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Citation for final published version:

Vaughan, Ian Phillip ORCID: <https://orcid.org/0000-0002-7263-3822> and Ormerod, Stephen James ORCID: <https://orcid.org/0000-0002-8174-302X> 2014. Linking interdecadal changes in British river ecosystems to water quality and climate dynamics. *Global Change Biology* 20 (9) , pp. 2725-2740. 10.1111/gcb.12616 file

Publishers page: <http://dx.doi.org/10.1111/gcb.12616>
<<http://dx.doi.org/10.1111/gcb.12616>>

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1 Primary research article

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4 **Linking inter-decadal changes in British river ecosystems to water**
5 **quality and climatic dynamics**

6

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18 Running title: *Inter-decadal change in British rivers*

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20 Keywords: Flow, temperature, invertebrates, pollution, recovery, water quality

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Summary

Macroinvertebrate communities in Western European rivers have changed substantially in recent decades. Understanding the causes is challenging because improvements in water quality have coincided with climatic variations over this period. Using data covering >2300 rivers and 21 years (1991–2011) across England and Wales, we analysed family-level distributions and nationwide trends in prevalence (proportion of sampling locations where an organism was present) to diagnose the causes of ecological change. Our aims were to: i) reveal the taxa driving assemblage-level trends, ii) identify the main changes in family-level prevalence and distribution patterns, and iii) test whether changes were accounted for by improving water quality, increasing temperatures or variations in discharge. While previous analyses revealed increasing richness among British river invertebrates, a partial turnover of taxa is now evident. Two distinct components of temporal trend have comprised: i) overall increases or decreases in taxon prevalence over 21 years, which correlated with pollution sensitivity and discharge, and ii) short-term variations in prevalence that correlated primarily with temperature and nutrient concentrations. The longer-term changes in prevalence were reflected in expansions or contractions in families' distributions linked to water quality, with little evidence of shifts consistent with increasing temperatures. Although these monitoring data had limitations (e.g. family-level data, few headwaters), they provide no clear evidence of long-term climate effects on invertebrates; the one feature consistent with climate warming – a small northward expansion of the range of many taxa – was accounted for by large improvements in water quality in northern England. Nevertheless, changes linked to discharge and temperature over the shorter term (< 2 years) point to the climatic sensitivity of invertebrate communities. It is therefore likely that any long-term climatic changes since 1990 have been outweighed by the strength and geographical extent of the recovery from poor water quality.

49 **Introduction**

50 Rivers exemplify the challenges of understanding ecological responses to multiple stressors
51 that are increasingly implicated in global change (Ormerod *et al.*, 2010). Globally, many
52 rivers are modified by exploitation for ecosystem services, flood alleviation, point-source
53 pollution, diffuse effects of catchment land use and the introduction of alien species
54 (Vörösmarty *et al.*, 2005, 2010). In turn these have altered the hydrology, water chemistry,
55 geomorphology and ultimately the ecology of river systems (Allan, 2004). Riverine
56 ecosystems are also naturally stressed, most notably by climatic variations (e.g. Boulton,
57 2003; Gilbert *et al.*, 2008; Power *et al.*, 2008), which can also interact with anthropogenic
58 stressors (e.g. Durance & Ormerod, 2007; Dunbar *et al.*, 2010). Climatic effects on rivers
59 have generated particular interest in recent years, given emerging evidence for trends in
60 discharge or water temperatures (e.g. Webb, 1996; Déry *et al.*, 2005; Hannaford & Marsh,
61 2007; Arismendi *et al.*, 2012; Wang & Zhang, 2012), a series of major droughts and floods
62 across several parts of the world (Blunden & Arndt, 2012; Kennedy *et al.*, 2012) and
63 predictions of further shifts and variability over coming decades (e.g. Shepherd *et al.*, 2010;
64 Bell *et al.*, 2012; Prudhomme *et al.*, 2012). Whilst evidence for climatic effects upon river
65 organisms is increasing (e.g. Acuña *et al.*, 2005; Clews *et al.*, 2010; Durance & Ormerod,
66 2010; Ledger *et al.*, 2011; Domisch *et al.*, 2012), there is a major challenge to separate
67 climatic effects from other potential stressors, most notably varying water quality (Ormerod *et*
68 *al.*, 2010). Meeting this challenge is important for both diagnostic and prognostic purposes, as
69 well as informing management about how to limit global change impacts. So far, however,
70 few empirical case studies have attempted to separate climatic and water quality drivers of
71 ecological change in rivers, particularly at regional to national scales.

72

73 The ecological effects of high and low flow events, as well as those expected through changes
74 in average discharge conditions, are complex and multifactorial. Changes in discharge alter
75 the wetted perimeter, and habitat available in the river channel, while representing important
76 disturbance events in their own right (Lake, 2000). Changes in discharge also affect
77 concentrations of natural solutes and pollutants through altered dilution or altered flux from
78 catchment sources (Whitehead *et al.*, 2009). Temperature has similarly far-reaching effects,
79 including direct metabolic effects upon ectotherms, alterations in the rate of key ecological
80 processes, such as decomposition, and additional consequences for water quality through
81 changing oxygen concentration or solute kinetics (Ormerod & Durance, 2012). While most
82 studies focus on ecological responses to long-term temperature increase (Daufresne *et al.*,
83 2004; Durance & Ormerod, 2007), inter-annual variations in temperature that can already
84 exceed 1-2°C could also have important implications for organisms, for example through non-
85 linear changes in composition or altered phenology (Mouthon & Daufresne, 2006; Thackeray
86 *et al.*, 2010).

87

88 Considering the importance of separating climatic effects from other potential stressors on
89 river ecosystems, there is a need for long term studies so that the temporal variability in both
90 organisms and environment can be captured, rates of change quantified and events (e.g.
91 droughts) characterised (Jackson & Füreder, 2006). Long-term monitoring of river
92 macroinvertebrates in the UK provides one such opportunity, with an extensive monitoring
93 network covering thousands of rivers (Vaughan & Ormerod, 2012a). For many years, gross
94 pollution from wastewater discharge was probably the major stressor of these rivers, but
95 treatment has improved over recent decades whilst discharges from heavy industry have
96 declined (Langford *et al.*, 2009), resulting in large reductions in point source pollution,
97 especially in the vicinity of urban areas (Vaughan & Ormerod, 2012a; Fig S1). At the same

98 time as urban water quality has improved, however, there has been evidence of a trend
99 towards increasing water temperatures, at least until the mid-2000s (Ormerod & Durance,
100 2012; Fig S1). Concomitantly, large variations among years in water quality, temperature and
101 discharge can be linked to climate phenomena such as the North Atlantic Oscillation
102 (Kingston *et al.*, 2006), whilst the evidence for trends in average or extreme discharge is more
103 equivocal (Stahl *et al.*, 2010; Wilby *et al.*, 2010). These changes in the set of potential
104 stressors affecting river ecosystems, coupled with the availability of long-term monitoring
105 data (>20 years), provide a context in which to try to separate water quality and climatic
106 impacts (Vaughan *et al.*, 2009).

107

108 Most studies of changing macroinvertebrate assemblages in aquatic ecosystems use synoptic
109 measures such as diversity, bioassessment metrics or ordination scores with the expectation
110 that these provide a simple and powerful way to describe overall changes in the community
111 (Chessman & McEvoy, 1998). Whilst such approaches can extract the major signals in data,
112 they may disguise underlying detail that offers greater potential for diagnosing potential
113 causes of trend. Bioassessment tools may struggle to distinguish between multiple stressors
114 (Chessman & McEvoy, 1998) and could be undermined by additional changes in the
115 environment (e.g. increasing temperatures), requiring cautious application until validated
116 under new conditions (Hamilton *et al.*, 2010; Hassall *et al.*, 2010). Given these limitations, we
117 adopted a different approach, examining nationwide change in the prevalence – the proportion
118 of locations at which a family was present – or spatial distribution of individual taxa through
119 time, before relating this to changes in the environment. Such an approach shares challenges
120 common to all macroinvertebrate studies (e.g. the reliability of ‘absences’), but relaxes some
121 of the main assumptions of assemblage-level metrics and may provide a more complete
122 picture of community-level change with potential greater diagnostic capability.

123

124 In two previous studies, we started to examine the relationships between changes in
125 invertebrate assemblages, water quality and climate using UK river monitoring data (Durance
126 & Ormerod, 2009; Vaughan & Ormerod, 2012b). In these studies, and the current one, we
127 consider water quality in terms of nutrient concentrations (nitrate and phosphate) and overall
128 organic loading. Both previous studies relied on assemblage level metrics (ordination scores,
129 richness), and either gave climate cursory treatment (Vaughan & Ormerod, 2012b) or were
130 restricted to a small number of streams in lowland southern England (Durance & Ormerod,
131 2009). Richness illustrates this point: whilst an increase in overall richness of nearly 20%
132 across England and Wales was demonstrated, it was not possible to identify the taxa driving
133 the changes (Vaughan & Ormerod, 2012b). Here, using data from >2300 rivers across
134 England and Wales covering 21 sampling years (1991–2011), we extend both the power and
135 breadth of these earlier studies by: i) modelling time series for individual macroinvertebrate
136 families (cf. using assemblage-level metrics), ii) using changes in both geographical
137 distribution and prevalence of individual families to test hypotheses at a national scale, and
138 iii) identifying distinct components of the overall time series that could be related to water
139 quality, temperature and discharge.

