $P$ -value = 0.96) or backwaters ( $R^2 = -0.214$ ;  $P$ -value = 0.55).

Considering all taxa recorded, richness was significantly higher in backwaters than in the main channel (Wilcoxon:  $W = 2500$ ;  $P$ -value < 0.0001). Helophytes and hydrophytes showed higher richness in backwaters than in the main channel (helophytes: Wilcoxon:  $W = 2476$ ;  $P$ -value < 0.0001; hydrophytes: Wilcoxon:  $W = 2461.5$ ;  $P$ -value < 0.0001). Across plant groups differences in species richness between main channel and backwaters were independent of the timing of sampling (all taxa: Kruskal–Wallis = 0.8821;  $df = 2$ ;  $P$ -value = 0.64;

hydrophytes: Kruskal–Wallis = 0.2238;  $df = 2$ ;  $P$ -value = 0.89; helophytes: Kruskal–Wallis = 0.9097;  $df = 2$ ;  $P$ -value = 0.63).

Analysis of compositional data by NMDS showed a clear partition between river channel and backwaters (Figure 4). No spatial pattern of similarity could be found between paired backwater–main channel sites at the floodplain scale. The Sørensen index of similarity between composition in backwaters and main channel ranged from 5% to 52% for all taxa, from 0% to 36% for hydrophytes and from 8% to 58% for helophytes. Values of the Sørensen index were not significantly correlated with connectivity for any plant groups.

Richness within individual backwaters showed no evidence of the downstream accumulation of species between successive transects that might be expected due to flow (all taxa: Kruskal–Wallis = 7.1839;  $df = 5$ ;  $P$ -value = 0.21; hydrophytes: Kruskal–Wallis = 6.8495;  $df = 5$ ;  $P$ -value = 0.23; helophytes: Kruskal–Wallis = 6.0324;  $df = 5$ ;  $P$ -value = 0.30).

#### Comparison between backwaters

Total species richness in backwaters ranged from 9 to 34. The number of hydrophytes ranged from 1 to 15 and helophytes from 7 to 20. Richness varied significantly between sites (Kruskal–Wallis,  $P < 0.0001$ ). Differences in richness between sites were independent of the time of sampling (Kruskal–Wallis,  $P > 0.05$ ). The CCA analysis showed that species composition of backwaters was related significantly ( $P$ -value = 0.01) to the frequency of connection to the main channel (Figure 5). Generalized Linear Models showed that species richness in backwaters was influenced significantly by connectivity with the main channel for all taxa

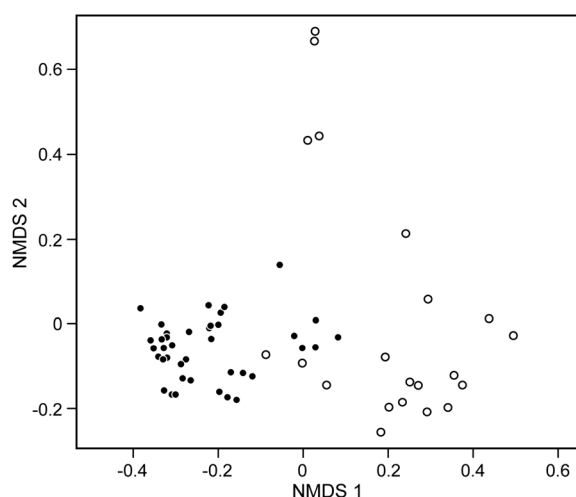


Figure 4. Non-metric multidimensional scaling ordination (NMDS) plot of species composition comparing main channel (○) and backwater (●) habitats along the rivers Tummel and Tay (stress = 0.16).

