**Title:** Twenty years of change in riverside vegetation: what role have invasive alien plants played?

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Agriculture; Competition; Climate change; Diversity; Flow regime; *Impatiens glandulifera*, Invasive species; Model averaging; Riparian vegetation;

**Nomenclature**

Preston et al. (2002) for vascular plants; Hill et al. (2006) for bryophytes

**Abbreviations**

IAP = invasive alien plant

## Abstract

**Question:** Which environmental factors influence the occurrence of invasive alien plants (IAPs) in riparian habitats and how much can IAPs account for change in native vegetation compared with other environmental variables?

**Location:** Rivers distributed throughout mainland Britain.

**Methods:** We quantified change in river bank vegetation using survey data collected approximately 20 years apart and assessed the contribution of major IAPs (*Impatiens glandulifera*, *Heracleum mantegazzianum* and *Fallopia japonica*) to these changes, and determined the importance of abiotic factors such as flow regime and land use in driving these changes.

**Results:** Comparing data from pre- and post-1990 surveys revealed that IAPs occurred mainly on lowland rivers (<200 ma.s.l.), regardless of time period, and their probability of occurrence increased over time and with rising frequency of high flows. Native plant species diversity declined over time with increasing IAP cover, along lowland rivers and along all rivers that experienced extended low flows during the growing season. These conditions particularly favoured native dominant species, whereas native subordinate species responded both positively and negatively to increased flood frequency depending on survey period. Over time, Salix spp. and larger native hydrophilic species, such as *Sparganium erectum*, increased along lowland rivers, replacing smaller-statured ruderal species and driving a shift towards increased shade tolerance of sub canopy and groundcover species. Smaller compositional changes occurred in the uplands and these changes lacked a clear environmental signature.

**Conclusions:** National scale changes in native riparian vegetation are likely driven primarily by environmental changes and land-use effects, rather than invasion by IAPs. However, IAPs, and indeed native species that benefit from abiotic changes, in turn, likely exert secondary effects on native riparian vegetation. The trend towards reduced diversity, increased shade tolerance and increased dominance of some native species and IAPs is likely linked to a set of interacting factors including drier summers, wetter winters, increased riparian tree cover, reduced livestock access to river banks and increased fine sediment input. Determining combined effects of land use, IAPs and climate-related changes in flow regime over decadal time scales (i.e., ~30 years) is important for predicting ecological responses of vulnerable habitats under future disturbance scenarios.

## Introduction

Riparian zones are dynamic and frequently disturbed (Tickner et al. 2001) but perform important ecosystem functions. Riparian vegetation in particular, is important in stabilising river banks, intercepting nutrients, modifying shade and providing a corridor for the dispersal of biota (Richardson et al. 2007). Despite their widely acknowledged importance, riparian zones remain among the most threatened of all ecosystems, under increasing pressure from anthropogenic and environmental stressors, with elevated risk of invasion by alien species (Baattrup-Pedersen et al. 2013).

Channel engineering, and alterations to flow regime and adjacent land-use are almost ubiquitous features of rivers worldwide (Stokes et al. 2010), especially in the lowlands (Garssen et al. 2015), but there is also mounting evidence of the scale of modification in the uplands (Wheater & Evans 2009). Riparian habitats have traditionally been a focus of agricultural activities, due to ease of water availability and high soil fertility. Agricultural activity has reduced water quality through nutrient enrichment, increased sedimentation and loss of woodland (Casanova 2015). Livestock grazing has also altered riparian vegetation dynamics, while land use intensification has reduced the normally high heterogeneity of riparian vegetation (Stockan et al. 2012). Lastly extensive physical transformation has rendered riparian ecosystems more susceptible to anthropogenic changes in climate and associated flow regime (Capon et al. 2013).

Intermittent flooding is a defining feature of riparian zones, with dependent hydrological and geomorphic processes such as inundation, erosion and sediment deposition, among key determinants of vegetation growth and survival (Baattrup-Pedersen et al. 2013). Historic changes to flow regimes as a result of climate shifts or flow regulation may affect these processes, thereby altering species diversity and composition of riparian vegetation (Nilsson & Svedmark 2002). The consequences of altered river flows for riparian biota are usually negative (Poff & Zimmerman 2010; Webb et al. 2013). However, little is known about the effect of climate-induced changes in flow regime on riparian vegetation (Tickner et al. 2001). Since flooding favours waterborne dispersal of propagules and their recruitment (Richardson et al. 2007), riparian ecosystems are responsive to changes in precipitation (Garssen et al. 2015). However, flooding not only enables the recruitment of native species, but also invasive alien plant species (IAPs), which may ultimately compromise the resilience of riparian vegetation to disturbances (Richardson et al. 2007).

Disturbance, whether from natural or anthropogenic sources, can disrupt species interactions, lower competitive ability and favour recruitment of IAPs, which are widely regarded as a major threat to native biodiversity (Richardson et al. 2007). Disturbed habitats with heightened potential for propagule dispersal, such as riparian zones, are especially amenable to invasion (Maskell et al. 2006), with IAPs developing monospecific stands that can potentially suppress the growth of native species (Beerling & Perrins 1993). Hence there is concern that invasions will lead to the large-scale homogenization of native flora (Hulme & Bremner 2006). Nevertheless, the precise impact of alien species on native ecosystems is still widely disputed. Of the numerous alien plants in Britain only a few are considered to be invasive. *Heracleum mantegazzianum*, *Fallopia japonica* and *Impatiens glandulifera* are currently listed in Europe's top 100 most invasive plant species by DAISIE (http://www.europe-aliens.org/ 23/01/13) and all three commonly occur in riparian habitats. The ecology and distribution of these three species is well studied, but reported impacts on the diversity of native vegetation are few and sometimes conflicting (Hulme & Bremner 2005; Hejda & Pyšek 2006), likely because impacts are scale and species-specific (Hejda et al. 2009; Powell et al. 2011).

Evidence from previous studies and predictive models suggest that rates of invasion and establishment within freshwater habitats will continue to increase (Strayer 2010). The degree to which native riparian vegetation has changed due to a suite of multiple stressors – IAPs, anthropogenic disturbance and climate-related changes to flow regime and their various interactions – at large spatial and temporal scales, is relatively unknown and significantly constrains our understanding of how riparian habitats will respond to future environmental change and management (Hejda & Pyšek 2006). The widespread establishment of IAPs is perhaps the most profound change to have occurred in European riparian habitats in recent decades, but how much invasion contributes to changes in native vegetation, versus other less obvious factors, is unclear.