140

141 Our specific aims were threefold: i) to reveal the primary contributors to the overall increase
142 in taxon richness observed since 1990 and identify declines of individual taxa that may have
143 been disguised by the general increase in richness; ii) to separate sources of short-term
144 variation from long-term trends (i.e. directional change over 21 years) in prevalence amongst
145 invertebrate families and clarify the roles of water quality, temperature and discharge; and iii)
146 to look for evidence of shifts in geographical distribution consistent with improving water
147 quality or rising temperatures, the latter akin to those observed for many terrestrial taxa, and

148 some aquatic species, over similar timespans (e.g. Hickling *et al.*, 2005, 2006). The analysis
149 of distribution patterns represents one of the first studies looking for climate-related
150 distribution changes across a wide range of individual riverine taxa, and we know of no other
151 similar study at a nationwide scale.

152

153 We hypothesised that long-term (ca 20 years) changes in prevalence arose from increasing
154 temperatures, improving water quality or a combination of the two, whilst shorter term
155 variations in prevalence correlated with inter-year variations in discharge and/or temperature.
156 Improving water quality and increasing temperatures are expected to have an antagonistic
157 relationship, which should help to diagnose the causes of change: the former will see
158 increased prevalence amongst taxa associated with greater pollution sensitivity, higher
159 dissolved oxygen concentrations and faster flowing waters, whereas long-term temperature
160 increases will have the opposite effect (Durance & Ormerod, 2009). This will also be
161 reflected geographically, with pollution sensitive taxa expanding into the more heavily
162 urbanised, warmer and drier lowlands of south and east of England with improving water
163 quality, and the opposite for increasing temperatures.

164

165

166

167 **Methods**

168 *Outline*

169 Data analysis comprised separate workflows for temporal and spatial analyses (Fig. 1). The
170 temporal analysis commenced with modelling the prevalence of each invertebrate family
171 through time (1991–2011). This addressed Aim 1 – revealing the primary contributors to
172 increasing richness and identifying declining taxa – and provided a basis for many of the
173 subsequent analyses. The temporal analysis then split into two distinct parts (Fig. 1). In the
174 first, the invertebrate time series were analysed with ordination to reveal the main sources of
175 variation (i.e. common patterns of inter-annual variation in prevalence) among the 78 taxa
176 (Aim 2): the resulting ordination scores provided concise descriptors of each family’s time
177 series. Known discharge and temperature preferences, and pollution sensitivities, of individual
178 families were correlated against the ordination scores to test simple hypotheses about the
179 potential roles of discharge, water quality and temperature in generating the observed changes
180 in prevalence (Aim 2; Fig. 1). The second part of the temporal analysis focused upon short-
181 term temporal changes by: i) de-trending invertebrate and environmental time series to
182 remove long-term changes, ii) cross-correlating the de-trended time series for lags up to two
183 years, and iii) regressing the ordination scores from part one onto the cross correlation
184 coefficients to reveal how short term relationships between organisms and discharge, water
185 quality or climate (cross correlation results) related to the main sources of temporal variation
186 (Aim 2; Fig. 1). The spatial analysis considered changes in geographical distribution of each
187 family between the early 1990s and late 2000s to test for shifts that would be consistent with
188 increasing temperature or improving water quality (Aim 3). Simple distribution models
189 enabled us to predict how the observed changes in average temperature and water quality
190 might affect the distributions (Aim 3). The observed and modelled changes were then

191 contrasted and related to the changes in prevalence witnessed over the same period (Fig. 1).

192 All data analyses used R v2.13 (R Core Development Team, 2011).

193

194 *Macroinvertebrate data*

195 Macroinvertebrate data were collated from 21 years (1991–2011) of routine monitoring by the

196 Environment Agency of England and Wales. Samples were collected in spring (March–May)

197 and autumn (September–November) using a standardised three-minute kick-sampling

198 protocol (Murray-Bligh, 1999). Taxa were sorted and identified to predominantly family-level

199 under laboratory conditions. The error rate in the monitoring data has been near constant since

200 1991 (J. Murray-Bligh, pers. comm.), based on a quality assurance scheme where 10% of

201 samples were re-inspected by a second operator and a random selection of samples was

202 completely re-analysed by an external auditor (Centre for Ecology and Hydrology). Data were

203 extracted for 78 taxa, based upon the individual families and composite family groups used in

204 the Biological Monitoring Working Party (BMWP) scoring system, but updated to reflect

205 recent changes in taxonomy (Centre for Ecology and Hydrology, 2011; Appendix S1). All

206 data were converted to presence-absence to avoid problems with changing taxonomy and

207 methods of recording abundance.

208

209 *Family-level time series*

210 Macroinvertebrate trends for England and Wales were based on 2339 sampling locations

211 (mean = 6.2 years sampled) where: i) there was at least one year sampled in each of the three,

212 seven-year divisions of the total study period (1991–2011) to minimise the turnover of sites,

213 and ii) both spring and autumn samples were collected in each year a site was sampled: by

214 pooling these two samples, a more reliable picture of the fauna was obtained (Clarke *et al.*,

215 2002). Where multiple sampling locations were present on the same watercourse, one was
216 selected at random.

217

218 Time series were modelled using Generalised Additive Models (GAMs; Fewster *et al.*, 2000;
219 Fig. 1), with an identity link and normal errors for taxon richness, and a logit link and
220 binomial errors for family presence-absence data. Year was modelled either as a factor, to
221 provide annual estimates of taxon prevalence, or smoothed using a cubic regression spline
222 with seven degrees of freedom to look at longer-term patterns, using R's mgcv library (Wood,
223 2006). Fixing the degrees of freedom around 1/3 of the length of the data series is considered
224 to be effective at capturing both the overall trend and multi-year fluctuations (Fewster *et al.*,
225 2000) and similar results were obtained using splines in the range 5–9 degrees of freedom.

226 Due to the large number of sites and the sparse data at many sites (e.g. 3–5 years), it was not
227 practical to include site as a factor in the GAMs. Instead, following the recommendation of
228 Fewster *et al.*, (2000), we included 10 site-level environmental covariates in the models that
229 have been shown to explain much of the variation in macroinvertebrate assemblages among
230 sites: catchment area and mean annual rainfall across the catchment; the proportion of the
231 catchment with arable, improved grassland or urban land cover, and underlain by calcareous
232 geology; the elevation and channel slope at the sampling location; and the easting and
233 northing of the location (see Vaughan & Ormerod, 2012b for details). All of the covariates
234 were modelled with regression splines with three degrees of freedom, with the exception of
235 easting and northing, which were modelled simultaneously using a tensor product smooth
236 (Wood, 2006). No variable selection was used and so the correlations among the covariates
237 were not a concern (Harrell 2001), whilst the non-parametric bootstrapping approach
238 circumvented the problems of serial autocorrelation that affect parametric methods (Fewster
239 *et al.*, 2000). To minimise biases introduced by non-random location of sampling points, data

240 were post stratified (Buckland *et al.*, 2005; Vaughan & Ormerod, 2012b; see Appendix S2 for
241 details). Bootstrapping was used to generate non-parametric 95% confidence limits around the
242 time series, based on 399 bootstraps from which the 2.5 and 97.5 percentiles were calculated
243 (Fewster *et al.*, 2000).

244

245 *'Upland' index*

246 There is a strong gradient in riverine and other fauna in the UK moving from the cooler,
247 wetter and piedmont north and west, to the warmer, drier, more densely populated lowlands.
248 To help interpret spatial and temporal patterns, we devised an 'upland' index that quantified
249 where individual families were located on this gradient. The 78 taxa were ordinated based on
250 their presence/absence across 6285 locations sampled in spring and autumn 1995 using
251 Principal Coordinates Analysis based upon Jaccard similarities (van Tongeren, 1995) (Fig.
252 S2). This year was selected because it had the most extensive coverage and was after the most
253 rapid period of temporal biological change in England and Wales (Vaughan & Ormerod,
254 2012b): results for 2000, another well-sampled year, were near identical. The first axis
255 represented the overall prevalence in the data ($r = 0.93$), and was discarded. The second axis
256 captured the major biogeographical gradient, with negative values (e.g. many hemipterans and
257 molluscs) representing easterly, lowland distributions in drier climates (Fig. S2), whilst
258 positive values represented westerly, upland distributions in more rural, wetter locations (e.g.
259 plecopterans, ephemeropterans; Fig. S2). For simplicity, this is referred to as the 'upland'
260 index, whilst recognising that many environmental variables change simultaneously with
261 altitude.

262

263 *Analysis of major temporal patterns*

264 The main sources of temporal variation amongst the 78 smoothed, family-level time series
265 were identified using Principal Component Analysis (PCA; Fig. 1). Before PCA, the
266 modelled prevalence for each taxon was standardised by subtracting the taxon's mean
267 prevalence and dividing by its standard deviation. This removed differences in overall
268 prevalence among taxa so that the PCA focused upon patterns of temporal change, rather than
269 absolute changes. PCA was applied to the resulting family \times year (78 \times 21) matrix.