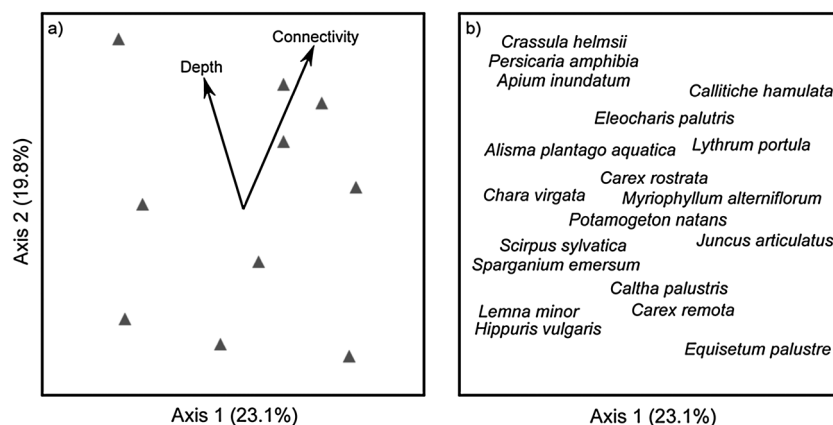


Figure 5. CCA ordination of backwaters: (a) ordination plot with distribution of sites in relation to connectivity and water; (b) species plot showing the distribution of the most common species recorded in surveyed backwaters.

and for helophytes ( $P$ -value  $< 0.05$ ). The relationship between connectivity frequency and species diversity (grouped as either all, helophyte or hydrophyte taxa) is presented in Figure 6. Water depth was also a significant factor but of lower importance (all taxa:  $P$ -value  $< 0.05$ ). No significant explanatory variables were detected for hydrophyte richness.

#### Floodplain species richness estimation

Species richness estimation at the floodplain scale using a species accumulation curve constructed by randomized re-sampling demonstrated a consistently higher number of species in backwaters than in the main channel (Figure 7). Once sampling effort exceeded 25 standard samples the estimated species richness was asymptotic and was three times higher

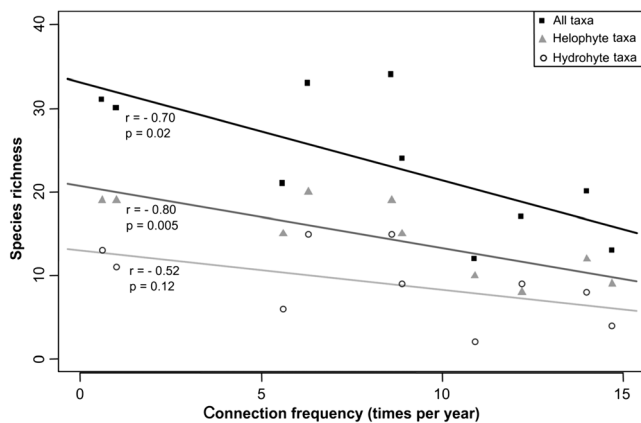


Figure 6. Relationship between connection frequency and species diversity of all, helophyte, and hydrophyte taxa.

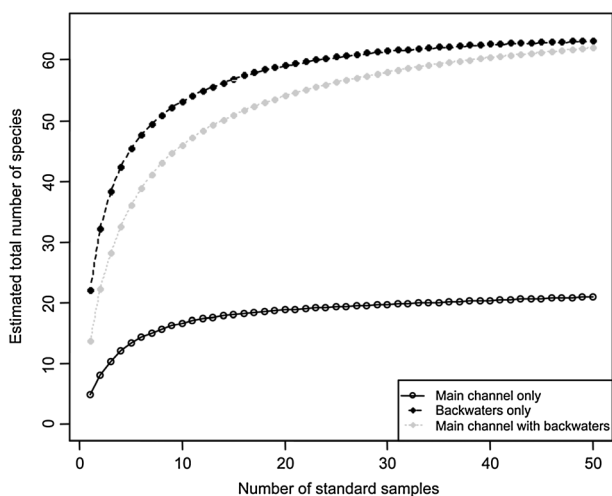


Figure 7. Species accumulation curve (constructed by sample-based rarefaction analysis) for main channel only, backwaters only, and main channel with backwaters, showing species accumulation with increasing numbers of transects sampled.

in backwaters (60 spp.) than in the main channel (20 spp.). An aggregate sample derived from a combination of backwaters and main channel was slightly less species-rich than backwaters alone owing to the small number of unique species associated with the main channel compared with backwaters, but this aggregate ultimately converged to the same richness of 60 spp. The differential between the channel-only species pool, compared with the paired main channel plus backwaters together provides an indication of the scale of undersampling that will occur in large rivers if surveys are restricted to the main stem. Equally it indicates the potential scale of species loss if backwater habitats are disconnected from the main channel by engineering or flow regulation or degraded by drainage or infilling.

