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

3

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12

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14 **Keywords**

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

17

18 **Nomenclature**

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

20

21 **Abbreviations**

22 IAP = invasive alien plant

23

24 **Abstract**

25

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

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

30 **Methods:** We quantified change in river bank vegetation using survey data collected
31 approximately 20 years apart and assessed the contribution of major IAPs (*Impatiens*
32 *glandulifera*, *Heracleum mantegazzianum* and *Fallopia japonica*) to these changes, and

33 determined the importance of abiotic factors such as flow regime and land use in driving these
34 changes.

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

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

56

57 **Introduction**

58

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

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

77 Intermittent flooding is a defining feature of riparian zones, with dependent
78 hydrological and geomorphic processes such as inundation, erosion and sediment deposition,
79 among key determinants of vegetation growth and survival (Baatrup-Pedersen et al. 2013).
80 Historic changes to flow regimes as a result of climate shifts or flow regulation may affect
81 these processes, thereby altering species diversity and composition of riparian vegetation
82 (Nilsson & Svedmark 2002). The consequences of altered river flows for riparian biota are
83 usually negative (Poff & Zimmerman 2010; Webb et al. 2013). However, little is known about
84 the effect of climate-induced changes in flow regime on riparian vegetation (Tickner et al.
85 2001). Since flooding favours waterborne dispersal of propagules and their recruitment
86 (Richardson et al. 2007), riparian ecosystems are responsive to changes in precipitation
87 (Garssen et al. 2015). However, flooding not only enables the recruitment of native species,
88 but also invasive alien plant species (IAPs), which may ultimately compromise the resilience
89 of riparian vegetation to disturbances (Richardson et al. 2007).

90 Disturbance, whether from natural or anthropogenic sources, can disrupt species
91 interactions, lower competitive ability and favour recruitment of IAPs, which are widely
92 regarded as a major threat to native biodiversity (Richardson et al. 2007). Disturbed habitats
93 with heightened potential for propagule dispersal, such as riparian zones, are especially
94 amenable to invasion (Maskell et al. 2006), with IAPs developing monospecific stands that can
95 potentially suppress the growth of native species (Beerling & Perrins 1993). Hence there is
96 concern that invasions will lead to the large-scale homogenization of native flora (Hulme &
97 Bremner 2006). Nevertheless, the precise impact of alien species on native ecosystems is still
98 widely disputed. Of the numerous alien plants in Britain only a few are considered to be
99 invasive. *Heracleum mantegazzianum*, *Fallopia japonica* and *Impatiens glandulifera* are

100 currently listed in Europe's top 100 most invasive plant species by DAISIE
101 (<http://www.europe-aliens.org/> 23/01/13) and all three commonly occur in riparian habitats.
102 The ecology and distribution of these three species is well studied, but reported impacts on the
103 diversity of native vegetation are few and sometimes conflicting (Hulme & Bremner 2005;
104 Hejda & Pyšek 2006), likely because impacts are scale and species-specific (Hejda et al. 2009;
105 Powell et al. 2011).

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

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

127

128 **Methods**

129

130 **River Macrophytes Database**

131 The Joint Nature Conservation Committee (JNCC) River Macrophytes Database (RMD)
132 contains records from standardised vegetation surveys of rivers from across the UK undertaken

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

142

143 **Data extraction**

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



150

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

153

154 A standard species checklist was used by all surveyors and additional species were also
 155 recorded in some instances. All surveys in the first period were undertaken by a single surveyor
 156 (Nigel Holmes). However, in the second period surveys were conducted by seven different
 157 personnel. To offset the bias in recording of additional species by different surveyors, a
 158 conservative criterion (presence at >2% of sites) was used to obtain a list of species common
 159 to both survey periods. A total of 119 angiosperms and bryophytes representing those on the
 160 standard checklist, plus additionally recorded species, were used in subsequent analyses.
 161 Species excluded from analyses represented <10% of the total cover of all species recorded.
 162 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.