270

271 To test our hypotheses about the factors underlying temporal changes in macroinvertebrate
272 assemblages, PCA axes one and two (PC1 and PC2) were correlated against the 'upland'
273 index, pollution sensitivity, discharge preferences and temperature preferences (Fig. 1).

274 Pollution sensitivity was quantified using families' BMWP (Biological Monitoring Working
275 party) scores, which are expert-opinion assessments of sensitivity to organic pollution (higher
276 values indicate greater sensitivity; Armitage *et al.*, 1983), and a data-driven update of the
277 BMWP weights ('Revised BMWP'; Walley & Hawkes, 1996). Discharge preferences were
278 quantified using scores from the Lotic-invertebrate Index for Flow Evaluation (LIFE), in
279 which lower values indicate preference for faster flows (Extence *et al.*, 1999), and the
280 correlation between prevalence and mean discharge over the preceding 12 months (see *Short*
281 *term changes* for details). Relationships with temperature were quantified using: i) a trait-
282 based index of temperature preferences, focusing mainly upon Ephemeroptera, Plecoptera and
283 Trichoptera for which trait data were available (Schmidt-Kloiber & Hering, 2012), where
284 higher scores indicated a preference for warmer conditions (see Appendix S2 for full details);
285 ii) the mean water temperature at sites where each taxon occurred in 1995 ('thermophily'
286 *sensu* Chessman, 2009), after filtering out the 50% of locations with the poorest water quality
287 to try to minimise confounding effects (see Appendix S2 for details), and iii) the cross-

288 correlations between unsmoothed prevalence and mean water temperature in the preceding 12
289 months, similar to the analysis for discharge.

290

291 For ease of interpretation, the Pearson correlation coefficient was used to describe the
292 relationship between PCA scores and the different metrics, whilst for significance testing,
293 PC1 or PC2 scores were regressed onto the different metrics using generalised least squares
294 (GLS), specifying a correlation structure that adjusted for potential phylogenetic correlation
295 among families (Pinheiro & Bates, 2000; Paradis, 2012). We employed the approach of
296 Grafen (1989) to estimate the correlation among taxa, as this was compatible with the
297 composite BMWP families (Paradis, 2012). Oligochaeta was excluded from these analyses as
298 it is a higher taxonomic level, making the sample size for GLS 77 taxa unless otherwise
299 stated.

300

301 *Short term changes*

302 The analysis of short-term changes involved two steps: an analysis of each family's time
303 series and a second step relating the family-level results to PC1 and PC2. In the first step,
304 each taxon's unsmoothed time series was de-trended using linear regression to isolate short-
305 term variations in prevalence from overall 21-year changes. The de-trending was repeated for
306 five environmental variables (water temperature, discharge, BOD, nitrate and phosphate), and
307 invertebrate and environmental time series correlated using R's ccf function (Venables &
308 Ripley, 2002) over lags of up to two years to reveal: i) how closely a family's prevalence
309 tracked different environmental changes and ii) the time lags at which the correlations were
310 largest. A maximum lag of two years was used as this covers the larval stage of most UK
311 macroinvertebrates (Hynes, 1970). Invertebrate data were compared to environmental data
312 averaged over the preceding 12 months (Mar–Feb) for an initial analysis of the PCA results

313 (Table 1) or against seasonal averages (winter = December–February, spring = March–May,
314 summer = June–August, autumn = September–November) – the latter generating correlations
315 at eight lags (4 seasons × 2 years). Environmental time series were calculated separately for
316 each taxon based on the subset of locations where the taxon was recorded at some stage
317 during 1991–2011 so as to exclude regions outside their range.

318

319 In the second stage, the cross-correlation coefficients from the 77 taxa were collated and
320 correlated against PC1 or PC2 scores at each time lag in turn, using Pearson correlation
321 coefficients for ease of interpretation and GLS for significance testing. The resulting Pearson
322 correlations calculated at eight time lags indicated the strength of the relationship between the
323 short-term variations in prevalence that contributed to the major temporal signals (PCs) and
324 variation in individual environmental variables (e.g. discharge). They were comparable with
325 the family-level ccf analyses in revealing the sign and magnitude of the correlations, and the
326 lag at which the correlation was largest, pointing to the season at which sensitivity to climate
327 or water quality was greatest. It is important to note that the environmental variables were
328 collinear (Table 2) and so cautious interpretation of the results is required.

329

330 *Changes in distribution*

331 The distributions of 56 taxa were analysed (Appendix S1): only those for which there were at
332 least 50 occupied and unoccupied sites, to ensure sufficient data were available for
333 distribution modelling (below). They were divided into two groups with contrasting
334 distributions that were expected to respond to changing temperatures or water quality in
335 opposing ways (Thomas & Lennon, 1999; Fig. 1). In the first classification, taxa were divided
336 into ‘upland’ and ‘lowland’ groups using the median upland index. An alternative
337 classification recognised ‘eastern’ and ‘western’ taxa according to whether the mean easting

338 of occupied sites for a taxon exceeded the mean for all sites in the data set – this aimed to
339 contrast taxa favouring more rural, upland locations with higher water quality and discharge
340 in the west, relative to the east. A division into ‘northern’ and ‘southern’ taxa (e.g. based on
341 their mean northing; Thomas & Lennon, 1999) was not meaningful with these data because
342 they only covered the southern part of the island of Great Britain, making it difficult to
343 identify ‘northern’ distributions. Instead, the focus was purely upon ‘southern’ taxa, defined
344 as the 50% of taxa with the most southerly mean northing of occupied sites (using other
345 proportions, e.g. most southerly 25%, 33% or 66% gave similar results). The response to
346 increasing temperatures was predicted to be an expansion, or overall shift, northwards by
347 southern taxa, westwards by eastern taxa and towards the uplands by lowland taxa, and
348 retreats by western and upland taxa. Conversely, improving water quality was predicted to
349 lead to western taxa expanding east and upland taxa towards the lowlands.

350
351 Distribution patterns were compared between 1991–2 and 2006–8 across 1565 locations
352 sampled in spring and autumn in both; this gave the best compromise between maximum time
353 span and spatial coverage. In the later years of the study period, fewer locations were sampled
354 in each year: hence samples were taken from a three year period at the second interval. For
355 each taxon, changes in distribution were quantified by the differences in the upland index and
356 in the edges of the observed distribution, with the latter based on the mean coordinates of the
357 20 occupied locations at the margin of interest, similar to previous studies focusing on
358 movements in range margins (e.g. Thomas & Lennon, 1999; Hickling *et al.*, 2005). GLS was
359 used to test whether the mean change in the upland index or location of marginal sites across
360 the 77 taxa differed from zero (Hickling *et al.*, 2006; Fig. 1). The changes in upland index and
361 range margins were then regressed on the relative changes in prevalence ($\log_{10}(\text{occupied sites}$
362 $2006-8 / \text{occupied sites } 1991-2)$) for the 77 taxa using GLS to reveal whether changes were: i)

363 simple expansions or contractions in distribution that reflected the changes in prevalence,
364 such that no change in distribution was apparent for families whose prevalence did not change
365 (intercept = 0), or ii) a systematic shift in distribution, consistent with long-term temperature
366 increases, where even taxa that did not change in prevalence showed a change in distribution
367 (intercept \neq zero; Thomas & Lennon, 1999). An example of the latter would be a mean shift
368 northward by southern taxa whose prevalence did not change (i.e. intercept $>$ 0; Thomas &
369 Lennon, 1999).

370

371 *Distribution models*

372 Distribution models were built using water quality or water temperature data in 1991–2 and
373 predictions made for 1991–2 and 2006–8 to simulate the changes in distribution that might be
374 expected if average chemistry or temperature were the sole factors controlling distributions.
375 Rather than aiming to produce sophisticated, biologically realistic models, we simply wished
376 to assess the extent to which the observed changes in average water chemistry or temperature
377 could account for the observed changes in prevalence and distribution. The study period saw
378 no major changes in mean rainfall/discharge between the two time points (Fig S1) and only
379 modest changes in catchment land use (Carey *et al.*, 2008). The same 1565 location data set
380 was used as for the distribution analysis and the predicted changes in distribution analysed in
381 the same way as for the observed data (previous section). The outputs from the 56 models
382 were also added together to estimate changes in overall richness.

383

384 Models used GAM logistic regression to relate the observed distribution in 1991–2 for each
385 family to i) water temperature or ii) the biochemical oxygen demand (BOD) and the
386 concentrations of ammonia, nitrate (approximated by total oxidized nitrogen because this
387 contributed $>$ 99% of the total N in these samples) and phosphate, all analysed using standard

388 methods (Standing Committee of Analysts, 1981, 1987, 1992). Models using both water
389 temperature and quality were also fitted, but for brevity the results are only presented in
390 supplementary material. Temperature and water chemistry were sampled monthly either at the
391 invertebrate sampling locations, or within 2km on the same watercourse, and median values
392 calculated for 1991–2 and 2006–8. No model simplification was used as the focus was solely
393 on making predictions, rather than revealing the relationships of the individual predictors with
394 invertebrate distributions, avoiding issues of spatial autocorrelation among predictors (Harrell,
395 2001). The model for each taxon was used to make predictions for both 1991–2 and 2006–8
396 from which to compare change. For distribution changes, a threshold had to be applied for
397 each family to dichotomise the predictions, and we set this to be where predicted prevalence
398 equalled observed prevalence in the training data (1991–2) because: i) this is considered to be
399 a good criterion for maintaining the observed prevalence (Freeman & Moisen, 2008) which
400 was essential for looking at changes in prevalence and distribution, ii) we were using the same
401 locations a short time later, therefore only limited generality was required (Vaughan &
402 Ormerod, 2005), and iii) more generally supported criteria (for example minimising the
403 difference between sensitivity and specificity e.g. Domisch *et al.*, 2012) produced near
404 identical results in terms of change in prevalence, whilst giving substantially worse estimates
405 of the absolute prevalence, compromising the analysis of changes in distribution.