#### Standing crop

##### Comparison between river corridor and sampled backwaters

Plant biomass was significantly higher in backwaters than in the river corridor (Wilcoxon:  $W = 534047$ ;  $P$ -value  $< 0.0001$ ). Mean biomass produced in the main channel was  $0.3 \text{ g m}^{-2}$  compared with  $40.3 \text{ g m}^{-2}$  in backwaters. Biomass in backwaters was thus, on average, 150 times higher than in the main channel. Biomass in backwaters was generally a result of production by two to four species per sampling point (most commonly *Potamogeton natans*, *Myriophyllum alterniflorum*, *Carex rostrata* and *Callitriche hamulata*), whereas in the main channel it was a result of only one or two species maximum. Timing of sampling did not influence the difference in biomass between river channel and backwaters (Figure 8); biomass was always significantly higher in backwaters than in the main channel

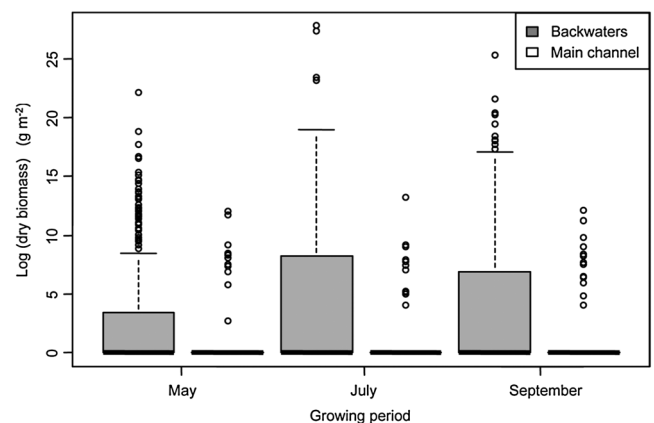


Figure 8. Variation in standing crop in backwaters and main channel according to timing of sampling with respect to growing season.

(May:  $W = 44\,566$ ,  $P\text{-value} < 0.0001$ ; July:  $W = 27\,460$ ,  $P\text{-value} < 0.0001$ ; September:  $W = 21\,779$ ,  $P\text{-value} < 0.0001$ ). No relationship was found between biomass and distance downstream on the 33 km study reach for either main channel ( $R^2 = -0.148$ ;  $P\text{-value} = 0.68$ ) or backwaters ( $R^2 = -0.110$ ;  $P\text{-value} = 0.76$ ).

#### *Comparison between backwaters and main channel transects*

Biomass was highly variable between backwaters (min  $< 0.1\text{ g m}^{-2}$ ; max  $= 168.6\text{ g m}^{-2}$ ) and significantly different between sites (Kruskal–Wallis  $= 776.1$ ;  $df = 9$ ;  $P\text{-value} < 0.0001$ ). Timing of sampling had a significant effect on biomass recorded in backwaters ( $df = 2$ ,  $P\text{-value} < 0.0001$ ) but not in main channel sections ( $df = 2$ ,  $P\text{-value} = 0.61$ ). Lowest biomass was found in May ( $27.2\text{ g m}^{-2}$  in backwaters and  $0.2\text{ g m}^{-2}$  in the main channel), reaching a peak in backwaters in July ( $50.6\text{ g m}^{-2}$ ) but remaining stable in the main channel ( $0.2\text{ g m}^{-2}$ ). In September biomass decreased in backwaters ( $45.8\text{ g m}^{-2}$ ) and remained similarly low in the main channel ( $0.3\text{ g m}^{-2}$ ). Differences in biomass were found along the longitudinal gradient within backwaters (Kruskal–Wallis: chi squared  $= 13.962$ ;  $P\text{-value} = 0.016$ ;  $df = 5$ ). Biomass was significantly higher at transects located mid-way along backwaters whereas both upstream and downstream ends supported less biomass, suggestive of the effects of increased physical disturbance. Generalized Linear Models showed that biomass in backwaters was not influenced by connectivity with the main channel ( $P\text{-value} > 0.05$ ). No significant explanatory variables were detected to explain biomass. However, sites with intermediate connectivity with the main channel had the highest production ( $80.9\text{ g m}^{-2}$ ;  $168.6\text{ g m}^{-2}$ ).