163

164 **Vegetation descriptors**

165 Alien species were defined as those which colonised Britain with the help of humans. We
166 focused on the invasive alien species *H. mantegazzianum*, *I. glandulifera* and *F. japonica*
167 which have previously been linked with negative impacts on native riparian vegetation (Hejda
168 et al. 2009). *Impatiens glandulifera* was the most frequently recorded, occurring at 70% of
169 invaded sites. The percentage cover of *I. glandulifera*, *H. mantegazzianum* and *F. japonica*
170 were combined and used to assess the effect of IAP cover on aspects of the native plant
171 community. Commonly occurring riparian alien species that were not considered invasive for
172 the purposes of this study included *Acorus calamus*, *Claytonia sibirica*, *Epilobium*
173 *brunnescens*, *Impatiens capensis* and *Mimulus guttatus*. Some studies have shown that native
174 dominant species may have a comparable competitive ability to IAPs (Bottollier-Curtet et al.
175 2013). In order to assess the comparative effect of native dominant species on the associated
176 native vegetation, native species were split into subordinate and dominant categories
177 (Appendix S1). Native dominant species (n=15) were defined *a priori* as species with mainly
178 or wholly competitor growth strategies (sensu Grime 1974) that also commonly form mono-
179 dominant stands alongside rivers in Britain (e.g. *Phalaris arundinacea*, *Urtica dioica*). Native
180 subordinate species were those with a wholly or partly ruderal or stress tolerator growth
181 strategy (sensu Grime 1974), which often occur at low abundance and tend to be outcompeted
182 by native dominant species. The percentage cover of native dominant or subordinate species
183 was determined by summing the individual percentage cover of the species belonging to these
184 groups.

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

190 To identify changes in community composition, while accounting for differences in site
191 attributes, sites were first clustered by altitude, slope, hydrology and location (easting) into
192 homogenous groups using K-Means cluster analysis. Two clusters were chosen, 'upland'
193 (n=132) and 'lowland' (n=139) river types, which reflected ease of interpretability and the need
194 for a minimum sample number per cluster. All 'lowland' rivers occurred at <200m elevation.
195 Species characteristic of the earlier or later surveys within each of the two river types were
196 identified using indicator species analysis (IndVal; Dufrene & Legendre 1997) applied to
197 square root-transformed percentage cover data. IndVal considers specificity and fidelity in
198 different groups (i.e., survey \times river type = 4 groups) with the index ranging from 0 %, denoting

199 no presence in a survey group, to 100 %, indicating presence in only one group and occurrence
200 in all samples from within that group. The significance of these values was tested using a Monte
201 Carlo randomisation procedure (Dufrene & Legendre 1997).

202 To support interpretation of environmental conditions, Ellenberg's indicator values for
203 moisture (F), light (L), pH (R) and fertility (N) were compared for the indicator species in each
204 group and survey period (Hill et al. 1999). Ellenberg indicator values (Ellenberg et al. 1991)
205 that rank plant tolerance to light (L), moisture (F), pH (R) and nitrogen (N) were assigned to
206 angiosperms and bryophytes using the PLANTATT and BRYOATT databases (Hill et al.
207 2004).

208

209 **Site characteristics**

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

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

231

232 **Statistical analysis and model selection**

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

254 A multi-model inference approach was used based on information theory (Burnham &
255 Anderson 2002), a method increasingly being adopted when dealing with observational data
256 collected at large spatial scales with varying environmental gradients such as those in this
257 study. Models were compared and ranked using AICc (correcting for small sample sizes), with
258 all possible combinations of predictors identified using the dredge function in MuMIn. Main
259 effects (including quadratic terms) were only considered alongside their interactions, if the
260 effect contributed to model fit. The best fitting models were evaluated based on their Δ AICc,
261 with values <4 considered to be equally parsimonious (Burnham & Anderson 2002). Akaike
262 weights were calculated for each explanatory variable, in order to compare the relative
263 importance of each variable in the top set (Δ AICc <4) of models. Model coefficients were
264 averaged across this set (full averaging) and the resulting averaged coefficients were used for
265 predictions and 95 % confidence intervals. Confidence intervals were calculated as $1.96 \times$ the
266 standard error of the model predictions. Model predictions were plotted holding all other

267 standardised predictor variables at zero. To account for the variation explained solely by the
268 fixed effects, as well as the variation explained by both the fixed and random effects, both the
269 marginal and conditional R^2 values are reported for each model, respectively (Nakagawa &
270 Schielzeth 2013).

271 All statistical analyses were conducted using R 3.2.2 (R Development Core Team
272 2015), with the additional R packages *vegan* (v 2.3-0), *labdsv* (v 1.8-0), *NbClust* (v 3.0),
273 *MuMIn* (v 1.15.1) and *lme4* (v 1.1-10).