406

407

408 **Results**

409 Mean taxon richness increased by 4.0 families (s.e. = 0.26) across England and Wales 1991–
410 2011, but disguised a partial turnover of taxa. Fifty nine families (76%) showed a significant
411 change in overall prevalence: 40 increased and 19 declined (Fig. 2). Absolute changes in
412 prevalence ranged from -0.15 (Haliplidae) to 0.26 (Rhyacophilidae-Glossosomatidae). On
413 average, the largest increases were observed amongst the Trichoptera and Ephemeroptera,
414 driving the majority of the increase in richness and disguising decreases across families in
415 groups such as Hirudinea, Hemiptera and Coleoptera (Fig. 2). These changes reflected the
416 geographic distribution of taxa, with upland taxa contributing most heavily to the national
417 increase in richness (change in prevalence v. upland index; $r = 0.46$; $p < 0.001$).

418

419 Taxa varied widely in their pattern of prevalence across the study period (Fig. S3), but PCA
420 of the standardised time series identified two major gradients in the data (Fig. 3). The first
421 (Temporal PC1), explaining 49% of the variance, was the overall change in prevalence across
422 the 21 years, with negative values reflecting decreasing prevalence (e.g. Corixidae,
423 Glossiphoniidae) and positive values increasing prevalence (e.g. Goeridae, Leuctridae). We
424 refer to this as the trend in prevalence, to distinguish it from shorter-term variability. Towards
425 the ends of the axis, smaller fluctuations in prevalence were evident on top of the overall
426 trends, with increasing and decreasing taxa mirroring one another. The second PCA axis
427 (Temporal PC2; 22% of the variance) distinguished taxa according to shorter-term variations
428 in prevalence (all other PCs explained $\leq 10\%$ of the variance). Negative scores (e.g.
429 Planariidae, Asellidae) indicated relatively low prevalence in the early-mid 1990s, followed
430 by greater prevalence from the late 1990s until mid 2000s, and finally a decrease in
431 prevalence in the mid-late 2000s. Positive values (e.g. many plecopterans) showed the

432 opposite pattern, with a peak in prevalence in the mid-1990s, followed by lower prevalence
433 for much of the study period, and often an increase after the mid-2000s (Fig. 3).

434

435 Increasing PC1 scores (\equiv increasing prevalence) reflected taxa with more upland distributions
436 and greater sensitivity to organic pollution (Table 1). Similarly, increasing Temporal PC1
437 correlated with declining LIFE class, and increasing mean discharge over the preceding year,
438 indicating preferences for greater flow velocities (Table 1). There was weak evidence (prior to
439 Bonferroni-correction) that increasing taxa tended to be those occupying cooler water
440 locations, consistent with the upland distributions, although this was not corroborated by
441 significant correlations between Temporal PC1 and published temperature preferences or
442 annual water temperatures (Table 1). Temporal PC2 was positively correlated with upland
443 distributions (not significant after Bonferroni correction) and pollution sensitivity, but not
444 with discharge (Table 1). There was stronger evidence of a preference at high scores on this
445 PC for cooler water conditions from both the mean water temperatures in the 1995
446 distributions and particularly the cross-correlations with annual water temperature (Table 1).

447

448 *Short-term changes*

449 The short-term variations in prevalence captured by PC2, and those superimposed on the long
450 term increases and decreases in prevalence (PC1), were correlated with temporal variations in
451 discharge, water temperatures and water chemistry over a range of time lags (Fig. 4). In
452 interpreting these changes, the correlations among the five variables were important (Table 2).
453 PC1 scores were positively correlated with discharge cross-correlation coefficients for the 12
454 months (Mar–Feb) prior to the start of invertebrate sampling (Fig. 4a), indicating that taxa
455 with higher PC1 scores were more prevalent following wetter conditions in the preceding
456 year. The strength of the relationship was similar in winter, summer and spring, as well as in

457 summer two years before invertebrate sampling. The relationship between PC1 scores and
458 temperature correlations varied according to the time lag (Fig. 4b): negative in summer and
459 autumn, and positive in spring and winter. This indicated that taxa with higher PC1 scores
460 were more prevalent following cooler summers and warmer springs. Cross-correlations with
461 BOD, nitrate and phosphate concentrations had generally negative relationships with PC1
462 scores (Fig. 4c–e). BOD was negative at all time lags, but most strongly in spring and summer
463 the year prior to invertebrate sampling, whilst for phosphate the relationship was strongest in
464 the previous autumn and summer. Nitrate was strongly negatively related in winter.

465

466 PC2 scores were only related to cross-correlations with discharge in the preceding summer,
467 with taxa having higher PC2 scores being more prevalent in the year following a wet summer
468 (Fig. 4a). The correlations with water temperatures were virtually all negative, especially in
469 autumn and winter, with a weaker relationship in summer and little evidence of a link to
470 spring temperatures in the preceding years (Fig. 4b). The relationship with BOD was more
471 complex (Fig. 4c), with a positive correlation between BOD cross-correlations and PC2
472 scores in winter, but a negative relationship at all other lags (especially autumn). Nitrate and
473 phosphate cross-correlations related negatively to PC2 scores throughout, with the strength of
474 the nitrate relationship decreasing with increasing time lag after the first winter, whereas the
475 relationship with phosphate was strongest in the summer (Fig. 4d–e).

476

477 *Changes in distribution*

478 The widespread changes in prevalence during the study period were reflected in changes in
479 distribution between 1991–2 and 2006–8 (Fig. 5). On average, upland taxa expanded across
480 the lowlands, although only showed a 2m drop in the mean elevation of the 20 lowest altitude
481 locations occupied, consistent with an eastward shift in western taxa's eastern boundaries

482 (mean = 12.7 km), whilst there was no significant change amongst lowland or eastern taxa.
483 The mean northern boundary of southern taxa moved northwards (mean = 10.6 km; Fig. 5).
484 GLS regressions found no evidence of overall shifts in distribution (all intercepts $p \geq 0.19$)
485 beyond those that reflected mean changes in prevalence within groups.

486

487 *Distribution models*

488 Distribution models reproduced some of the observed changes in prevalence and distribution
489 (Fig. 5). The main features of changing richness through the study period were a large
490 increase in richness in northern and central England, and south Wales, and a small decline in
491 richness in western Wales and southern England (Fig. 6). Models based upon water
492 chemistry successfully reproduced the increases in richness, but did not predict the declines
493 (Fig. 6a). Median water temperatures in 2006–8 were 0.40°C higher on average than in 1991–
494 2 (Fig. S3), but distribution models based upon temperature predicted little change in richness
495 across England and Wales, with some modest declines in the south and east, a few of which
496 overlapped with the areas of observed decline (Fig. 6a). The results for models containing
497 both chemistry and temperature closely resembled the chemistry-only models (Fig. S4)

498

499 Water chemistry models accounted for just over a third of the variance in the observed
500 changes in prevalence (Fig 6b; $R^2 = 0.37$; $p < 0.001$), contrasting with water temperature
501 models, where predicted changes in prevalence were the opposite of those observed (Figure
502 6c; $R^2 = 0.22$; $p = 0.002$). Combined water temperature and chemistry models were most
503 similar to chemistry-only models, but explained less of the change in prevalence ($R^2 = 0.15$;
504 Fig. S4d). Water chemistry models predicted several of the changes observed in distribution
505 patterns (Fig. 6): i) a shift towards the lowlands by upland taxa; ii) an eastward shift of 24.6
506 km in the boundary of western taxa, iii) some northward expansion of southern taxa (although

507 this was not significantly different from zero); and iv) no mean changes amongst lowland or
508 eastern taxa. Water temperature models, by contrast, predicted that lowland taxa should have
509 expanded further across the lowlands and eastern taxa expanded west (mean of 34.9 km),
510 whilst upland taxa were predicted to contract into the uplands and western taxa to retreat west
511 by 24.8 km (although the latter was not significantly different from zero). No significant
512 change in the mean northern boundary of southern taxa was predicted (Fig. 5).