#### *Contribution to standing crop at the floodplain scale*

At the floodplain scale, along the 33 km reach of the rivers Tummel and Tay surveyed, backwaters

and main channel accounted for 5% and 95%, respectively, of the total area of aquatic habitat. Visual inspection of maps for large rivers in Europe and North America suggests that this figure is fairly typical of natural systems. Based on this relative proportion, backwaters made a substantially larger contribution to floodplain standing crop than the main channel. Averaged across the growing season backwaters accounted for 89% (2073 kg) of the standing crop in aquatic habitats at the floodplain scale compared with just 11% (264 kg) in the main channel (Table 3).

## DISCUSSION

### Macrophyte distribution

The occurrence and distribution of macrophytes in the floodplain had a strong lateral dimension. A profound difference was found between the river channel and backwaters (Figure 3 and 4). Macrophytes were principally recorded in backwaters since the standing water conditions were favourable for colonization and growth (Bornette *et al.*, 1998a). Differences were even more pronounced with regards to strictly aquatic species. Recent studies of European large rivers (e.g. Danube) have underlined the presence of many macrophyte species in the main channel (Breugnot *et al.*, 2008; Janauer *et al.*, 2010) contrasting with the present results. However, many large European rivers are heavily degraded by eutrophication and impoundment which may lead to more favourable, albeit unnatural, conditions for macrophyte growth in the main channel (Birk *et al.*, 2012). In previous studies on the distribution of riverine macrophytes, velocity, flow regime, water depth, and sediment size have all proved to be significant factors (Chambers *et al.*, 1991; Riis *et al.*, 2001; Riis and Biggs, 2003; Demars and Harper, 2005; Makkay *et al.*, 2008; Capers *et al.*, 2009).

In backwaters, macrophyte species richness was primarily influenced by connectivity with the main channel, as also reported by Robach *et al.* (1997),

Table 3. Distribution of dry weight standing crop in a standard unit of floodplain aquatic habitat ( $\text{km}^{-2}$ )

|              | Area of<br>floodplain aquatic habitat | Percentage of<br>floodplain aquatic habitat | May  |     | July |     | September |     |
|--------------|---------------------------------------|---|------|-----|------|-----|-----------|-----|
|              | ( $\text{km}^2$ )                     | %   | kg   | %   | kg   | %   | kg        | %   |
| Main channel | 2.75                                  | 95  | 234  | 15  | 233  | 8   | 325       | 12  |
| Backwaters   | 0.15                                  | 5   | 1369 | 85  | 2545 | 92  | 2306      | 88  |
| Total        | 2.90                                  | 100   | 1603 | 100 | 2779 | 100 | 2631      | 100 |



whereas water depth was of secondary importance. Species richness was negatively correlated with increasing connectivity (or disturbance intensity). Thus, aquatic vegetation will probably experience significant abiotic constraints in becoming established in the main channel. The interaction of these environmental factors strongly discriminates between macrophyte distribution in the river channel and backwaters. Accordingly, the estimated number of species at a floodplain scale (Figure 7) indicates that backwaters will contribute significantly to diversity (65% of species in this study) and that the loss of lateral connectivity and aquatic habitats associated with human activities will therefore severely reduce biodiversity in large river systems (Ward and Tockner, 2001). Spatial turnover of species between backwaters themselves was also relatively high contributing to a high overall species pool as backwaters covered a wide range of connectivity (Figures 5 and 9(b)–(d)). In contrast, the main channel was relatively uniform with respect to factors that define viable habitat for macrophytes (Figure 9(a)) and consequently different sites in the main channel accumulated species at a very low rate.

Plant species composition and abundance has remained stable in these backwaters across several years, even though connection, via major flood events, has occurred on many occasions. More detailed investigation is therefore required to identify which aspects of connectivity, such as

physical flow disturbance, mediation of dispersal, or other ecological processes, are driving species richness and biomass production.