In this study we use botanical data from two large-scale surveys of British rivers to assess the contribution of three major IAPs (*I. glandulifera, F. japonica* and *H. mantegazzianum*) to changes in native riparian vegetation over a 20 year period, relative to the effects of flow regime, river type and land use characteristics over the same period. The wide geographical coverage of these surveys allows inference to be made about the extent of changes in riparian vegetation on a national scale (Maskell et al. 2006). Specifically, we consider (i) which environmental factors most affect the probability of occurrence of IAPs; (ii) how changes in the diversity, turnover and cover of native species are related to IAP cover, flow regime changes and land-use; (iii) changes in community composition within contrasting river types and if these changes are explained by switches in species dominance and/or environmental factors.

## Methods

### River Macrophytes Database

The Joint Nature Conservation Committee (JNCC) River Macrophytes Database (RMD) contains records from standardised vegetation surveys of rivers from across the UK undertaken by experienced surveyors. Surveys focus on rivers with existing or potential conservation value and almost 4500 surveys have been undertaken since 1977 following the methods described by Boon et al. (1996) and Holmes et al. (1999). Survey sites comprised 500m river stretches, with sites along the same river being located 5-10km apart, depending on river size. Plants were recorded using a standardised species checklist to aid recording. Each species recorded was given a cover score of 1-3 corresponding to a range of percentage cover values. The checklist was commonly supplemented by surveyors with records of additional species. Basic locational and environmental data such as substrate type, altitude, distance from river source and channel width were either collected in the field or derived subsequently through GIS.

## Data extraction

Sites with repeat surveys separated by at least 10 years were extracted from the RMD. This process yielded 271 sites (Fig. 1), first surveyed in the period 1979-1982 (hereafter first survey period) and resurveyed in the period 1992-2009 (hereafter second survey period). The average interval between first and second survey was ~20 years. Although annual survey data are preferable to allow for the effects of short term temporal variation, such data were unavailable and if available, have only been collected exceptionally and at a local scale.

Fig 1. Location of survey sites included in this study represented by cross symbols (scale and locations approximate). Key rivers in Britain are also shown.

A standard species checklist was used by all surveyors and additional species were also recorded in some instances. All surveys in the first period were undertaken by a single surveyor (Nigel Holmes). However, in the second period surveys were conducted by seven different personnel. To offset the bias in recording of additional species by different surveyors, a conservative criterion (presence at >2% of sites) was used to obtain a list of species common to both survey periods. A total of 119 angiosperms and bryophytes representing those on the standard checklist, plus additionally recorded species, were used in subsequent analyses. Species excluded from analyses represented <10% of the total cover of all species recorded. Plant species which had an Ellenberg moisture score of 11 and 12 (Hill et al. 1999, Hill et al. 2004) were removed to ensure a focus on riparian vegetation.

## Vegetation descriptors

Alien species were defined as those which colonised Britain with the help of humans. We focused on the invasive alien species *H. mantegazzianum, I. glandulifera* and *F. japonica* which have previously been linked with negative impacts on native riparian vegetation (Hejda et al. 2009). *Impatiens glandulifera* was the most frequently recorded, occurring at 70% of invaded sites. The percentage cover of *I. glandulifera*, *H. mantegazzianum* and *F. japonica* were combined and used to assess the effect of IAP cover on aspects of the native plant community. Commonly occurring riparian alien species that were not considered invasive for the purposes of this study included *Acorus calamus*, *Claytonia sibirica*, *Epilobium brunnescens*, *Impatiens capensis* and *Mimulus guttatus.* Some studies have shown that native dominant species may have a comparable competitive ability to IAPs (Bottollier-Curtet et al. 2013). In order to assess the comparative effect of native dominant species on the associated native vegetation, native species were split into subordinate and dominant categories (Appendix S1). Native dominant species (n=15) were defined *a priori* as species with mainly or wholly competitor growth strategies (sensu Grime 1974) that also commonly form mono-dominant stands alongside rivers in Britain (e.g. *Phalaris arundinacea*, *Urtica dioica*). Native subordinate species were those with a wholly or partly ruderal or stress tolerator growth strategy (sensu Grime 1974), which often occur at low abundance and tend to be outcompeted by native dominant species. The percentage cover of native dominant or subordinate species was determined by summing the individual percentage cover of the species belonging to these groups.

Native species diversity was assessed using Shannon’s diversity index. The Bray–Curtis dissimilarity Index (BCI) was used to quantify temporal change in species composition, calculated using cover (percentage, square-root transformed) of native species. Theoretical values of BCI range from 0 to 1, with 1 indicating no shared species between paired surveys and 0 indicating complete overlap.

To identify changes in community composition, while accounting for differences in site attributes, sites were first clustered by altitude, slope, hydrology and location (easting) into homogenous groups using K-Means cluster analysis. Two clusters were chosen, ‘upland’ (n=132) and ‘lowland’ (n=139) river types, which reflected ease of interpretability and the need for a minimum sample number per cluster. All ‘lowland’ rivers occurred at <200m elevation. Species characteristic of the earlier or later surveys within each of the two river types were identified using indicator species analysis (IndVal; Dufrene & Legendre 1997) applied to square root-transformed percentage cover data. IndVal considers specificity and fidelity in different groups (i.e., survey × river type = 4 groups) with the index ranging from 0 %, denoting no presence in a survey group, to 100 %, indicating presence in only one group and occurrence in all samples from within that group. The significance of these values was tested using a Monte Carlo randomisation procedure (Dufrene & Legendre 1997).

To support interpretation of environmental conditions, Ellenberg's indicator values for moisture (F), light (L), pH (R) and fertility (N) were compared for the indicator species in each group and survey period (Hill et al. 1999). Ellenberg indicator values (Ellenberg et al. 1991) that rank plant tolerance to light (L), moisture (F), pH (R) and nitrogen (N) were assigned to angiosperms and bryophytes using the PLANTATT and BRYOATT databases (Hill et al. 2004).

## Site characteristics

A Principal Components Analysis (PCA) was conducted, following Jeffers (1998), to reduce collinear site characteristics (slope, altitude, distance from source and height of source) to a single axis of variation. Altitude and slope were expressed mainly through the first PCA axis, which explained 55% of the variance. Percentage woodland cover within a 100 m radius of a site was determined using the Land Cover Map 2007 (LCM2007) (Morton et al. 2011) imported to ArcGIS/ArcMap (v 10). Data on water chemistry (alkalinity and total oxidised nitrogen (TON)) were available for a subset of sites. However, since the variable easting was collinear with alkalinity and was universally available, easting was used as a surrogate for both fertility and intensive agricultural land use which are generally higher in eastern parts of Britain (Morton et al. 2011).