513

514

515

516

517 **Discussion**

518 Pronounced change in the macroinvertebrate fauna of English and Welsh rivers over recent
519 decades has occurred against a complex background of varying multiple stressors – both
520 natural and anthropogenic – superimposed over equally complex aspects of geographical
521 pattern and a strong oceanic influence on the climate. Routine river monitoring data represent
522 one of the few resources for quantifying these changes and investigating the causes. The
523 merits and limitations of using such data have been discussed in detail elsewhere (Vaughan &
524 Ormerod, 2010), but often include unparalleled spatial and temporal coverage, coupled with
525 quality assurance to ensure consistency through time, offset by non-random site location and a
526 predominance of family-level (cf. species-level) data that constrains the questions that can be
527 asked. In the latter case, contrasting responses to changes in temperature or discharge in
528 closely related species may be masked by using family-level data, although studies
529 contrasting species and family level data suggest that the results are often comparable (e.g.
530 Marshall *et al.*, 2006; Mueller *et al.*, 2013) and climate change effects in rivers have been
531 detected using family level data (e.g. Chessman, 2009; Floury *et al.*, 2013). In addition here,
532 there were few locations on headwater streams, reflecting the focus of biological monitoring
533 on intermediate and large rivers in Britain (Vaughan & Ormerod, 2010). This extends the
534 scope of previous studies focusing on headwaters (e.g. Briers *et al.*, 2004; Durance &
535 Ormerod, 2007, 2010), but excludes those smaller, often upland, waterbodies expected to be
536 particularly sensitive to climatic changes (Heino *et al.*, 2009). Nevertheless, long- and short-
537 term climate effects have been demonstrated in large European rivers (e.g. Daufresne & Boët,
538 2007; Floury *et al.*, 2013) and our data should have identified any major family-level changes
539 in prevalence or distribution, whilst concentrating on the size of streams that are often the
540 focus for management (Vaughan & Ormerod, 2010).

541

542 We sought to draw out greater detail from the data by commencing our analysis with family-
543 level time series (cf. assemblage-level, such as ordination or BMWP scores). This identified
544 changes at two temporal scales: long-term changes in prevalence across the entire study
545 period and short-term variations within the 21 years of the study.

546

547 *Long-term changes*

548 The largest change over the two decades from 1991 was the set of overall increases or
549 decreases in prevalence across the 78 taxa, with concomitant expansions or contractions in
550 geographic distributions. The evidence was consistent with this being driven by improving
551 water quality, largely declining BOD, rather than increasing water temperatures during the
552 study period or as a lagged response to earlier periods of more rapid warming (Mair *et al.*,
553 2012). Specifically: i) increases in prevalence correlated with pollution sensitivity and were
554 the opposite of those expected under climate warming (Durance & Ormerod, 2009); ii) the
555 expansion of upland taxa into the lowlands and western taxa towards the east matched our *a*
556 *priori* predictions for water quality driven changes; and iii) water chemistry models managed
557 to re-create many of the changes in richness, prevalence and distribution patterns. There was
558 no overall trend in discharge or rainfall across our study period (cf. water quality; Fig. S1),
559 consistent with more detailed studies of discharge trends in England and Wales (Hannaford &
560 Marsh, 2006; Wilby *et al.*, 2008), suggesting that these changes were the result of decreasing
561 organic pollution, rather than dilution (Neal *et al.*, 2012), although increased nutrient
562 processing rates as water temperatures increased could also play a role (e.g. Rosa *et al.*,
563 2013). This matches the conclusion of previous, smaller scale studies (e.g. Durance &
564 Ormerod, 2009; Langford *et al.*, 2009) and our previous assemblage-level analysis of these
565 data (Vaughan & Ormerod, 2012).

566

567 There was little evidence to link temperature to overall increases or declines in prevalence (cf.
568 short-term variation): only the mean northward movement in the northern boundaries of
569 southern taxa. This northward movement of 10.6 km (6.8 km decade⁻¹ using the mid-points of
570 the two time windows) was lower than estimates from previous studies of 14.4–41.6 km
571 decade⁻¹ for British odonates between 1960–1970 and 1985–1995, and 32.0–42.0 km decade⁻¹
572 for aquatic hemipterans (using the mid-point of the time windows; Hickling *et al.*, 2006). In
573 part, this difference may be methodological, as: i) our sites were not arranged on a regular
574 grid, ii) we used 20 rather than 10 sites to define the margins of family distributions, iii)
575 headwaters were under-represented, and iv) family-level data may disguise contrasting
576 responses to warming amongst constituent species (Schmidt-Kloiber & Hering, 2012). A
577 lower rate of movement might also be expected here for two reasons. First, our study covered
578 a period of slower temperature increase than the 1970s and 1980s (Mair *et al.*, 2012).
579 Secondly, the set of taxa included relatively sedentary groups (e.g. molluscs) and excluded
580 (due to limited records) the three Odonata families, which are expected to respond rapidly to
581 warming (Hickling *et al.*, 2005; Bush *et al.*, 2013).

582

583 Irrespective of the rate, concluding that climate warming underlies the northward shift in
584 riverine taxa in England and Wales is problematic in the absence of accompanying evidence
585 of shifts towards the similarly cooler and wetter west, or uplands as a whole. Northern
586 England was one of the areas most affected historically by industrial pollution and has since
587 seen some of the largest biological recovery, which could generate an expansion northwards
588 correlated with increasing prevalence. This explanation gained qualified support from the
589 results of water chemistry modelling, which generated a (not significant) mean northward
590 shift of 4.3 km decade⁻¹, whilst water temperature models did not predict a mean northward
591 movement. More generally, our temperature models predicted increases in the prevalence of

592 taxa that preferred warmer, slower flowing water and declines amongst those preferring
593 cooler, cleaner, faster-flowing waters – the opposite of what was observed. Taken in
594 combination with the direct support for water quality effects, this strongly supports the idea
595 that—leaving headwaters to one side—biological recovery from pollution has been the
596 primary driver of change in British rivers since 1990, whilst evidence for the effects of
597 increasing temperatures has so far been equivocal. This is consistent with previous
598 suggestions that water quality effects have tended to be larger than temperature effects over
599 recent decades in lowland Britain (Durance & Ormerod, 2009), but contrasts with studies
600 elsewhere in Europe that have found changes consistent with a warming climate (e.g.
601 Daufresne *et al.*, 2003; Durance & Ormerod, 2007; Floury *et al.* 2013). It also highlights the
602 importance of considering changes in other environmental conditions, such as water quality,
603 when interpreting apparent climate-driven range changes by aquatic taxa (Hickling *et al.*,
604 2005).

605

606 Contrary to recent efforts to model the distributions of freshwater taxa (e.g. Wenger *et al.*,
607 2011; Domisch *et al.*, 2012; Ruesch *et al.*, 2012), our distribution models were very
608 simplistic, making a series of unrealistic assumptions to assess changes in the water quality or
609 temperature envelope (Araújo & Peterson, 2012). They ignored both basic environmental
610 information, such as channel substratum, and biological factors, such as dispersal, assuming
611 equilibrium between water quality or temperature and family distribution at both time points
612 (Araújo & Peterson, 2012). Nevertheless, they provided clear evidence for the role of
613 improving water quality in the main distribution changes and credible predictions for
614 warming water temperatures, matching our *a priori* predictions of retreats in distribution by
615 upland and western taxa and eastern taxa expanding west in the warmer temperatures of
616 2006–8.

617

618 *Short-term changes*

619 Climate variability, and its interaction with the catchment, is a major source of shorter-term
620 variation in river environments: temperature controls the rates of many biological and
621 physical processes, whilst varying discharge and catchment runoff not only affect habitat area
622 (wetted perimeter) and hydraulics directly, but also alter water quality and channel form (Neal
623 *et al.*, 2012). Correlations between climate variability and river ecosystems have been
624 demonstrated widely (e.g. Bradley & Ormerod, 2001; Wagner & Schmidt, 2004; Acuña *et al.*,
625 2005) and climate signals were apparent on both PC1 and PC2.

626

627 Considering PC1 first, the short-term variations in prevalence around the long term trends
628 correlated with discharge variation. This was consistent with the conclusion that the overall
629 trends were mainly water-quality driven, as pollution sensitive taxa generally prefer faster
630 flowing conditions (Extence *et al.*, 1999) and increased discharge dilutes phosphate and
631 organic pollutants deriving from point sources (Neal *et al.*, 2012). Conversely, the declines of
632 taxa with low PC1 scores slowed, or were temporarily reversed, following drier conditions.
633 Identifying the causal basis for these short-term correlations – which aspect(s) of water
634 quality or discharge are involved – is beyond the capacity of the current data set. Nitrate
635 concentrations in temperate headwaters tend to be higher through the winter due to catchment
636 runoff and reduced biological activity (Neal *et al.*, 2012), which might explain the negative
637 relationship between PC1 scores and nitrate cross-correlation in winter alone. The negative
638 correlation between PC1 and temperature preferences in summer could either reflect a direct
639 effect (e.g. reduced dissolved oxygen concentrations) or more general links between wetter
640 and cooler conditions in summer. Equally, the positive correlation between PC1 and winter
641 temperatures may well be a manifestation of preferences for wetter conditions (which also

642 tend to be warmer). The breadth of taxa correlating positively or negatively with discharge
643 and temperature were consistent with previous findings that mild and wet conditions,
644 particularly in winter and early spring, are associated with large changes in the invertebrate
645 community (Bradley & Ormerod, 2001; Durance & Ormerod, 2007, 2010).