### Productivity of macrophytes at the river floodplain scale

Bornette *et al.* (1998a) hypothesized that floodplain productivity would be mainly supported by backwaters. This is confirmed by the present study. On average, and across the growing season, main channel biomass was  $0.3 \text{ g m}^{-2}$  compared with  $40.3 \text{ g m}^{-2}$  in backwaters. Standing crop was therefore 150 times higher in backwaters than in the main river. However, biomass in backwaters was mainly driven by habitat variability in the floodplain and not by connectivity (Robertson *et al.*, 2001). As in Amoros and Bornette (2002) highest biomass occurred at a medium disturbance regime, which might reflect an optimal equilibrium for production between physical disturbance at high connectivity, versus tree shading, potential nutrient depletion and competitive exclusion by floating-leaved species with low submerged biomass (e.g. nymphaeids or lemniids) at low connectivity. In the backwaters studied, and unlike some previous studies, nutrient concentrations did not control biomass (Bedford *et al.*, 1999; Hilton *et al.*, 2006) possibly because the nutrient concentrations were consistently low in most sites. Differences in biomass between

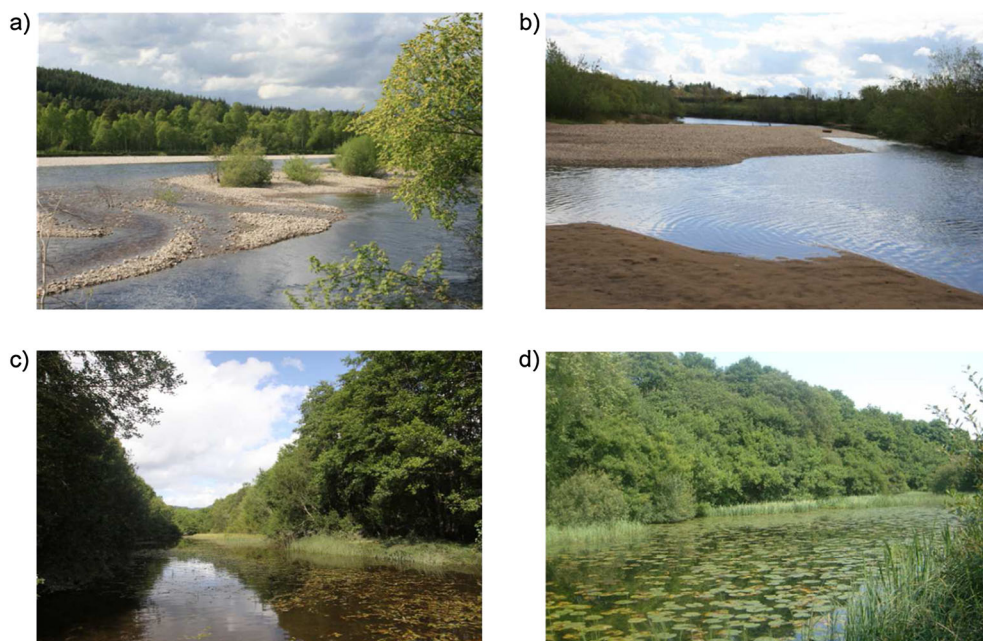


Figure 9. Photographs of (a) Ballinluig on the River Tummel, 2 km upstream of the confluence with the River Tay; and backwaters experiencing: (b) high connection frequency (TA9B); (c) intermediate connection frequency (TU1B); (d) low connection frequency (Bloody Inches on River Tay) with the main river channel.

backwaters and the main channel were independent of the timing of sampling with respect to the growing season (Figure 8). At a larger scale backwaters made a very high contribution to floodplain standing crop, accounting for 89% of aquatic plant biomass produced across the growing period (Table 3). A peak of production was reached in July where 92% of biomass was produced in backwaters. Previous quantitative assessments of production in different components of the floodplain are rare but this result is likely to be typical of undisturbed systems.