To assess the effect of hydrology on riparian vegetation, daily mean flow data were obtained from the Centre of Ecology and Hydrology's National River Flow Archive. Data for the five years prior to the dates of the first and second surveys were used to calculate flow regime indicators, using data from the most downstream flow gauging station on each surveyed river. Flood frequency, expressed as the mean number of days per year on which flows exceeded a threshold of five times the median flow ($FRE_5$), was used as an indicator of fluvial disturbance. The maximum number of consecutive days over the period 1 March to 30 September each year on which flows did not exceed a threshold of three times the annual median flow, averaged over the five years prior to each survey period, was used as an indicator of undisturbed growing season length. These indices capture contrasting but ecologically-relevant components of flow variability (Clausen & Biggs 1997).

## Statistical analysis and model selection

Our primary focus was on whether the various response variables (IAP presence or absence, Shannon diversity, native subordinate and dominant species percentage cover) differed between the two survey periods and whether any such differences, or difference in species turnover (BCI) between surveys, was explainable by other vegetation indicators or environmental factors (altitude/slope (PC1), easting, woodland percentage cover, flood frequency and low flow duration). Therefore, in all models (BCI response excluded) a fixed factor of survey (with two levels: first and second survey period), was included as an interaction with each predictor. Thus, a significant interaction between a given predictor and survey period indicates that the predictor affects the change in the response between survey periods. Since sites were nested by river this identifier was treated as a random effect. All predictors were standardised to one standard deviation prior to statistical analyses, to allow relative effect sizes of predictors to be compared directly (Nakagawa & Schielzeth 2010). This modelling approach was used to model five response variables with choice of error structure dependent on the type of response: (1) the probability of an IAP being present at a site (generalized linear mixed model (GLMM) with a Binomial error structure), (2) Shannon's Diversity Index (linear mixed models (LMM)), (3) Bray–Curtis Index (BCI), (LMM), (4) native subordinate species cover and (5) native dominant species cover (both percentage, squared root transformed and LMM). Although BCI is theoretically bounded by zero, observed values ranged from 0.2-0.8 enabling us to model this index within the theoretical constraints of bounded data. We checked for multicollinearity among the predictor variables before use in multiple regression analyses, retaining those variables which were not highly correlated (r = <0.60).

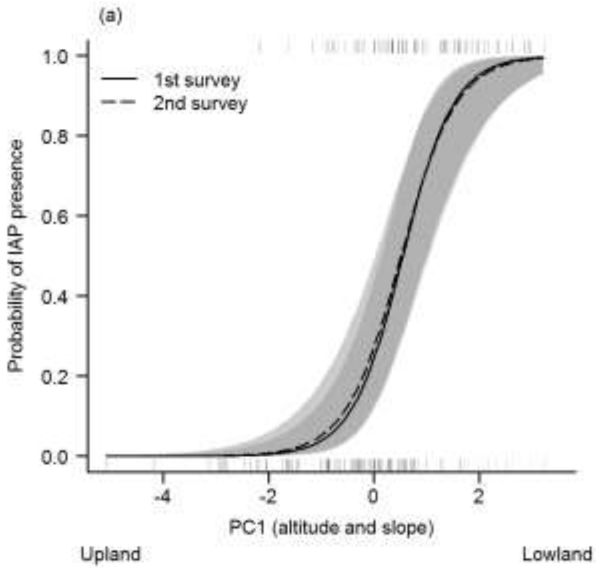
A multi-model inference approach was used based on information theory (Burnham & Anderson 2002), a method increasingly being adopted when dealing with observational data collected at large spatial scales with varying environmental gradients such as those in this study. Models were compared and ranked using AICc (correcting for small sample sizes), with all possible combinations of predictors identified using the dredge function in MuMIn. Main effects (including quadratic terms) were only considered alongside their interactions, if the effect contributed to model fit. The best fitting models were evaluated based on their ΔAICc, with values <4 considered to be equally parsimonious (Burnham & Anderson 2002). Akaike weights were calculated for each explanatory variable, in order to compare the relative importance of each variable in the top set (ΔAICc <4) of models. Model coefficients were averaged across this set (full averaging) and the resulting averaged coefficients were used for predictions and 95 % confidence intervals. Confidence intervals were calculated as 1.96* the standard error of the model predictions. Model predictions were plotted holding all other standardised predictor variables at zero. To account for the variation explained solely by the fixed effects, as well as the variation explained by both the fixed and random effects, both the marginal and conditional $R^2$ values are reported for each model, respectively (Nakagawa & Schielzeth 2013).

All statistical analyses were conducted using R 3.2.2 (R Development Core Team 2015), with the additional R packages vegan (v 2.3-0), labdsv (v 1.8-0), NbClust (v 3.0), MuMIn (v 1.15.1) and lme4 (v 1.1-10).

## Results

### Invasive alien species

Probability of IAP presence increased with PC1 scores, which were equivalent to decreasing altitude and slope. This effect was the same for both survey periods (Fig. 2a). Flood frequency and PC1 (altitude and slope) were the most important variables (interaction terms with survey, (Table 1)) for predicting the probability of IAP presence at a site. Both predictors had a relative variable importance (RVI) of 1. The top model within the top set had a marginal $R^2$ of 0.57 and a $W_i$ of 0.68 (Appendix S2). Flood frequency increased the probability of an invasive species being present at a site, particularly so for the second survey (Fig. 2b). IAPs were present at 34 % of the 271 sites in the first survey period compared with 47 % of sites in the second survey period. The median percentage cover of IAPs in the first survey period was low, ~5 %, compared to 15 % in the second survey period.



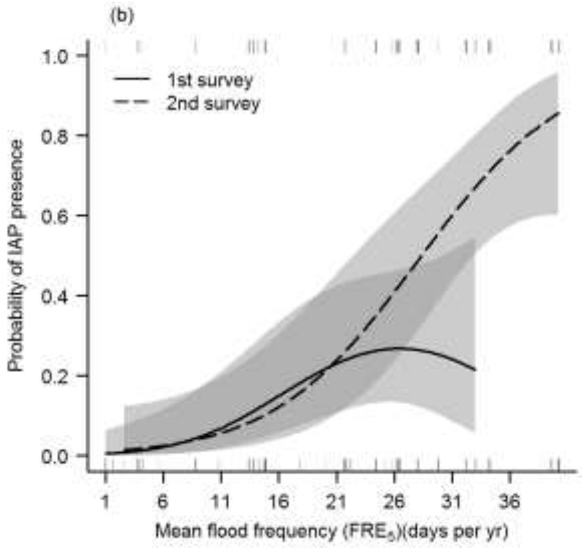


Fig 2. Observed values (dashes) and full model averaged predicted values (lines± 95 % CI) from the GLMM analysis of probability of invasive alien plant presence. Interaction effect between a) PC1 (altitude and slope) x survey and b) mean annual flood frequency ($FRE_5$) × survey.