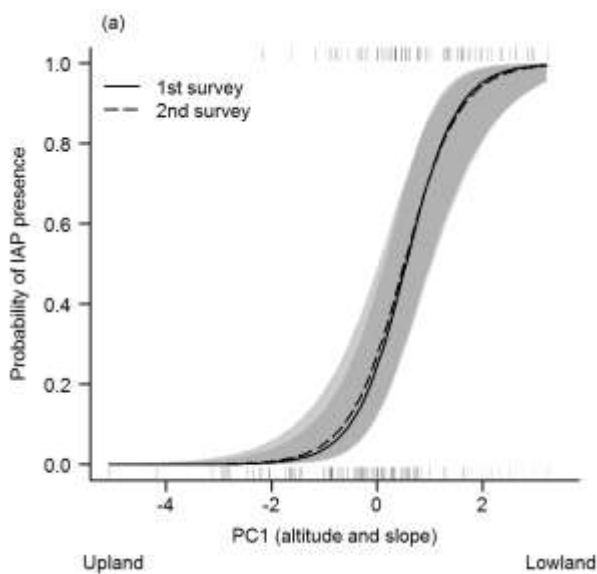
274

275 **Results**

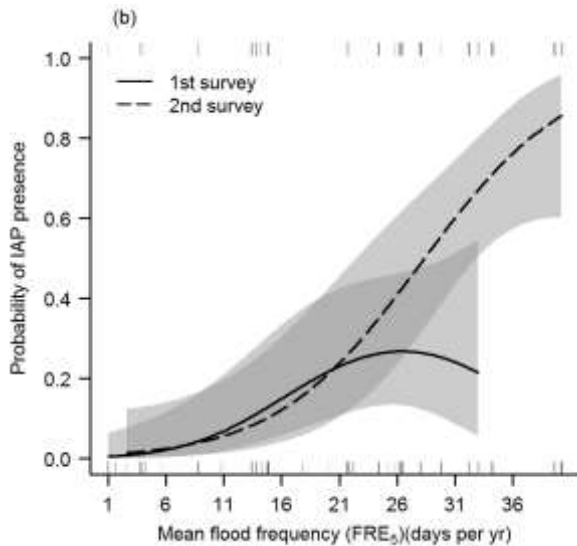
276

277 **Invasive alien species**

278 Probability of IAP presence increased with PC1 scores, which were equivalent to decreasing
279 altitude and slope. This effect was the same for both survey periods (Fig. 2a). Flood frequency
280 and PC1 (altitude and slope) were the most important variables (interaction terms with survey,
281 (Table 1)) for predicting the probability of IAP presence at a site. Both predictors had a relative
282 variable importance (RVI) of 1. The top model within the top set had a marginal R^2 of 0.57 and
283 a W_i of 0.68 (Appendix S2). Flood frequency increased the probability of an invasive species
284 being present at a site, particularly so for the second survey (Fig. 2b). IAPs were present at 34
285 % of the 271 sites in the first survey period compared with 47 % of sites in the second survey
286 period. The median percentage cover of IAPs in the first survey period was low, ~5 %,
287 compared to 15 % in the second survey period.