In the River Continuum Concept (RCC) production within the main stem of medium sized and lowland rivers is viewed as being mainly supported by *in situ* vascular hydrophytes and phytoplankton and algal production (Vannote *et al.*, 1980). The RCC has been applied to upstream reaches and large regulated rivers but is inappropriate for natural river floodplains as it values only the main river channel and ignores the importance of production in lateral habitats (Thorp *et al.*, 2006). In the flood pulse concept, Junk *et al.* (1989) drew attention to the significant lateral component of energy inputs to extensive floodplains and the ecological consequences of episodic flood pulses. Since then some research has demonstrated that lateral habitats in large rivers are responsible for driving structural and functional processes in river systems, such as production and nutrient cycling (Hein *et al.*, 2003; Preiner *et al.*, 2007). The present study demonstrates that lateral habitats associated with low energy flows, higher transparency of the water column and nutrient inputs from the main channel (Preiner *et al.*, 2007) produce favourable conditions for primary production by higher plants.

### **Nested functional role of backwaters in river–floodplain ecology**

This research illustrates the significant production occurring in backwaters and its potential contribution to the river–floodplain ecosystem (Thorp *et al.*, 2006). Equally, Battle and Mihuc (2000) stressed the importance of backwater vegetation in decomposition and nutrient recycling. During high-flow disturbances fresh plant material and propagules (Henry *et al.*, 1996), as well as inorganic matter, are exported from backwaters (Tockner *et al.*, 1999) which are thus key source habitats in large river systems (Cellot *et al.*, 1998). It is therefore tempting to say that backwaters are

critical for nutrient recycling or for fish reproduction in large rivers, and thus for the wider ecosystem services that rivers provide. However, for nutrients or organic inputs, as well as passive propagule dispersal, their fate in downstream reaches and water bodies of the floodplain is uncertain (Cellot *et al.*, 1998). Therefore, it may be unwise to generalize the influence that backwaters may exercise over floodplain functioning or downstream colonization.

### **Implications for assessment of large rivers**

The present survey provides a guiding image (Willby, 2011) of the distribution of macrophytes along a large, natural, upland river. The main channel itself is highly unrepresentative of macrophyte diversity and production at the riverscape scale, especially for hydrophyte taxa. A significant contrast between main channel and backwaters should be expected when surveying similar natural large rivers. Backwaters should therefore be considered as an inclusive part of the river system and not disregarded through convenience or convention (Bornette *et al.*, 1998b). Recognizing the contribution of floodplain water bodies to biodiversity at a riverscape scale requires well designed sampling protocols. Across backwaters, surveys should concentrate on covering a gradient of connectivity (Figures 5 and 9(b)–(d)). Human activities such as channel engineering, flow regulation, floodplain drainage and agricultural intensification will severely impair interactions between the main channel and floodplain aquatic habitats with subsequent effects on ecosystem functioning due to restrictions on the flow of biota and organic matter (Tyser *et al.*, 2001; Ward *et al.*, 2002; Janauer *et al.*, 2008). This investigation highlights the importance of a naturally dynamic flow regime since the associated processes of lateral instability and alluvial deposition promote the formation and turnover of lateral aquatic habitats in unconstrained reaches (Gilvear and Winterbottom, 1992) and regulate exchanges between the main stem and backwaters. Therefore, the existence of backwater habitats, their physical diversity, and the biota they support may yet prove to be the best guide to the integrity of large rivers, while the comparative ease of sampling backwaters may offer a partial solution to the practical difficulties of sampling main channel environments. Nevertheless, for an integrated assessment of the ecological quality of large rivers, the main stem cannot be ignored altogether.

### Conservation perspectives for macrophytic vegetation in river floodplains

This study underlines the high value of backwaters in preserving macrophyte diversity and production in river floodplains. Therefore it is critical to adequately protect residual backwaters since they remain a reservoir of aquatic vegetation that could occur in the lowland reaches of large rivers (Tockner and Stanford, 2002). However, backwaters are also used as reproductive and refuge areas for various life stages of a large range of other species (macroinvertebrates, fish, amphibians, birds, and mammals) (Amoros and Bornette, 2002) which increases their overall value. Barta *et al.* (2009) suggested that a gradient of flow conditions and connectivity of floodplain water bodies to the main channel will maintain a higher diversity of species. Thus, at the floodplain scale, river systems containing backwaters with a range of connection frequencies to the main channel should support the highest diversity of aquatic vegetation and associated species (van der Nat *et al.*, 2003) and their protection should be given a high priority.

