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Primary research article

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

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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.

Introduction

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

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

Considering the importance of separating climatic effects from other potential stressors on river ecosystems, there is a need for long term studies so that the temporal variability in both organisms and environment can be captured, rates of change quantified and events (e.g. droughts) characterised (Jackson & Füreder, 2006). Long-term monitoring of river macroinvertebrates in the UK provides one such opportunity, with an extensive monitoring network covering thousands of rivers (Vaughan & Ormerod, 2012a). For many years, gross pollution from wastewater discharge was probably the major stressor of these rivers, but treatment has improved over recent decades whilst discharges from heavy industry have declined (Langford *et al*., 2009), resulting in large reductions in point source pollution, especially in the vicinity of urban areas (Vaughan & Ormerod, 2012a; Fig S1). At the same time as urban water quality has improved, however, there has been evidence of a trend towards increasing water temperatures, at least until the mid-2000s (Ormerod & Durance, 2012; Fig S1). Concomitantly, large variations among years in water quality, temperature and discharge can be linked to climate phenomena such as the North Atlantic Oscillation (Kingston *et al*., 2006), whilst the evidence for trends in average or extreme discharge is more equivocal (Stahl *et al*., 2010; Wilby *et al*., 2010). These changes in the set of potential stressors affecting river ecosystems, coupled with the availability of long-term monitoring data (>20 years), provide a context in which to try to separate water quality and climatic impacts (Vaughan *et al*., 2009).

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

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

Our specific aims were threefold: i) to reveal the primary contributors to the overall increase in taxon richness observed since 1990 and identify declines of individual taxa that may have been disguised by the general increase in richness; ii) to separate sources of short-term variation from long-term trends (i.e. directional change over 21 years) in prevalence amongst invertebrate families and clarify the roles of water quality, temperature and discharge; and iii) to look for evidence of shifts in geographical distribution consistent with improving water quality or rising temperatures, the latter akin to those observed for many terrestrial taxa, and some aquatic species, over similar timespans (e.g. Hickling *et al*., 2005, 2006). The analysis of distribution patterns represents one of the first studies looking for climate-related distribution changes across a wide range of individual riverine taxa, and we know of no other similar study at a nationwide scale.

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

Methods

Outline

Data analysis comprised separate workflows for temporal and spatial analyses (Fig. 1). The temporal analysis commenced with modelling the prevalence of each invertebrate family through time (1991–2011). This addressed Aim 1 – revealing the primary contributors to increasing richness and identifying declining taxa – and provided a basis for many of the subsequent analyses. The temporal analysis then split into two distinct parts (Fig. 1). In the first, the invertebrate time series were analysed with ordination to reveal the main sources of variation (i.e. common patterns of inter-annual variation in prevalence) among the 78 taxa (Aim 2): the resulting ordination scores provided concise descriptors of each family's time series. Known discharge and temperature preferences, and pollution sensitivities, of individual families were correlated against the ordination scores to test simple hypotheses about the potential roles of discharge, water quality and temperature in generating the observed changes in prevalence (Aim 2; Fig. 1). The second part of the temporal analysis focused upon short-term temporal changes by: i) de-trending invertebrate and environmental time series to remove long-term changes, ii) cross-correlating the de-trended time series for lags up to two years, and iii) regressing the ordination scores from part one onto the cross correlation coefficients to reveal how short term relationships between organisms and discharge, water quality or climate (cross correlation results) related to the main sources of temporal variation (Aim 2; Fig. 1). The spatial analysis considered changes in geographical distribution of each family between the early 1990s and late 2000s to test for shifts that would be consistent with increasing temperature or improving water quality (Aim 3). Simple distribution models enabled us to predict how the observed changes in average temperature and water quality might affect the distributions (Aim 3). The observed and modelled changes were then contrasted and related to the changes in prevalence witnessed over the same period (Fig. 1). All data analyses used R v2.13 (R Core Development Team, 2011).