## Native species diversity

Across sites as a whole native species diversity declined by an average of 6 % between surveys. Along lowland and upland rivers, native diversity declined by 10 % and 2.4 % respectively. Interaction terms $IAP^2$ × survey and easting × survey had the greatest effect on native species diversity. At both lower altitudes (Fig. 3a) and with extended flow periods (Fig. 3b), native species diversity was lower in the second survey. In the first survey period diversity was positively associated with low level increases in IAP cover but in the second period, as IAP cover increased further, this relationship became neutral to negative (Fig. 3c). All predictors except flood frequency had an RVI of 1 (Table 1). The top model had a weighting of 0.87 and a marginal $R^2$ of 0.27 (Appendix S2).

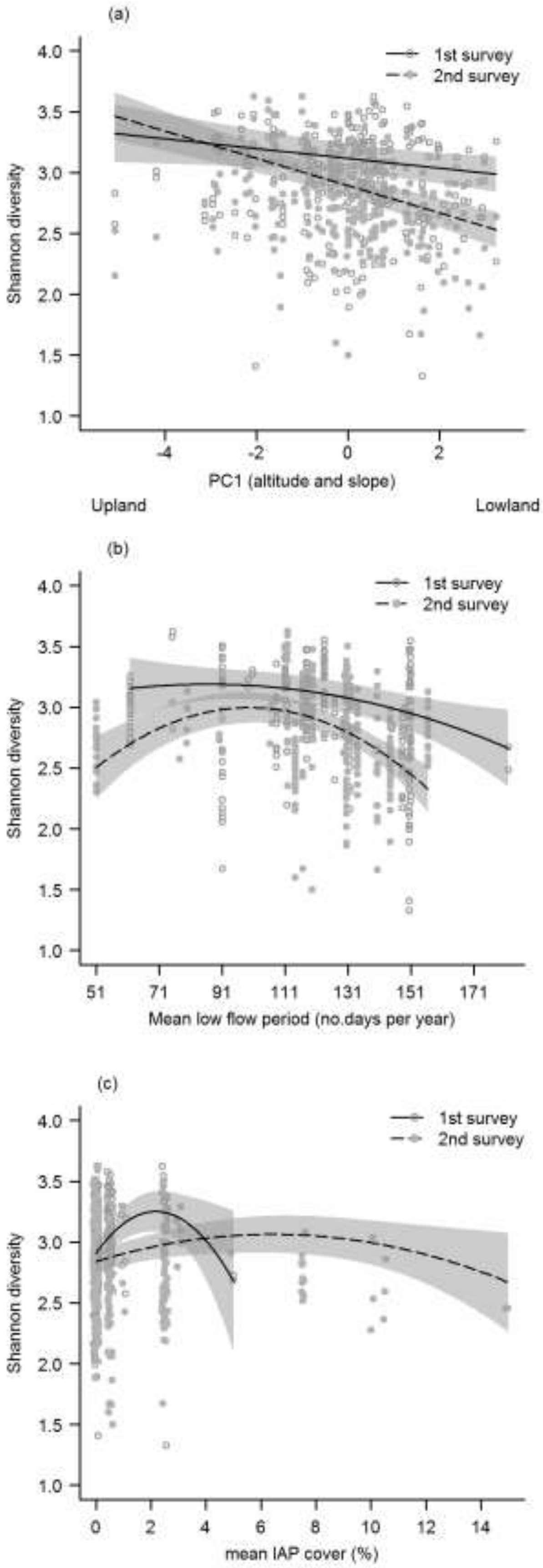
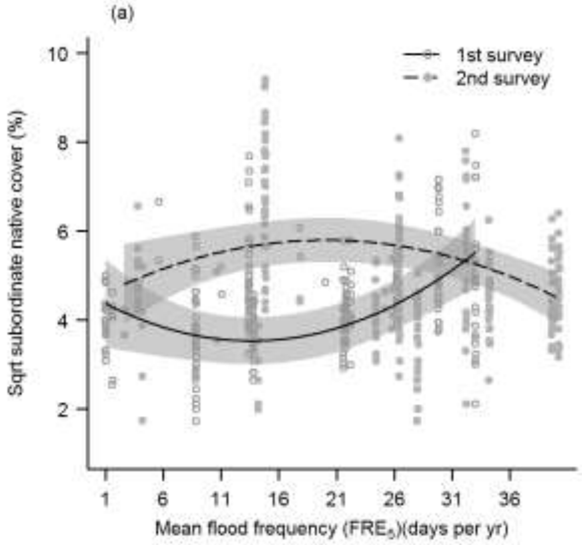


Fig 3. Observed values (points) and full model averaged predicted values (lines± 95 % CI) from the LMM analysis of native species Shannon diversity. Open and closed circles represent observed values

from the first and second survey respectively. Figure a) shows the PC1 (altitude and slope) × survey interaction, b) mean number of low flow days × survey interaction and c) invasive alien plant percentage cover × survey interaction.

## Native species cover

Interaction terms flood frequency$^2$ × survey, easting × survey and low flow$^2$ × survey had the greatest effect on native subordinate species cover and an RVI of 1 (Table 1). In contrast to the first survey period, cover was highest at intermediate flood frequencies in the second survey period (Fig. 4a). There was a negative association between native subordinate species cover and decreasing site altitude and slope in both survey periods, although strongest in the second period. Thus, the difference in native subordinate species cover between the second relative to the first survey period increased from low to high altitude sites (Fig. 4b). All predictors were retained within the top model set. The top model had a $W_i$ of 0.38 and a marginal R$^2$ of 0.35 (Appendix S2).