Conservationists are by no means oblivious to the significance of floodplain aquatic habitats and there is an extensive literature on the importance of lateral river habitats for fish. Some of the most famous ornithological sites in Europe are associated with huge floodplain wetlands covered by Ramsar site designation, which effectively protects an entire wetland complex containing a variety of aquatic habitats, although fish are increasingly being cited in Ramsar designations. However, birds aside, floodplain water bodies themselves are not generally renowned for supporting large populations of rare species and as a habitat they do not feature in Annex 1 of the 1992 European Habitats Directive. Similarly, while the more recent (2000) EC Water Framework Directive places considerable emphasis on the assessment both of biological and hydromorphological quality elements in determining the ecological status of water bodies it fails even to mention the terms 'floodplain' or 'lateral connectivity', opting instead to highlight longitudinal continuity and connectivity to groundwater. Backwaters, as with many other freshwater habitats, therefore risk falling through the cracks – neglected by multiple key pieces of environmental legislation (Boon and Lee, 2005) and succeeding in achieving protection only when large enough to support important populations of qualifying bird species.

In reality floodplain backwaters themselves may be rather ill-suited to specific legal protection since this tends to pigeon-hole habitats and species, rather than recognizing the connectivity between populations, life stages, and habitats. Also, being the product of channel mobility, backwaters are rarely static features around which site boundaries can be neatly drawn. Most sites considered in the present study were in fact protected, either via designation under the Habitats Directive as Special Areas of Conservation (SAC), through being aligned with the Annex I priority habitat 'alluvial forests of alder, ash and white willow' (Habitat Type: H91E0), or by national designations as Sites of Special Scientific Interest due to the presence of mobile gravel bed islands supporting nationally important bird species. Elsewhere in the UK (e.g. on the rivers Spey, Conon, and Eden) or in other parts of Europe (e.g. France and Austria), floodplain aquatic habitats have also received international protection indirectly through association with alluvial forest (which is frequently associated with important heron colonies in continental Europe thus attracting additional protection as a Special Protection Area for birds). Alternatively, they have been included within sites qualifying as 'Oligotrophic to mesotrophic standing waters with vegetation of *Littorellion uniflorae* (H3130)', as a component of 'Transition mires and quaking bog (H7140)' or 'Water courses of plain to montane level with Batrachian *Ranunculus* vegetation (H3260)'. In other cases sites have benefitted from European protection through hosting or being attached to rivers which host Habitats Directive Annex II species, such as freshwater pearl mussel, river and brook lamprey, salmon, otter or beaver, or aquatic plants, such as *Luronium natans* or *Marsilea quadrifolia*. Backwater habitats, such as secondary channels are considered an essential element of functional floodplain wetlands but are difficult and costly to reinstate during restoration schemes (Buijse *et al.*, 2002) and are only partially replicated by compensation structures situated in impounded reaches (Janauer *et al.*, 2008). Therefore including backwaters as part of the designation of larger areas is a more effective way of protecting floodplain integrity and maintaining the fluvial processes that create and transform backwater habitats. Nevertheless, backwaters are commonly overlooked and would benefit from a more explicit recognition of their various roles, whether in river ecosystem functioning, provision of nursery habitat for fish, in the maintenance of populations of rare



species, or in natural flood management. This will rely on valuing connectivity within and between terrestrial and aquatic habitats more highly.

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**APPENDIX 1.**  
**HYDROPHYTE SPECIES RECORDED AMONG SURVEYED MAIN CHANNEL SECTIONS AND PAIRED BACKWATERS**