288



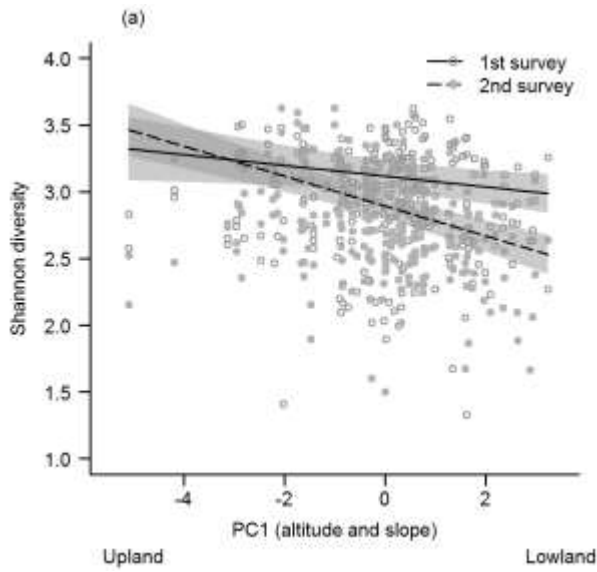
289

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

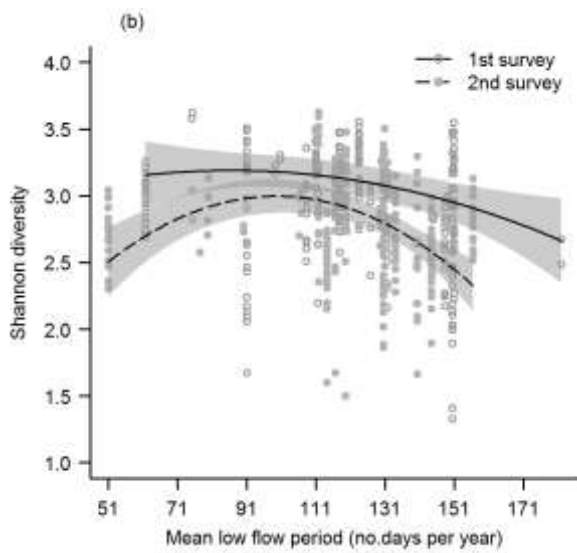
293

294 **Native species diversity**

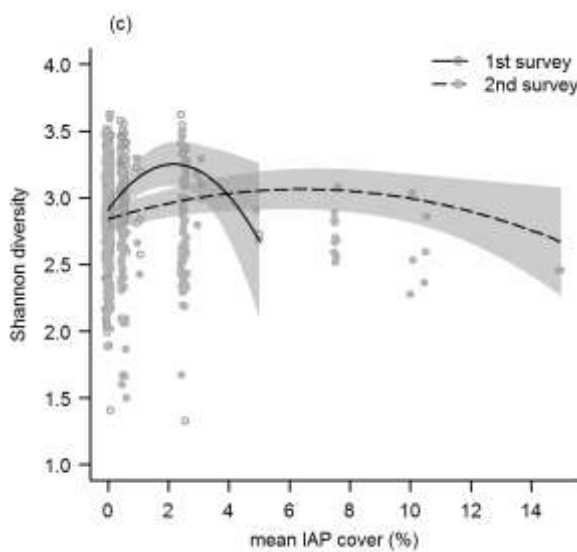
295 Across sites as a whole native species diversity declined by an average of 6 % between surveys.
 296 Along lowland and upland rivers, native diversity declined by 10 % and 2.4 % respectively.
 297 Interaction terms $IAP^2 \times survey$ and $easting \times survey$ had the greatest effect on native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



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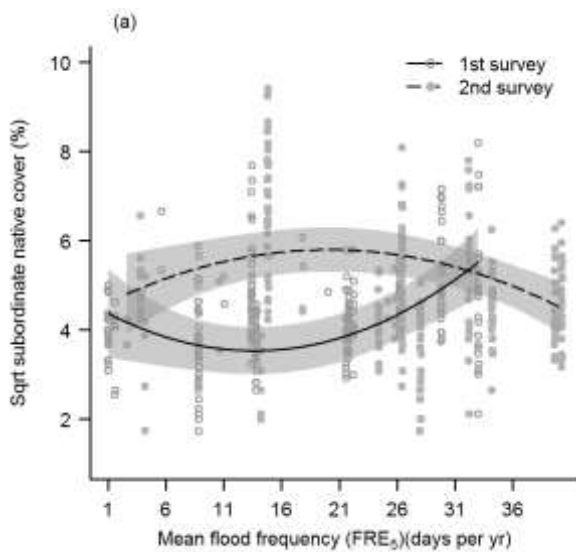
307 Fig 3. Observed values (points) and full model averaged predicted values (lines \pm 95 % CI) from the
 308 LMM analysis of native species Shannon diversity. Open and closed circles represent observed values