646

647 Whilst our analysis of long-term changes in prevalence (PC1) expanded upon a signal that
648 had been detected previously (e.g. Parr & Mason, 2003; Langford *et al.*, 2009; Vaughan &
649 Ormerod, 2012b), the second PCA axis was novel and confirmed the value of the family-level
650 (cf. assemblage-) analysis. This axis appeared to capture temperature and water quality
651 effects, largely nutrients: taxa with high PC2 scores were more prevalent in lower nutrient
652 conditions and following wetter summers, consistent with the correlation between PC2 and
653 BMWP, although the positive relationship between winter BOD and PC2 was an exception.
654 Taxa with lower PC2 scores included many grazers (e.g. molluscs) which were more
655 prevalent in relatively warm, nutrient-rich conditions that might promote algal production and
656 the growth or reproductive rates among the organisms concerns (e.g. Rosemond *et al.*, 1993).
657 The absence of correlations between PC2 and taxa's cross-correlations with autumn or winter
658 discharge suggest that the links to temperature were more likely to be genuine thermal effects,
659 rather than a result of an underlying discharge relationship with which temperature was
660 correlated (as suggested for PC1). The involvement of nutrients in this axis also suggests a
661 possible role for more diffuse pollutants, potentially in interaction with thermal effects.

662

663 Influences on the rates of many biological and physical processes means that changing
664 temperatures can have manifold effects upon macroinvertebrate abundance and stream food
665 webs (Woodward *et al.*, 2010). Faster growth rates and earlier emergence times linked to
666 warmer winters have been implicated in the decreased abundance of headwater stream taxa

667 during spring sampling, many of which had high PC2 scores here (Briers *et al.*, 2004;
668 Durance & Ormerod, 2007). However, with the current data combining spring and autumn
669 samples, insect families and fully aquatic macroinvertebrates (e.g. molluscs) showed similar
670 temporal relationships with temperature (results not shown), tending to reject the idea that
671 warming effects on phenology were responsible for the PC2 time signal. A plausible
672 alternative is that temperature-mediated variations in the breakdown rates of autumnal leaf
673 litter could affect stream ecosystems with consequences for resource availability and use
674 (Ferreira & Chauvet, 2011). Cooler conditions may increase the availability of organic matter
675 over winter, potentially altering food webs and also accounting for the positive correlation
676 between PC2 scores and cross-correlations with BOD in winter (Hynes, 1970). Warmer
677 winters, in which leaf litter breaks down more rapidly, may promote the algal-based pathways
678 in food webs compared to the detrital-based ones (Woodward *et al.*, 2010). Such resource-
679 mediated changes in assemblages are being increasingly implicated in climate change effects
680 in addition to direct ecophysiological effects (Cahill *et al.*, 2013)

681
682 Whilst we have clarified the intimate link between organisms, water quality (especially BOD)
683 and discharge, more work is needed to elucidate the temperature and nutrients signals.
684 Hypotheses concerning the mechanisms underlying this second axis cannot be evaluated with
685 the relatively coarse-scale/resolution data used here and will need further work, and
686 potentially experimentation. Nevertheless, in an environment of improved gross water quality,
687 it is likely that ecological responses to temperature will become clearer and be more readily
688 characterised (Durance & Ormerod, 2009).

689

690 **Acknowledgements**

691 We wish to thank the Environment Agency for supplying the data used in this analysis, and
692 the Editor and six referees, whose comments enabled us to make valuable improvements to
693 the manuscript. The work was part funded by the Department for Environment, Food and
694 Rural Affairs through the Biodiversity Impacts of Climate Change Observation Network II
695 programme.

696

697

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1007

1008 **Supporting Information**

1009

1010 **Appendix S1.** The 78 taxa considered in the study, along with the groups into which 56 taxa
1011 were placed for analysing changes in distribution and modelling change: upland-lowland (Up-
1012 Low), eastern-western (E-W) and the 28 most southerly taxa (S).

1013

1014 **Appendix S2.** Methodological details for: i) post-stratifying family-level trends, ii)
1015 calculating temperature preferences based on trait-based information, and iii) calculating
1016 temperature preferences based on mean water temperatures.

1017

1018

1019 **Figure S1.** Annual mean discharge (a), water temperatures (b), BOD (c), and nitrate and
1020 orthophosphate concentrations from the locations used in the study.

1021

1022 **Figure S2.** Principal Coordinates Analysis ordination of the 78 invertebrate taxa based upon
1023 their distributions across 6285 locations sampled in 1995.

1024

1025 **Figure S3.** Temporal trends in prevalence for the 78 taxa.

1026

1027 **Figure S4.** Expanded version of Fig. 6, including the results of a model including water
1028 chemistry and temperature.

1029

1030

1031 **Table 1.** Correlations between macroinvertebrate metrics describing geographical position
 1032 (upland index), pollution sensitivity, discharge preferences and correlations with discharge
 1033 and temperature, versus Temporal PC1 and PC 2. Significance testing using generalised least
 1034 squares with $n=77$ in every case except for the temperature-traits index ($n=21$). With eight
 1035 tests for each PC, Bonferroni-corrected threshold ($\alpha = 0.05$) = 0.00625.

Variable	Temporal PC1			Temporal PC2		
	<i>r</i>	<i>t</i> -value	<i>P</i>	<i>R</i>	<i>t</i> -value	<i>P</i>
<i>Spatial component</i>						
Upland index	0.52	4.890	<0.001	0.44	2.626	0.010
<i>Pollution sensitivity</i>						
BMWP weights	0.34	1.635	0.106	0.27	1.530	0.130
Revised BMWP weights	0.49	4.005	<0.001	0.45	2.853	0.006
<i>Discharge preferences</i>						
LIFE	-0.50	4.040	<0.001	-0.30	1.630	0.107
Annual discharge	0.58	5.724	<0.001	0.13	0.250	0.804
<i>Temperature preferences</i>						
Temperature traits index	0.26	1.204	0.244	0.04	0.234	0.817
Mean water temperature	-0.37	2.352	0.021	-0.40	2.542	0.013
Annual water temperature	-0.08	0.030	0.976	-0.67	7.969	<0.001

1036
 1037

1038 **Table 2.** Correlations among the detrended seasonal discharge, water temperature and water
 1039 chemistry time series used in the cross correlation analyses (Pearson's r). Values represent the
 1040 mean correlation coefficients from the 77 family data sets.

1041

		Discharge	Temperature	BOD	Nitrate			Discharge	Temperature	BOD	Nitrate
Autumn	Temperature	-0.30				Spring	0.10				
	BOD	-0.05	-0.29				-0.26	-0.06			
	Nitrate	0.17	0.09	-0.31			0.02	-0.15	-0.18		
	Phosphate	-0.50	0.44	0.14	-0.29		-0.25	0.20	-0.01	0.06	
Winter	Temperature	0.51				Summer	-0.67				
	BOD	-0.27	-0.62				-0.31	0.02			
	Nitrate	-0.52	0.00	-0.06			0.22	-0.08	-0.35		
	Phosphate	-0.27	0.04	0.04	0.15		-0.71	0.45	0.40	-0.19	

1042
1043

Figure legends

Figure 1. The overall workflow for the temporal and spatial analyses, describing the main stages of analysis and the number of taxa involved. Boxes numbered 1–3 represent the study aim addressed at the different stages (see Methods for details). PCA = principal component analysis; GLS = generalised least squares.

Figure 2. Changes in prevalence of the 78 taxa 1992–2010. Filled circles indicate ‘significant’ changes, where the bootstrapped 95% confidence intervals do not include zero. Changes exclude the first and last year of the study, as these may exaggerate the magnitude of change (Thaxter *et al.*, 2010).

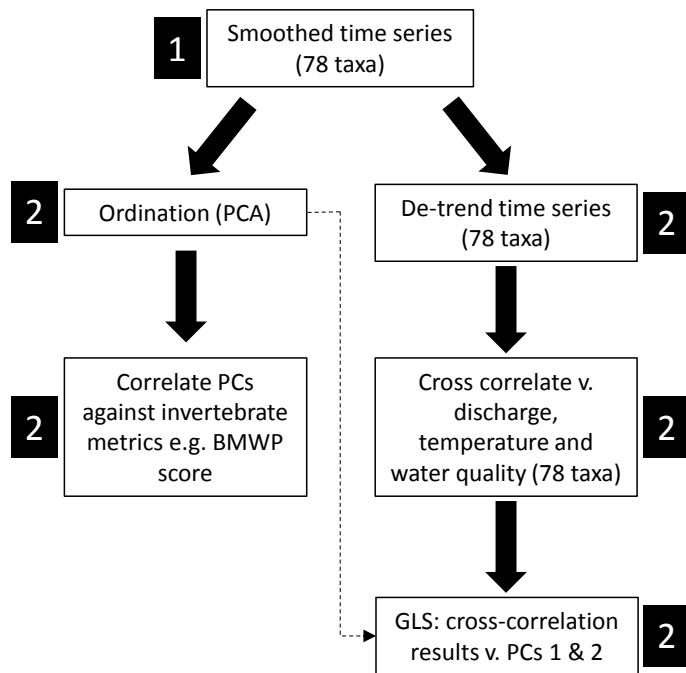
Figure 3. Principal Component Analysis of the standardised smoothed temporal trends. The un-standardised temporal trends for three taxa at the ends of the two axes are superimposed to assist with interpretation, with prevalence across the 2339 locations plotted on the y-axis.