Macroinvertebrate data

Macroinvertebrate data were collated from 21 years (1991–2011) of routine monitoring by the Environment Agency of England and Wales. Samples were collected in spring (March–May) and autumn (September–November) using a standardised three-minute kick-sampling protocol (Murray-Bligh, 1999). Taxa were sorted and identified to predominantly family-level under laboratory conditions. The error rate in the monitoring data has been near constant since 1991 (J. Murray-Bligh, pers. comm.), based on a quality assurance scheme where 10% of samples were re-inspected by a second operator and a random selection of samples was completely re-analysed by an external auditor (Centre for Ecology and Hydrology). Data were extracted for 78 taxa, based upon the individual families and composite family groups used in the Biological Monitoring Working Party (BMWP) scoring system, but updated to reflect recent changes in taxonomy (Centre for Ecology and Hydrology, 2011; Appendix S1). All data were converted to presence-absence to avoid problems with changing taxonomy and methods of recording abundance.

Family-level time series

Macroinvertebrate trends for England and Wales were based on 2339 sampling locations (mean = 6.2 years sampled) where: i) there was at least one year sampled in each of the three, seven-year divisions of the total study period (1991–2011) to minimise the turnover of sites, and ii) both spring and autumn samples were collected in each year a site was sampled: by pooling these two samples, a more reliable picture of the fauna was obtained (Clarke *et al.*, 2002). Where multiple sampling locations were present on the same watercourse, one was selected at random.

Time series were modelled using Generalised Additive Models (GAMs; Fewster *et al*., 2000; Fig. 1), with an identity link and normal errors for taxon richness, and a logit link and binomial errors for family presence-absence data. Year was modelled either as a factor, to provide annual estimates of taxon prevalence, or smoothed using a cubic regression spline with seven degrees of freedom to look at longer-term patterns, using R's mgcv library (Wood, 2006). Fixing the degrees of freedom around 1/3 of the length of the data series is considered to be effective at capturing both the overall trend and multi-year fluctuations (Fewster *et al*., 2000) and similar results were obtained using splines in the range 5–9 degrees of freedom. Due to the large number of sites and the sparse data at many sites (e.g. 3–5 years), it was not practical to include site as a factor in the GAMs. Instead, following the recommendation of Fewster *et al*., (2000), we included 10 site-level environmental covariates in the models that have been shown to explain much of the variation in macroinvertebrate assemblages among sites: catchment area and mean annual rainfall across the catchment; the proportion of the catchment with arable, improved grassland or urban land cover, and underlain by calcareous geology; the elevation and channel slope at the sampling location; and the easting and northing of the location (see Vaughan & Ormerod, 2012b for details). All of the covariates were modelled with regression splines with three degrees of freedom, with the exception of easting and northing, which were modelled simultaneously using a tensor product smooth (Wood, 2006). No variable selection was used and so the correlations among the covariates were not a concern (Harrell 2001), whilst the non-parametric bootstrapping approach circumvented the problems of serial autocorrelation that affect parametric methods (Fewster *et al*., 2000). To minimise biases introduced by non-random location of sampling points, data were post stratified (Buckland *et al*., 2005; Vaughan & Ormerod, 2012b; see Appendix S2 for details). Bootstrapping was used to generate non-parametric 95% confidence limits around the time series, based on 399 bootstraps from which the 2.5 and 97.5 percentiles were calculated (Fewster *et al*., 2000).

'Upland' index

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

Analysis of major temporal patterns

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

To test our hypotheses about the factors underlying temporal changes in macroinvertebrate assemblages, PCA axes one and two (PC1 and PC2) were correlated against the 'upland' index, pollution sensitivity, discharge preferences and temperature preferences (Fig. 1). Pollution sensitivity was quantified using families' BMWP (Biological Monitoring Working party) scores, which are expert-opinion assessments of sensitivity to organic pollution (higher values indicate greater sensitivity; Armitage *et al*., 1983), and a data-driven update of the BMWP weights ('Revised BMWP'; Walley & Hawkes, 1996). Discharge preferences were quantified using scores from the Lotic-invertebrate Index for Flow Evaluation (LIFE), in which lower values indicate preference for faster flows (Extence *et al*., 1999), and the correlation between prevalence and mean discharge over the preceding 12 months (see *Short term changes* for details). Relationships with temperature were quantified using: i) a trait-based index of temperature preferences, focusing mainly upon Ephemeroptera, Plecoptera and Trichoptera for which trait data were available (Schmidt-Kloiber & Hering, 2012), where higher scores indicated a preference for warmer conditions (see Appendix S2 for full details); ii) the mean water temperature at sites where each taxon occurred in 1995 ('thermophily' *sensu* Chessman, 2009), after filtering out the 50% of locations with the poorest water quality to try to minimise confounding effects (see Appendix S2 for details), and iii) the cross-correlations between unsmoothed prevalence and mean water temperature in the preceding 12 months, similar to the analysis for discharge.