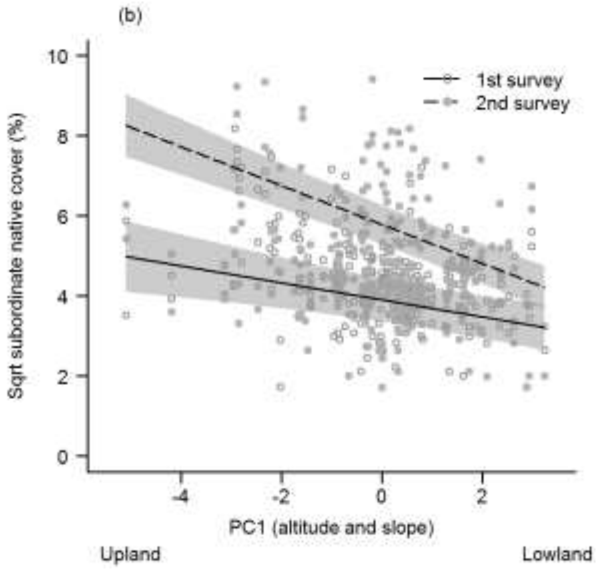


Fig 4. Observed values (points) and full model averaged predicted values (lines± 95 % CI) from the LMM analysis of native subordinate species percentage cover (sqrt transformed). Open and closed circles represent observed values from the first and second survey respectively. Figure a) flood frequency × survey interaction, b) PC1 (altitude and slope) × survey interaction.

Although most explanatory variables had a relatively small effect on native dominant species cover, easting × survey and low flow$^2$ × survey had an RVI of 1, with the largest relative effect sizes (Table 1). After an initial decline at an intermediate low flow period, native dominant species cover increased with number of consecutive low flow days in the second survey period. In contrast, an initial increase and thereafter weak decline in native dominant species cover with increased low flow period occurred in the first survey period (Fig. 5a). There was an overall positive association between native dominant species cover and decreasing site altitude and slope in both survey periods. However, in the second period there was a slower rate of increase in native dominant species cover, moving from high to low elevation (Fig. 5b). The top model within the top model set had a marginal R$^2$ of 0.24 and a $W_i$ 0.26 (Appendix S2).

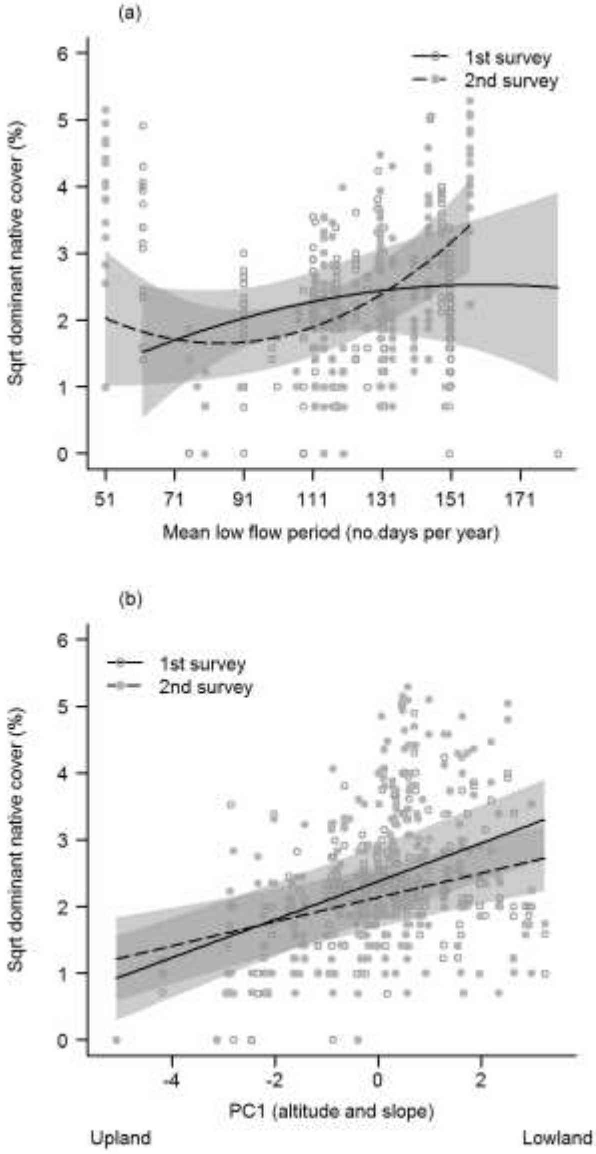


Fig 5. Observed values (points) using full model averaged predicted values (lines± 95 % CI) from the LMM analysis of native dominant species percentage cover (sqrt transformed). Open and closed circles represent observed values from the first and second survey respectively. Figure a) shows the interaction effect between number of low flow days × survey, b) PC1 (altitude and slope) × survey for both the first (solid line) and second (dashed line) survey period.

## Change in native species composition

Easting, PC1 (altitude and slope) and low flow days had the greatest effect on BCI (Table 1), compared to other predictor variables in the model. Thus sites showing least change in native vegetation composition (low BCI) were generally located further east and/or at higher elevations, whilst the greatest compositional change (high BCI) occurred at low elevations (Fig 6), and a greater number of consecutive low flow days. The top model within the top model set had a marginal $R^2$ of 0.23 and a $W_{\mathrm{i}}$ 0.20 (Appendix S2).

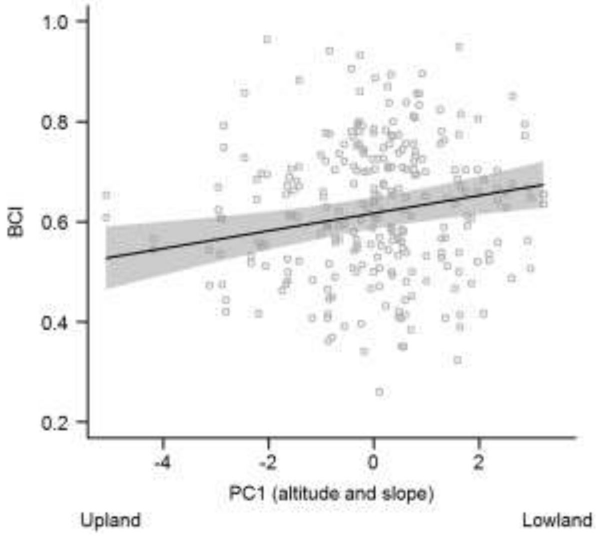


Fig 6. Observed values (points) and full model averaged predicted values (lines± 95 % CI) from the LMM analysis of native species Bray-Curtis Dissimilarity Index (BCI) showing the effect of PC1.