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

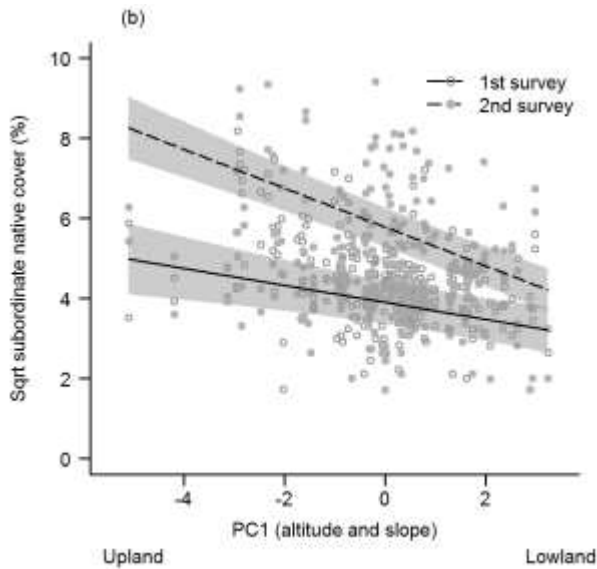
312

313 Native species cover

314 Interaction terms flood frequency² \times survey, easting \times survey and low flow² \times survey had the
315 greatest effect on native subordinate species cover and an RVI of 1 (Table 1). In contrast to the
316 first survey period, cover was highest at intermediate flood frequencies in the second survey
317 period (Fig. 4a). There was a negative association between native subordinate species cover
318 and decreasing site altitude and slope in both survey periods, although strongest in the second
319 period. Thus, the difference in native subordinate species cover between the second relative to
320 the first survey period increased from low to high altitude sites (Fig. 4b). All predictors were
321 retained within the top model set. The top model had a W_i of 0.38 and a marginal R^2 of 0.35
322 (Appendix S2).



323



324

325

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

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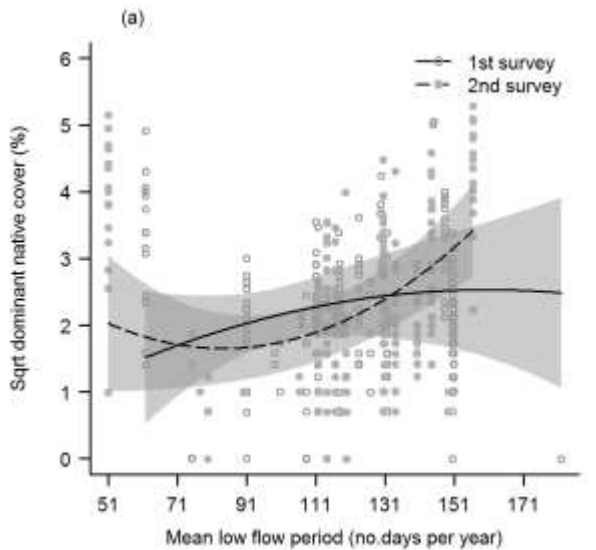
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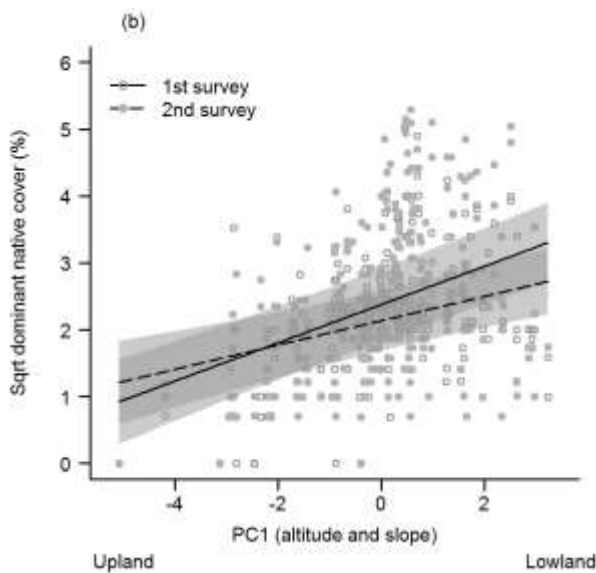
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340

Although most explanatory variables had a relatively small effect on native dominant species cover, easting \times survey and low flow² \times 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).



341

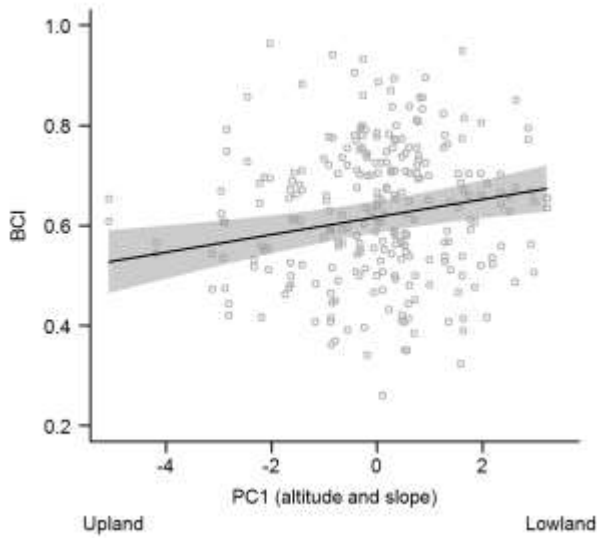


342

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

348 **Change in native species composition**

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



355

356

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

Predictor	Invasive Presence/Absence				S-W Diversity				BCI (Turnover)				Subordinate Cover				Dominant Cover			
	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