Figure 4. Correlations between temporal PC scores (PC1 = left hand column; PC2 = right hand column) and cross correlation coefficients for the 77 invertebrate families within each season for two years prior to biological sampling. Naïve r values, not accounting for phylogenetic correlations, are plotted for simplicity, whilst significance testing employed GLS. Rows show: (a) discharge, (b) water temperature, (c) BOD, (d) nitrate and (e) phosphate. Significance at the 5% level is denoted after Bonferroni correction ($p=0.00625$; black fill) or only before correction ($p=0.05–0.00625$; grey fill): correlations that did not differ significantly from zero are represented by open bars.

Figure 5. Mean changes between 1991–2 and 2006–8 of: (a) overall distribution of ‘upland’ and ‘lowland’ taxa, (b) western boundary of ‘eastern taxa’ and eastern boundary of ‘western taxa’, and (c) northern boundary of ‘southern’ taxa. Open bars represent the observed changes, light grey bars changes modelled using water quality and dark grey bars changes modelled by changing temperature. Differences from zero tested using phylogenetic GLS: * = $p < 0.05$; ** = $p < 0.01$.

Figure 6. Observed and modelled changes in richness and prevalence between 1991–2 and 2006–8. In (a) observed or predicted changes in richness across the 1565 sites was smoothed using ordinary kriging, and white areas indicate sites lacking samples due to changes in biological sampling protocol and/or lack of matched water chemistry. Panels (b) and (c) represent the predicted changes in prevalence compared to the observed changes for the water quality and temperature models respectively.