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

Short term changes

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

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

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

Changes in distribution

The distributions of 56 taxa were analysed (Appendix S1): only those for which there were at least 50 occupied and unoccupied sites, to ensure sufficient data were available for distribution modelling (below). They were divided into two groups with contrasting distributions that were expected to respond to changing temperatures or water quality in opposing ways (Thomas & Lennon, 1999; Fig. 1). In the first classification, taxa were divided into ‘upland’ and ‘lowland’ groups using the median upland index. An alternative classification recognised ‘eastern’ and ‘western’ taxa according to whether the mean easting of occupied sites for a taxon exceeded the mean for all sites in the data set – this aimed to contrast taxa favouring more rural, upland locations with higher water quality and discharge in the west, relative to the east. A division into ‘northern’ and ‘southern’ taxa (e.g. based on their mean northing; Thomas & Lennon, 1999) was not meaningful with these data because they only covered the southern part of the island of Great Britain, making it difficult to identify ‘northern’ distributions. Instead, the focus was purely upon ‘southern’ taxa, defined as the 50% of taxa with the most southerly mean northing of occupied sites (using other proportions, e.g. most southerly 25%, 33% or 66% gave similar results). The response to increasing temperatures was predicted to be an expansion, or overall shift, northwards by southern taxa, westwards by eastern taxa and towards the uplands by lowland taxa, and retreats by western and upland taxa. Conversely, improving water quality was predicted to lead to western taxa expanding east and upland taxa towards the lowlands.

Distribution patterns were compared between 1991–2 and 2006–8 across 1565 locations sampled in spring and autumn in both; this gave the best compromise between maximum time span and spatial coverage. In the later years of the study period, fewer locations were sampled in each year: hence samples were taken from a three year period at the second interval. For each taxon, changes in distribution were quantified by the differences in the upland index and in the edges of the observed distribution, with the latter based on the mean coordinates of the 20 occupied locations at the margin of interest, similar to previous studies focusing on movements in range margins (e.g. Thomas & Lennon, 1999; Hickling *et al*., 2005). GLS was used to test whether the mean change in the upland index or location of marginal sites across the 77 taxa differed from zero (Hickling *et al*., 2006; Fig. 1). The changes in upland index and range margins were then regressed on the relative changes in prevalence ($\log_{10}$(occupied sites 2006–8 / occupied sites 1991–2) for the 77 taxa using GLS to reveal whether changes were: i) simple expansions or contractions in distribution that reflected the changes in prevalence, such that no change in distribution was apparent for families whose prevalence did not change (intercept = 0), or ii) a systematic shift in distribution, consistent with long-term temperature increases, where even taxa that did not change in prevalence showed a change in distribution (intercept ≠ zero; Thomas & Lennon, 1999). An example of the latter would be a mean shift northward by southern taxa whose prevalence did not change (i.e. intercept > 0; Thomas & Lennon, 1999).

Distribution models

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

Models used GAM logistic regression to relate the observed distribution in 1991–2 for each family to i) water temperature or ii) the biochemical oxygen demand (BOD) and the concentrations of ammonia, nitrate (approximated by total oxidized nitrogen because this contributed >99% of the total N in these samples) and phosphate, all analysed using standard methods (Standing Committee of Analysts, 1981, 1987, 1992). Models using both water temperature and quality were also fitted, but for brevity the results are only presented in supplementary material. Temperature and water chemistry were sampled monthly either at the invertebrate sampling locations, or within 2km on the same watercourse, and median values calculated for 1991–2 and 2006–8. No model simplification was used as the focus was solely on making predictions, rather than revealing the relationships of the individual predictors with invertebrate distributions, avoiding issues of spatial autocorrelation among predictors (Harrell, 2001). The model for each taxon was used to make predictions for both 1991–2 and 2006–8 from which to compare change. For distribution changes, a threshold had to be applied for each family to dichotomise the predictions, and we set this to be where predicted prevalence equalled observed prevalence in the training data (1991–2) because: i) this is considered to be a good criterion for maintaining the observed prevalence (Freeman & Moisen, 2008) which was essential for looking at changes in prevalence and distribution, ii) we were using the same locations a short time later, therefore only limited generality was required (Vaughan & Ormerod, 2005), and iii) more generally supported criteria (for example minimising the difference between sensitivity and specificity e.g. Domisch *et al*., 2012) produced near identical results in terms of change in prevalence, whilst giving substantially worse estimates of the absolute prevalence, compromising the analysis of changes in distribution.