| | Invasive Presence/Absence | | | | S-W Diversity | | | | BCI (Turnover) | | | | Subordinate Cover | | | | Dominant Cover | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Predictor | Estimate | −95% CI | +95% CI | RVI | Estimate | −95% CI | +95% CI | RVI | Estimate | −95% CI | +95% CI | RVI | Estimate | −95% CI | +95% CI | RVI | Estimate | −95% CI | +95% CI | RVI |
| Intercept | -1.13 | -2.00 | 4.35 | | 3.12 | 3.00 | 3.24 | | 0.62 | 0.59 | -1.13 | | 3.91 | 3.37 | 4.44 | | 2.38 | 1.85 | -3.35 | |
| PC1 | 2.06 | 1.27 | -2.08 | 1.00 | -0.04 | -0.07 | -0.01 | 1.00 | 0.02 | 0.01 | -0.01 | 1.00 | -0.21 | -0.32 | -0.10 | 1.00 | 0.29 | 0.21 | -0.38 | 1.00 |
| Dominant Native Sp Cover | - | - | - | - | - | - | - | - | <0.01 | -0.01 | 0.03 | 0.27 | -0.10 | -0.32 | 0.13 | 1.00 | - | - | - | - |
| Dominant Native Sp Cover$^2$ | - | - | - | - | - | - | - | - | - | - | - | - | 0.13 | 0.02 | 0.25 | 1.00 | - | - | - | - |
| Easting | - | - | - | - | -0.08 | -0.15 | 0.00 | 1.00 | -0.05 | -0.08 | 0.17 | 1.00 | -0.39 | -0.70 | -0.07 | 1.00 | -0.03 | -0.20 | 0.49 | 0.27 |
| Invasive Cover | - | - | - | - | 0.38 | 0.20 | 0.55 | 1.00 | <0.01 | -0.01 | 0.02 | 0.34 | 0.43 | -0.08 | 0.95 | 1.00 | -0.01 | -0.19 | 0.46 | 0.51 |
| Invasive Cover$^2$ | - | - | - | - | -0.26 | -0.43 | -0.09 | 1.00 | - | - | - | - | -0.19 | -0.69 | 0.32 | 0.49 | - | - | - | - |
| Woodland Cover | - | - | - | - | - | - | - | - | <0.01 | -0.01 | 0.02 | 0.33 | 0.01 | -0.06 | 0.07 | 0.29 | - | - | - | - |
| Flood frequency | 0.64 | -0.32 | 1.11 | 1.00 | <0.01 | -0.04 | 0.04 | 0.13 | - | - | - | - | 0.97 | 0.53 | 1.41 | 1.00 | 0.17 | -0.23 | 0.65 | 0.57 |
| Flood frequency$^2$ | -0.79 | -1.56 | 3.46 | 1.00 | - | - | - | - | - | - | - | - | 0.62 | 0.30 | 0.95 | 1.00 | -0.08 | -0.31 | 0.73 | 0.57 |
| Low flow | -0.08 | -0.70 | 1.68 | 0.32 | -0.10 | -0.17 | -0.04 | 1.00 | 0.03 | 0.00 | 0.02 | 0.96 | -0.02 | -0.35 | 0.32 | 1.00 | 0.20 | -0.18 | 0.55 | 1.00 |
| Low flow$^2$ | -0.09 | -0.51 | 1.22 | 0.18 | -0.04 | -0.08 | 0.01 | 1.00 | <0.01 | -0.01 | 0.03 | 0.19 | 0.18 | 0.01 | 0.34 | 1.00 | -0.07 | -0.20 | 0.46 | 1.00 |
| Survey | 0.14 | -0.86 | 2.19 | 1.00 | -0.22 | -0.33 | -0.12 | 1.00 | - | - | - | - | 1.88 | 1.38 | 2.38 | 1.00 | -0.24 | -0.53 | 1.18 | 1.00 |
| PC1 × Survey | -0.15 | -0.76 | 1.79 | 1.00 | -0.07 | -0.12 | -0.03 | 1.00 | - | - | - | - | -0.27 | -0.41 | -0.13 | 1.00 | -0.10 | -0.19 | 0.42 | 1.00 |
| Easting × Survey | - | - | - | - | 0.23 | 0.16 | 0.30 | 1.00 | - | - | - | - | 0.94 | 0.63 | 1.25 | 1.00 | 0.04 | -0.11 | 0.30 | 0.27 |
| Dominant Native Sp Cover × Survey | - | - | - | - | - | - | - | - | - | - | - | - | 0.55 | 0.28 | 0.83 | 1.00 | - | - | - | - |
| Dominant Native Sp Cover$^2$ × Survey | - | - | - | - | - | - | - | - | - | - | - | - | -0.26 | -0.41 | -0.12 | 1.00 | - | - | - | - |
| Invasive Cover × Survey | - | - | - | - | -0.26 | -0.44 | -0.08 | 1.00 | - | - | - | - | -0.24 | -0.72 | 0.25 | 1.00 | 0.04 | -0.16 | 0.43 | 0.51 |
| Invasive Cover$^2$ × Survey | - | - | - | - | 0.24 | 0.07 | 0.41 | 1.00 | - | - | - | - | 0.17 | -0.31 | 0.65 | 0.49 | - | - | - | - |
| Woodland Cover × Survey | - | - | - | - | - | - | - | - | - | - | - | - | -0.03 | -0.17 | 0.10 | 0.29 | - | - | - | - |
| Flood frequency × Survey | 1.10 | 0.03 | 0.48 | 1.00 | - | - | - | - | - | - | - | - | -1.10 | -1.47 | -0.74 | 1.00 | -0.07 | -0.30 | 0.71 | 0.57 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Flood frequency$^2$ × Survey | 0.75 | -0.07 | 0.54 | 1.00 | <0.01 | -0.03 | 0.03 | 0.13 | - | - | - | - | -1.01 | -1.30 | -0.72 | 1.00 | 0.01 | -0.13 | 0.32 | 0.57 |
| Low flow × Survey | 0.08 | -0.74 | 1.87 | 0.32 | -0.13 | -0.23 | -0.04 | 1.00 | - | - | - | - | -0.85 | -1.19 | -0.51 | 1.00 | 0.45 | 0.19 | -0.23 | 1.00 |
| Low flow$^2$ × Survey | 0.11 | -0.41 | 1.06 | 0.18 | -0.10 | -0.15 | -0.04 | 1.00 | - | - | - | - | -0.76 | -0.96 | -0.56 | 1.00 | 0.29 | 0.16 | -0.26 | 1.00 |

Table 1. Full model-averaged parameter estimates for GLMER (invasive presence or absence) and LMER (native species diversity, BCI, native subordinate and dominant species percentage cover) analyses ±95 % confidence intervals. Confidence intervals were calculated using full model averaged standard errors. The estimates for survey are relative to the first survey period. All explanatory variables were standardised to 1SD prior to analyses. Superscript 2 indicates a quadratic term. Relative variable importance (RVI) is also given.