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

365

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

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

389 strongly hydrophilic species such as *S. erectum* increased in lowland sites in the later survey
390 period.

391

392 **Discussion**

393

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

402

403 **Invasive alien plant distribution**

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

416 At similar high flow frequencies there was a greater probability of IAP occurrence in
417 the second survey period compared with the first survey period. Since flooding favours spread
418 of IAPs along rivers (Truscott et al. 2006), an increased frequency of high flows might intensify
419 this effect. Direct effects of high flows include reduced cover of dominant species, and
420 increased species turnover, facilitated by reduced competition (Nilsson & Svedmark 2002).
421 Garssen et al. (2015), however, showed that increased duration of flooding did not reduce

422 riparian plant biomass, as species tolerant of flooding were adapted to frequent inundation. The
423 potential for IAPs to maintain abundance after flood-enhanced colonisation therefore
424 represents an additional pressure upon riparian communities.

425

426 **Changes in native plant diversity**

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

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

451

452 **Subordinate and dominant native plant cover**

453 Lowland rivers supported less native plant diversity in the second survey period compared with
454 the first survey period. Lowland rivers were also associated with greater reductions in native
455 subordinate species cover in the second survey period. In contrast, native dominant plants were

456 positively associated with lowland sites, most likely favoured by a combination of higher
457 fertility, finer sediments and lower variation in flows (Tickner 2001). Changes in flow regime
458 had contrasting effects on native subordinate and dominant species cover. The latter was less
459 affected by flood frequency, and benefitted more from an increase in duration of low flows
460 than native subordinate species, consistent with the reduced native species diversity observed
461 at lowland sites. Bunn & Arthington (2002) highlight multiple studies linking increased growth
462 of river plants with reduced flow variability and artificially stabilised flow regimes, with
463 dominant species likely to be the main beneficiaries.

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

476

477 **Changes in native species composition**

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

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

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

508 Land-use changes offer a complementary explanation to that implicating changes to
509 water flow for changes between the two survey periods, particularly in lowland catchments.
510 The period between 1991 and 2004 saw a ~10% decline in Britain in total cattle numbers (Defra
511 2015). Since 1986 agri-environment schemes have also subsidised farmers to reduce bankside
512 grazing by stock (Kirkham et al. 2006), partly to enhance the effectiveness of riparian buffer
513 zones for diffuse pollution reduction, while the fencing of stream margins has been widely
514 adopted in fisheries management (SEPA 2009). Since riparian areas are favoured by cattle for
515 access to water and palatable vegetation (Batchelor et al. 2015) these changes are likely to have
516 reduced grazing pressure. González et al. (2015) highlight studies showing positive responses
517 of *Salix* and *Populus* tree species to exclusion of cattle from riparian zones while other studies
518 report a fourfold increase in rush and willow species and increase in palatable hydrophytic
519 plants (Hough-Snee et al. 2013; Batchelor et al. 2015). The increases we observed in
520 *Sparganium erectum*, a species often targeted by livestock (Willby pers. obs.), and woody *Salix*
521 spp. therefore seem likely to be related, at least in part, to reduced grazing pressure. Alongside
522 changes in livestock management there was a pronounced switch from spring to winter
523 cultivated cereals between survey periods (Barr et al., 1993). Cultivated land is a major source

524 of fine sediment input to rivers (Collins & Walling, 2007) and this change in practice, coupled
525 with increased intensity of winter rainfall, is likely to have exacerbated fine sediment inputs.
526 Deposition of fertile fine sediment on river banks creates gaps conducive to growth of IAPs
527 such as *I. glandulifera*, as well as some native dominant species (Pattison & Willby unpubl.
528 data).

529

530 **Conclusion**

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

548

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717 **Supporting Information**

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

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

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

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

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