Results

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

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

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

Short-term changes

The short-term variations in prevalence captured by PC2, and those superimposed on the long term increases and decreases in prevalence (PC1), were correlated with temporal variations in discharge, water temperatures and water chemistry over a range of time lags (Fig. 4). In interpreting these changes, the correlations among the five variables were important (Table 2). PC1 scores were positively correlated with discharge cross-correlation coefficients for the 12 months (Mar–Feb) prior to the start of invertebrate sampling (Fig. 4a), indicating that taxa with higher PC1 scores were more prevalent following wetter conditions in the preceding year. The strength of the relationship was similar in winter, summer and spring, as well as in summer two years before invertebrate sampling. The relationship between PC1 scores and temperature correlations varied according to the time lag (Fig. 4b): negative in summer and autumn, and positive in spring and winter. This indicated that taxa with higher PC1 scores were more prevalent following cooler summers and warmer springs. Cross-correlations with BOD, nitrate and phosphate concentrations had generally negative relationships with PC1 scores (Fig. 4c–e). BOD was negative at all time lags, but most strongly in spring and summer the year prior to invertebrate sampling, whilst for phosphate the relationship was strongest in the previous autumn and summer. Nitrate was strongly negatively related in winter.

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

Changes in distribution

The widespread changes in prevalence during the study period were reflected in changes in distribution between 1991–2 and 2006–8 (Fig. 5). On average, upland taxa expanded across the lowlands, although only showed a 2m drop in the mean elevation of the 20 lowest altitude locations occupied, consistent with an eastward shift in western taxa’s eastern boundaries (mean = 12.7 km), whilst there was no significant change amongst lowland or eastern taxa. The mean northern boundary of southern taxa moved northwards (mean = 10.6 km; Fig. 5). GLS regressions found no evidence of overall shifts in distribution (all intercepts $p \geq 0.19$) beyond those that reflected mean changes in prevalence within groups.

Distribution models

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

Water chemistry models accounted for just over a third of the variance in the observed changes in prevalence (Fig 6b; $R^2 = 0.37$; $p < 0.001$), contrasting with water temperature models, where predicted changes in prevalence were the opposite of those observed (Figure 6c; $R^2 = 0.22$; $p = 0.002$). Combined water temperature and chemistry models were most similar to chemistry-only models, but explained less of the change in prevalence ($R^2 = 0.15$; Fig. S4d). Water chemistry models predicted several of the changes observed in distribution patterns (Fig. 6): i) a shift towards the lowlands by upland taxa; ii) an eastward shift of 24.6 km in the boundary of western taxa, iii) some northward expansion of southern taxa (although this was not significantly different from zero); and iv) no mean changes amongst lowland or eastern taxa. Water temperature models, by contrast, predicted that lowland taxa should have expanded further across the lowlands and eastern taxa expanded west (mean of 34.9 km), whilst upland taxa were predicted to contract into the uplands and western taxa to retreat west by 24.8 km (although the latter was not significantly different from zero). No significant change in the mean northern boundary of southern taxa was predicted (Fig. 5).