Indicator species analyses showed that taxa strongly associated with lowland sites in the first survey period (Appendix S3) were mostly small ruderal species of inundation zones and livestock grazed margins (including *Agrostis stolonifera, Myosotis scorpioides, Epilobium spp., Juncus bufonius, Equisetum arvense, Persicaria hydropiper, Callitriche stagnalis, Alopecurus genicuatus* and *Ranunculus sceleratus*) or those resistant to grazing (*Deschampsia caespitosa* and *Juncus inflexus*). The second survey period featured *Salix* spp., *Sparganium erectum* and *I. glandulifera* as the strongest indicators alongside other tall canopy-forming herbs (e.g. *Angelica sylvestris, Stachys palustris, Scrophularia auriculata* and *Lysimachia vulgaris*) or their understorey associates. In the upland site group some of the same differences in indicator taxa applied, with *S. palustris, Sagina procumbens, Leptodyction riparium, Galium palustre, Pellia epiphylla* and *Lunularia cruciata* and the IAPs *I. glandulifera* and *F. japonica* again being indicative of the second survey period. In the first survey period the indicators *A. stolonifera, A. geniculatus* and *E. arvense* were also common to both upland and lowland groups of sites. However, some contrasts were also evident with strong indicators of the first survey period in the lowland sites (*P. hydropiper* and *D. caespitosa*) being associated with the latter survey period in the upland sites

Ellenberg scores of significant indicator taxa, within river types, showed no difference from the first to second survey period for both pH (R) and fertility (N). In lowland sites indicator species from the second survey period were associated with shadier conditions than those of the first survey period ($F_{1,34} = 5.803$, $p < 0.05$) but at upland sites Ellenberg scores for light did not differ between survey periods ($F_{1,29} = 0.004$, $p = 0.951$), in line with the lack of tree indicator taxa. Moisture (F) was also not significantly different between the survey periods in lowland ($F_{1,34} = 1.474$, $p = 0.233$) or upland sites ($F_{1,29} = 0.529$, $p = 0.473$), although some strongly hydrophilic species such as *S. erectum* increased in lowland sites in the later survey period.

## Discussion

Directional change in vegetation attributes over decadal time scales, as observed over an almost 20 year period in this study, is likely to correlated with underlying changes in key environmental drivers. Overall, our study highlights that native plant diversity of river margins has decreased over time and native community composition has changed, especially in the lowlands. We also observed changes in shade tolerance and the relative proportion of native dominant and subordinate plant species. Candidate drivers for these changes include increased abundance of IAP species, shifts in river flow regime, and reduced grazing and increased fine sediment inputs linked to agricultural and river management practices.

### Invasive alien plant distribution

IAP species occurred at a greater proportion of sites in the second survey period compared with the first survey period. *Impatiens glandulifera* was the most frequent IAP, consistent with results of Seager et al. (2012) who reported little change in the distribution of *H. mantegazzianum* or *F. japonica* on UK rivers between 1996-2008, whilst *I. glandulifera* became more widespread and abundant. We found that regardless of survey period, IAPs had a higher probability of being found along lowland (<200m altitude) river sites. This result may reflect climatic factors, such as incidence of frost, which can restrict germination and establishment of the IAPs we studied (Funkenberg et al. 2012). Exposure to anthrogenic stressors also varies with altitude, with lowland rivers typically being more severely modified. This combination of stressors can reduce ecological resistance, potentially favouring colonisation by IAPs, which may in turn impact ecological resilience of riparian vegetation (Richardson et al. 2007).

At similar high flow frequencies there was a greater probability of IAP occurrence in the second survey period compared with the first survey period. Since flooding favours spread of IAPs along rivers (Truscott et al. 2006), an increased frequency of high flows might intensify this effect. Direct effects of high flows include reduced cover of dominant species, and increased species turnover, facilitated by reduced competition (Nilsson & Svedmark 2002). Garssen et al. (2015), however, showed that increased duration of flooding did not reduce riparian plant biomass, as species tolerant of flooding were adapted to frequent inundation. The potential for IAPs to maintain abundance after flood-enhanced colonisation therefore represents an additional pressure upon riparian communities.

## Changes in native plant diversity

Our study shows that, as IAP cover increased, native species diversity in riparian habitats was negatively affected. There has been much debate regarding the impact of IAPs on native vegetation (Thomas & Palmer 2015). Generally, negative effects of IAPs on species richness are strongest at progressively smaller spatial scales (Powell et al. 2011). Maskell et al. (2006) offer evidence of negative landscape-scale effects of IAP cover on native diversity, but this effect was observed across nested plots varying in size within a 1km sample area. In our study, working at a relatively coarse 500 m (reach) scale overall diversity of native riparian vegetation was lower in the second survey period regardless of whether a site was invaded, suggesting that IAPs were not a general causal factor in this change.

A decline in native diversity in the second survey period was also associated with a longer growing season undisturbed by peak flows. Diversity peaked at ~97 low flow days, suggesting that low flow periods of intermediate length favour colonisation and establishment of native species, but over more prolonged low flow periods diversity declined, perhaps because this flow regime favours expansion of dominant plant species (either native or invasive), thus increasing competitive exclusion. During the 1990s, areas of southern and eastern Britain in particular, experienced recurrent droughts (Blenkinsop & Fowler 2007) which were especially intense from 1995-97 (Morecroft et al. 2002). Drought would have accentuated low flows within the second survey period and may have subsequently enhanced the sensitivity of vegetation to growing season length. Morecroft et al. (2002) noted that most tree and shrub seedling numbers increased across terrestrial sites in Britain during the drought suggesting that it may have also contributed to the increases in *Salix* cover that we observed. However, it is unclear from our data whether the vegetation changes are a short term response to extreme droughts from which plants recover quickly (Holmes 1999), or reflect the decline in summer heavy rainfall since the 1960s (Maraun et al. 2008).