| Species name                      | Main channel | Backwaters |
|-----------------------------------|--------------|------------|
| <i>Apium inundatum</i>            |              | ✓          |
| <i>Callitriche</i> sp.            |              | ✓          |
| <i>Callitriche hamulata</i>       |              | ✓          |
| <i>Callitriche stagnalis</i>      |              | ✓          |
| <i>Chara virgata</i>              |              | ✓          |
| <i>Crassula helmsii</i>           |              | ✓          |
| <i>Eleocharis acicularis</i>      |              | ✓          |
| <i>Elodea canadensis</i>          |              | ✓          |
| <i>Elodea nuttallii</i>           |              | ✓          |
| <i>Fontinalis anti pyretica</i>   | ✓            | ✓          |
| <i>Juncus bulbosus</i>            |              | ✓          |
| <i>Lemanea fluviatilis</i>        | ✓            |            |
| <i>Lemna minor</i>                |              | ✓          |
| <i>Littorella uniflora</i>        |              | ✓          |
| <i>Lythrum portula</i>            |              | ✓          |
| <i>Myriophyllum alterniflorum</i> |              | ✓          |
| <i>Nitella flexilis</i>           |              | ✓          |
| <i>Persicaria amphibia</i>        |              | ✓          |
| <i>Potamogeton alpinus</i>        |              | ✓          |
| <i>Potamogeton berchtoldii</i>    |              | ✓          |
| <i>Potamogeton crispus</i>        |              | ✓          |
| <i>Potamogeton natans</i>         |              | ✓          |
| <i>Potamogeton obtusifolius</i>   |              | ✓          |
| <i>Potamogeton polygonifolius</i> |              | ✓          |
| <i>Racomitrium aciculare</i>      | ✓            | ✓          |
| <i>Ranunculus fluitans</i>        | ✓            | ✓          |
| <i>Sparganium angustifolium</i>   |              | ✓          |
| <i>Sparganium emersum</i>         |              | ✓          |
| <i>Sparganium natans</i>          |              | ✓          |
| <i>Subularia aquatica</i>         |              | ✓          |

**APPENDIX 2.**  
**HELOPHYTE SPECIES RECORDED AMONG SURVEYED MAIN CHANNEL SECTIONS AND PAIRED BACKWATERS**

| Species name                    | Main channel | Backwaters |
|---------------------------------|--------------|------------|
| <i>Agrostis stolonifera</i>     |              | ✓          |
| <i>Alisma plantago-aquatica</i> |              | ✓          |
| <i>Caltha palustris</i>         |              | ✓          |
| <i>Cardamine hirsuta</i>        |              | ✓          |
| <i>Cardamine pratensis</i>      |              | ✓          |
| <i>Carex nigra</i>              | ✓            | ✓          |
| <i>Carex remota</i>             | ✓            | ✓          |
| <i>Carex rostrata</i>           | ✓            | ✓          |
| <i>Carex vesicaria</i>          |              | ✓          |
| <i>Carex viridula</i>           |              | ✓          |
| <i>Eleocharis palustris</i>     | ✓            | ✓          |
| <i>Epilobium palustre</i>       |              | ✓          |
| <i>Equisetum arvense</i>        | ✓            | ✓          |
| <i>Equisetum fluviatile</i>     |              | ✓          |
| <i>Equisetum palustre</i>       |              | ✓          |
| <i>Fallopia japonica</i>        | ✓            | ✓          |
| <i>Filipendula ulmaria</i>      | ✓            | ✓          |
| <i>Galium palustris</i>         | ✓            | ✓          |
| <i>Glyceria fluitans</i>        | ✓            | ✓          |
| <i>Hippuris vulgaris</i>        |              | ✓          |
| <i>Iris pseudacorus</i>         |              | ✓          |
| <i>Juncus acutiflorus</i>       |              | ✓          |
| <i>Juncus articulatus</i>       | ✓            | ✓          |
| <i>Juncus bufonius</i>          |              | ✓          |
| <i>Juncus effusus</i>           | ✓            | ✓          |
| <i>Mentha aquatica</i>          | ✓            | ✓          |

(Continues)

Table 1.(Continued)

| Species name                | Main channel | Backwaters |
|-----------------------------|--------------|------------|
| <i>Mimulus guttatus</i>     | ✓            | ✓          |
| <i>Myosotis scorpioides</i> | ✓            | ✓          |
| <i>Phalaris arundinacea</i> | ✓            | ✓          |
| <i>Ranunculus flammula</i>  | ✓            | ✓          |
| <i>Ranunculus repens</i>    | ✓            | ✓          |
| <i>Scirpus sylvatica</i>    |              | ✓          |
| <i>Solanum dulcamara</i>    |              | ✓          |
| <i>Sparganium erectum</i>   |              | ✓          |
| <i>Typha latifolia</i>      |              | ✓          |