Temporal analysis



Spatial analysis

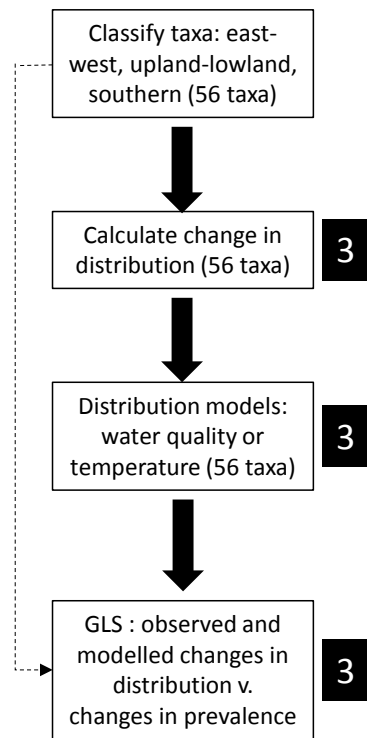


Figure 2

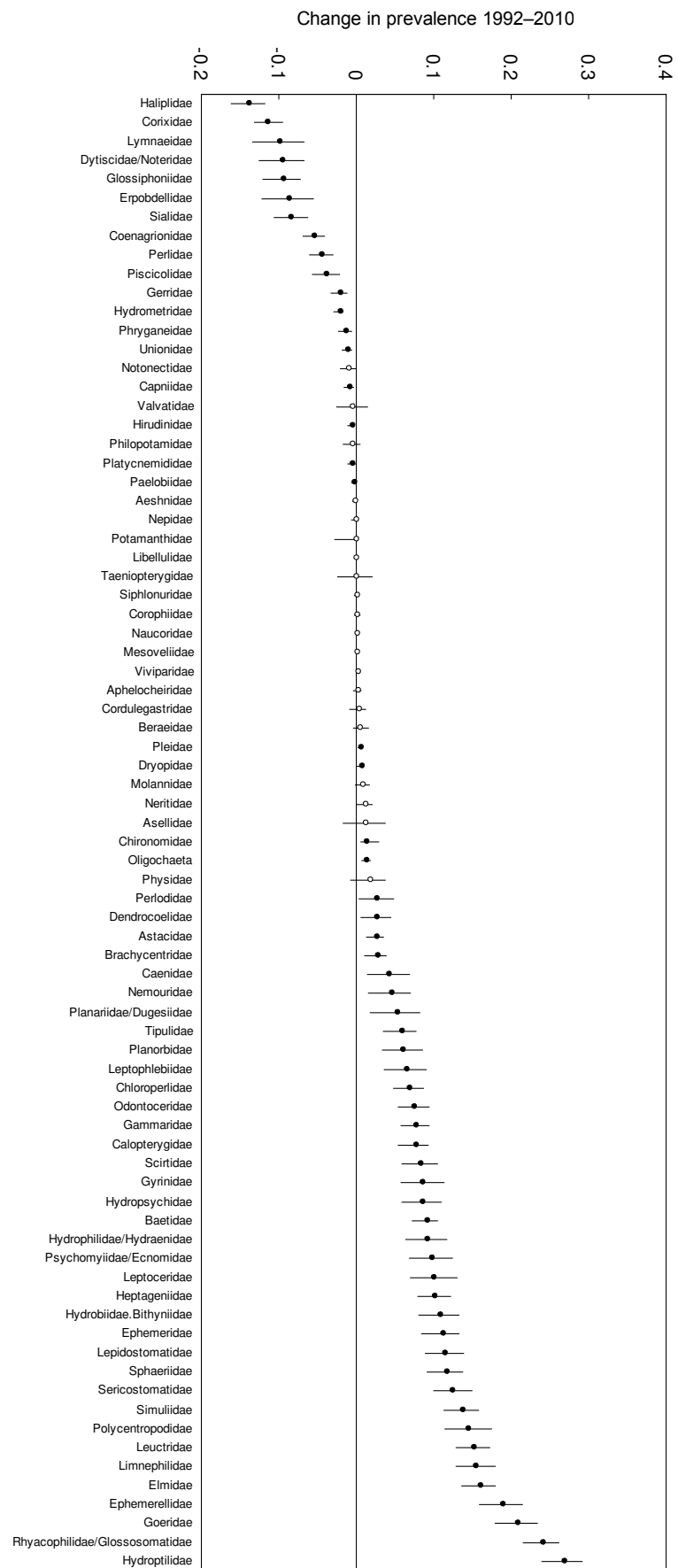


Figure 3

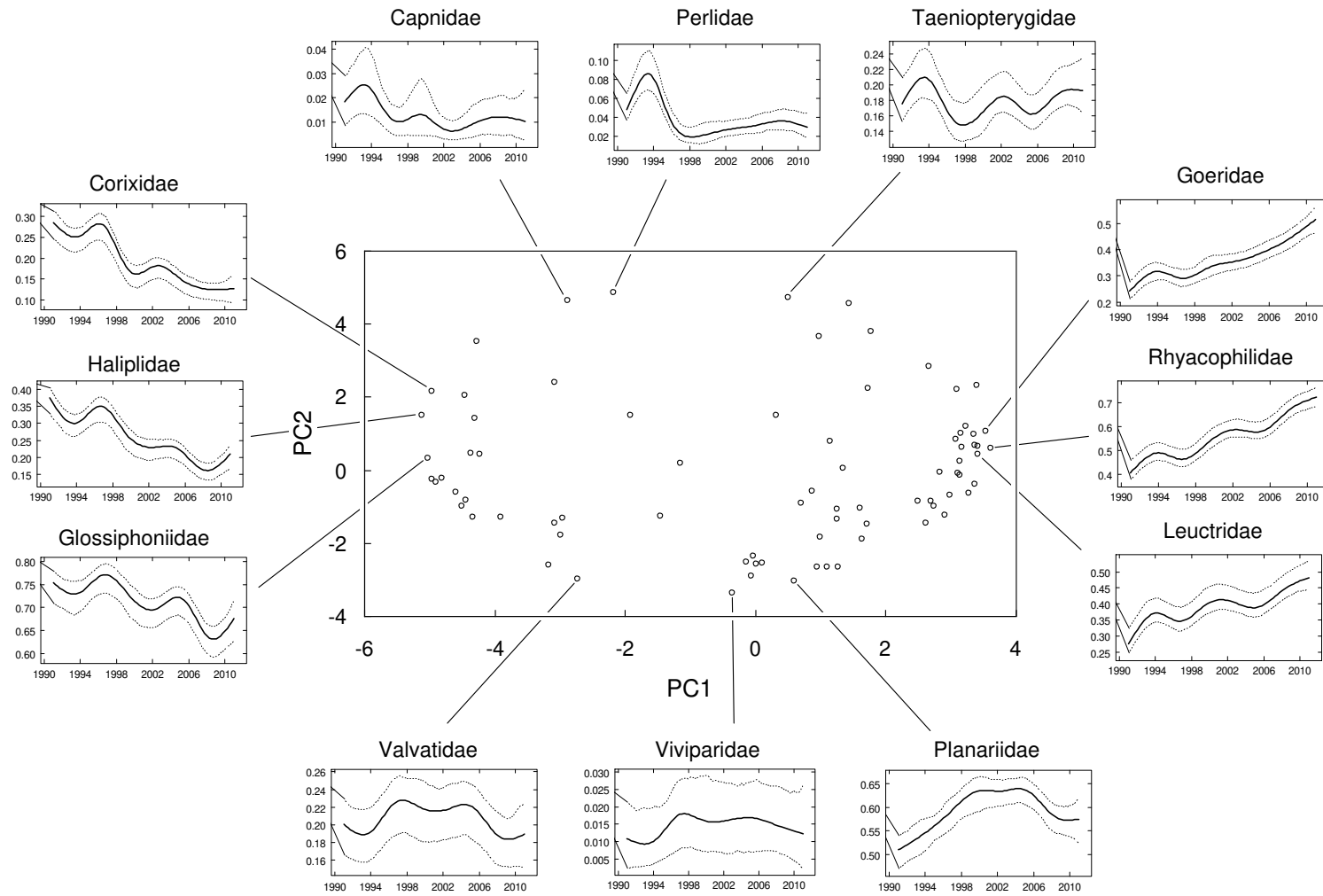


Figure 4

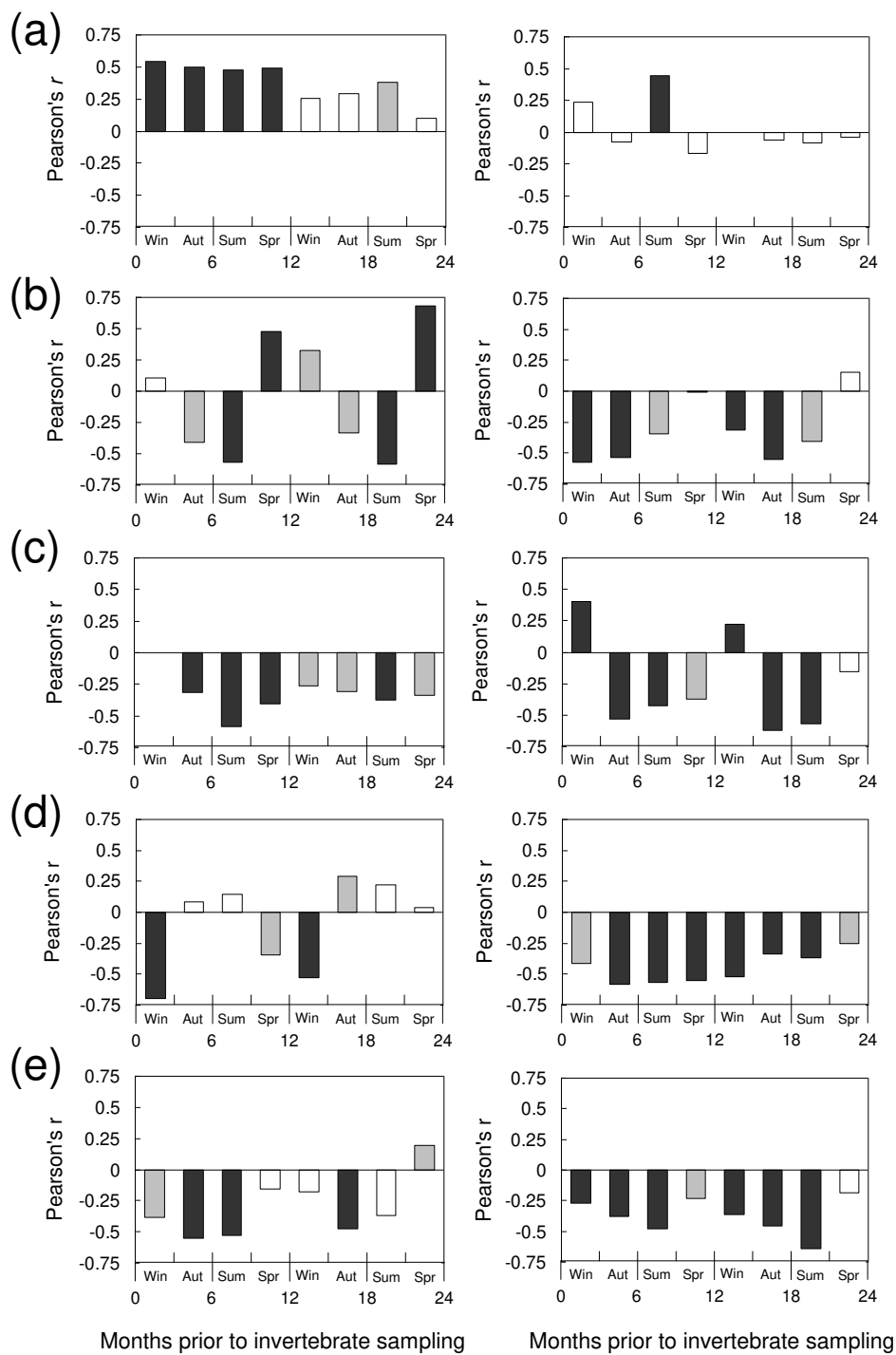
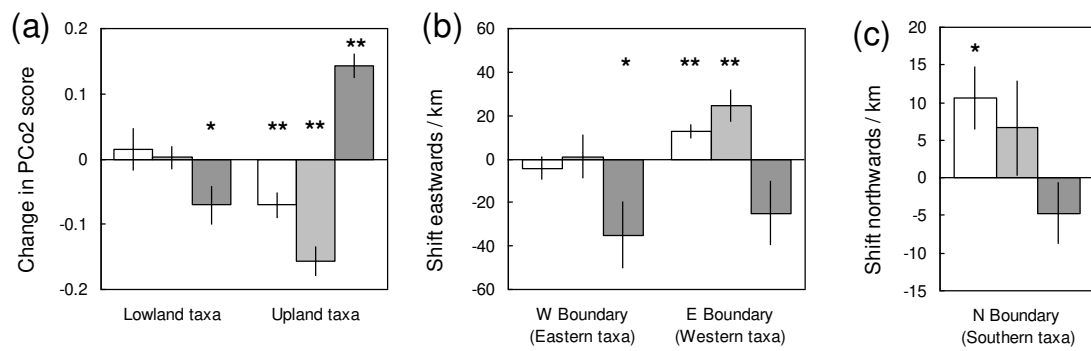
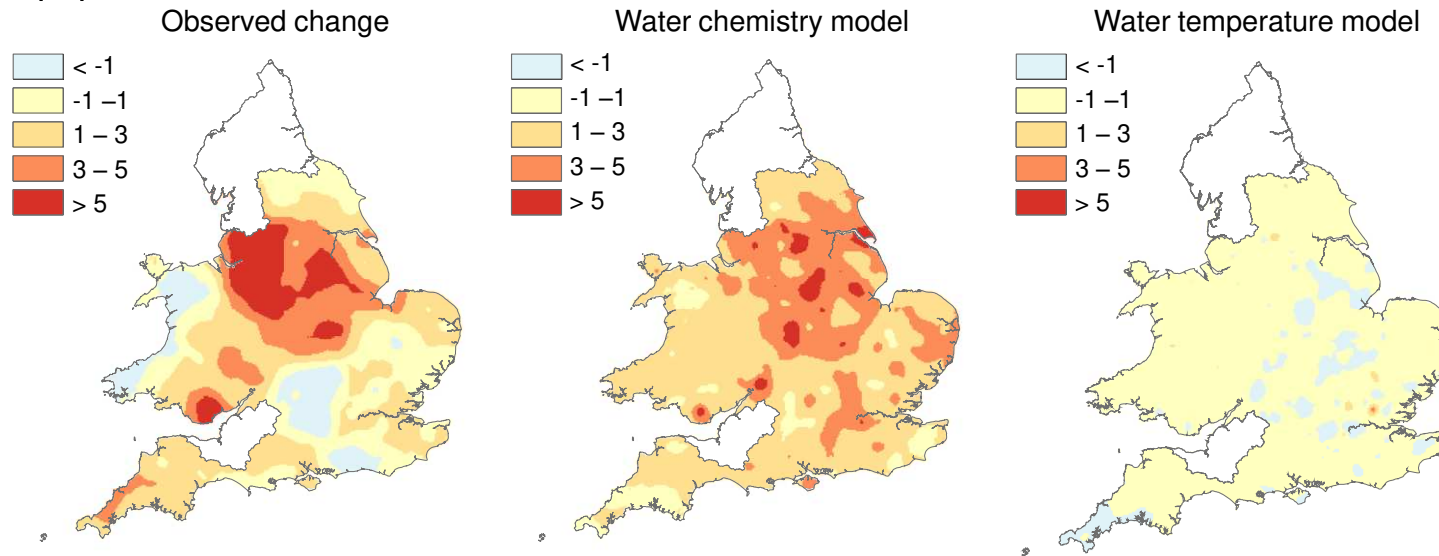


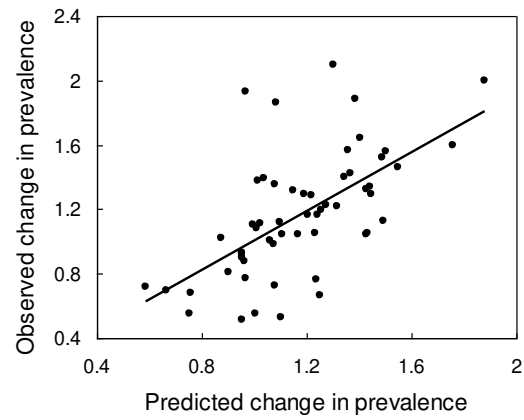
Figure 5



(a)



(b)



(c)