## Subordinate and dominant native plant cover

Lowland rivers supported less native plant diversity in the second survey period compared with the first survey period. Lowland rivers were also associated with greater reductions in native subordinate species cover in the second survey period. In contrast, native dominant plants were positively associated with lowland sites, most likely favoured by a combination of higher fertility, finer sediments and lower variation in flows (Tickner 2001). Changes in flow regime had contrasting effects on native subordinate and dominant species cover. The latter was less affected by flood frequency, and benefitted more from an increase in duration of low flows than native subordinate species, consistent with the reduced native species diversity observed at lowland sites. Bunn & Arthington (2002) highlight multiple studies linking increased growth of river plants with reduced flow variability and artificially stabilised flow regimes, with dominant species likely to be the main beneficiaries.

Rainfall in the UK exhibits marked interannual variability but in recent decades the frequency of high intensity events has increased, particularly in the autumn and winter (Werritty 2002; Maraun et al. 2008), translating to increased high river flow events at these times. Native subordinate species cover was most influenced by frequency of high flows (Truscott et al. 2006), but showed opposite trends in the first and second survey periods. Increasing high flow frequency was initially associated with greater native subordinate species cover, after which cover declined in the second survey period. Increased high flows could increase dispersal and establishment opportunities for some subordinate species, but several decades of increasing fluvial disturbance (especially if coupled with increased fine sediment loading) might selectively favour larger competitive species with high seed output and rapid spring growth (e.g. IAPs such as *I. glandulifera*), or that spread via vegetative fragments (many native dominant species).

## Changes in native species composition

Turnover in native vegetation was influenced more by environmental and topographical features than IAPs. Repeat surveys of lowland river sites were more dissimilar than those on upland rivers. An increased number of consecutive lowflow days was also associated with greater turnover of the riparian vegetation. This result reflects the reduced native plant diversity and increased native dominant species cover observed at lowland sites after extended low flow periods.

Sites further east retained more similar native riparian communities over time compared with western sites. This is surprising as the east of Britain supports more intensive agriculture, as well as generally being more prone to summer droughts. Since Britain has a strong historical agricultural legacy (Withers & Lord 2002), replacement by species adapted to higher fertility or agricultural disturbance likely long pre-dated the earlier surveys, causing these sites to retain a similar composition due to prevailing constraints.

Species-specific changes in the vegetation highlight a shift at lowland sites from small ruderal herbs and grasses, or unpalatable species often associated with livestock-disturbed margins and inundation zones (Rodwell 2000), to *Salix* spp. and tall-herbs, including the IAPs *I. glandulifera* and *F. japonica*, and hydrophilic *S. erectum*, plus their understorey shade-tolerant associates. Increased cover of IAPs is often associated with lower light due to their taller stature and fast growth (Maskell et al. 2006). Seager et al (2012) found a marginal increase in extensive (> 33% of 500 m river length) tree shading of river channels in Britain, using River Habitat Survey data. Trees are an important feature of lowland rivers, providing habitat complexity and temperature regulation (Gurnell et al. 2005). However, increased tree cover might also favour moderately shade-tolerant IAPs, such as *I. glandulifera* (Beerling & Perrins 1993), and concentrates fine sediment deposition from which IAP recruitment appears to benefit (Pattison & Willby unpubl. data). *Impatiens glandulifera* and *F. japonica* were also indicative of the second survey period in upland sites but other changes at upland sites lacked clear environmental trends with regards to Ellenberg indices. Upland rivers may have been too small or already shaded, thereby reducing sensitivity to change in tree cover. Some indicator species were, however, suggestive of increased water level range (e.g. bryophytes) coupled with greater sediment transport and fine sediment input (*Persicaria hydropiper*, *Sagina procumbens*, *Rorippa sylvestris*) consistent with increased runoff and flow variability.

Land-use changes offer a complementary explanation to that implicating changes to water flow for changes between the two survey periods, particularly in lowland catchments. The period between 1991 and 2004 saw a ~10% decline in Britain in total cattle numbers (Defra 2015). Since 1986 agri-environment schemes have also subsidised farmers to reduce bankside grazing by stock (Kirkham et al. 2006), partly to enhance the effectiveness of riparian buffer zones for diffuse pollution reduction, while the fencing of stream margins has been widely adopted in fisheries management (SEPA 2009). Since riparian areas are favoured by cattle for access to water and palatable vegetation (Batchelor et al. 2015) these changes are likely to have reduced grazing pressure. González et al. (2015) highlight studies showing positive responses of *Salix* and *Populus* tree species to exclusion of cattle from riparian zones while other studies report a fourfold increase in rush and willow species and increase in palatable hydrophytic plants (Hough-Snee et al. 2013; Batchelor et al. 2015). The increases we observed in *Sparganium erectum*, a species often targeted by livestock (Willby pers. obs.), and woody *Salix* spp. therefore seem likely to be related, at least in part, to reduced grazing pressure. Alongside changes in livestock management there was a pronounced switch from spring to winter cultivated cereals between survey periods (Barr et al., 1993). Cultivated land is a major source of fine sediment input to rivers (Collins & Walling, 2007) and this change in practice, coupled with increased intensity of winter rainfall, is likely to have exacerbated fine sediment inputs. Deposition of fertile fine sediment on river banks creates gaps conducive to growth of IAPs such as *I. glandulifera*, as well as some native dominant species (Pattison & Willby unpubl. data).

## Conclusion

Assembling trends from the recent past enables some forecasting of future ecological change. However, it is crucial to account for interactive effects between co-occurring environmental factors in order to understand recent and likely future plant community responses. Our analyses suggest that changes in flow regime have increased opportunities for establishment of IAPs and that these IAPs have contributed to reduced native diversity along riparian zones. However, other environmental factors also played a definitive role in the changes seen in riparian vegetation over the 20 year period. IAPs themselves were a prominent feature of changing riparian zones, benefitting most from changes in flow regime on lowland rivers, probably reinforced by changes in agricultural practices that reduce bankside herbivory and trampling by livestock but increase fine sediment inputs. IAPs may therefore have been passengers of change, with the potential to outcompete native species once established, and reinforced by local conditions. Identifying areas most susceptible to effects of IAPs is important for prioritising management (Strayer 2010), although management will be most effective if it can address the environmental factors promoting invasion, rather than reacting to established invasions. However, most climate change scenarios also suggest that summer droughts and wetter winters will increase across NW Europe, which, according to our analyses, may frustrate attempts to limit invasions and their consequences.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1**. List of species used in this study.

**Appendix S2.** Model selection summary for models within the top set for each of the five response variables.

**Appendix S3**. Significant indicator species in upland and lowland sites in the first and second survey period.