Discussion

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

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

Long-term changes

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

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

Irrespective of the rate, concluding that climate warming underlies the northward shift in riverine taxa in England and Wales is problematic in the absence of accompanying evidence of shifts towards the similarly cooler and wetter west, or uplands as a whole. Northern England was one of the areas most affected historically by industrial pollution and has since seen some of the largest biological recovery, which could generate an expansion northwards correlated with increasing prevalence. This explanation gained qualified support from the results of water chemistry modelling, which generated a (not significant) mean northward shift of 4.3 km decade^{-1}, whilst water temperature models did not predict a mean northward movement. More generally, our temperature models predicted increases in the prevalence of taxa that preferred warmer, slower flowing water and declines amongst those preferring cooler, cleaner, faster-flowing waters – the opposite of what was observed. Taken in combination with the direct support for water quality effects, this strongly supports the idea that—leaving headwaters to one side—biological recovery from pollution has been the primary driver of change in British rivers since 1990, whilst evidence for the effects of increasing temperatures has so far been equivocal. This is consistent with previous suggestions that water quality effects have tended to be larger than temperature effects over recent decades in lowland Britain (Durance & Ormerod, 2009), but contrasts with studies elsewhere in Europe that have found changes consistent with a warming climate (e.g. Daufresne *et al*., 2003; Durance & Ormerod, 2007; Floury *et al*. 2013). It also highlights the importance of considering changes in other environmental conditions, such as water quality, when interpreting apparent climate-driven range changes by aquatic taxa (Hickling *et al*., 2005).

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

Short-term changes

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

Considering PC1 first, the short-term variations in prevalence around the long term trends correlated with discharge variation. This was consistent with the conclusion that the overall trends were mainly water-quality driven, as pollution sensitive taxa generally prefer faster flowing conditions (Extence *et al*., 1999) and increased discharge dilutes phosphate and organic pollutants deriving from point sources (Neal *et al*., 2012). Conversely, the declines of taxa with low PC1 scores slowed, or were temporarily reversed, following drier conditions. Identifying the causal basis for these short-term correlations – which aspect(s) of water quality or discharge are involved – is beyond the capacity of the current data set. Nitrate concentrations in temperate headwaters tend to be higher through the winter due to catchment runoff and reduced biological activity (Neal *et al*., 2012), which might explain the negative relationship between PC1 scores and nitrate cross-correlation in winter alone. The negative correlation between PC1 and temperature preferences in summer could either reflect a direct effect (e.g. reduced dissolved oxygen concentrations) or more general links between wetter and cooler conditions in summer. Equally, the positive correlation between PC1 and winter temperatures may well be a manifestation of preferences for wetter conditions (which also tend to be warmer). The breadth of taxa correlating positively or negatively with discharge and temperature were consistent with previous findings that mild and wet conditions, particularly in winter and early spring, are associated with large changes in the invertebrate community (Bradley & Ormerod, 2001; Durance & Ormerod, 2007, 2010).

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

Influences on the rates of many biological and physical processes means that changing temperatures can have manifold effects upon macroinvertebrate abundance and stream food webs (Woodward *et al*., 2010). Faster growth rates and earlier emergence times linked to warmer winters have been implicated in the decreased abundance of headwater stream taxa during spring sampling, many of which had high PC2 scores here (Briers *et al*., 2004; Durance & Ormerod, 2007). However, with the current data combining spring and autumn samples, insect families and fully aquatic macroinvertebrates (e.g. molluscs) showed similar temporal relationships with temperature (results not shown), tending to reject the idea that warming effects on phenology were responsible for the PC2 time signal. A plausible alternative is that temperature-mediated variations in the breakdown rates of autumnal leaf litter could affect stream ecosystems with consequences for resource availability and use (Ferreira & Chauvet, 2011). Cooler conditions may increase the availability of organic matter over winter, potentially altering food webs and also accounting for the positive correlation between PC2 scores and cross-correlations with BOD in winter (Hynes, 1970). Warmer winters, in which leaf litter breaks down more rapidly, may promote the algal-based pathways in food webs compared to the detrital-based ones (Woodward *et al*., 2010). Such resource-mediated changes in assemblages are being increasingly implicated in climate change effects in addition to direct ecophysiological effects (Cahill *et al*., 2013)

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

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Supporting Information

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

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

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

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

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

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

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

	Temporal PC1			Temporal PC2		
Variable	*r*	*t*-value	*P*	*R*	*t*-value	*P*
Spatial component						
Upland index	0.52	4.890	<0.001	0.44	2.626	0.010
Pollution sensitivity						
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
Discharge preferences						
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
Temperature preferences						
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

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

		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

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.

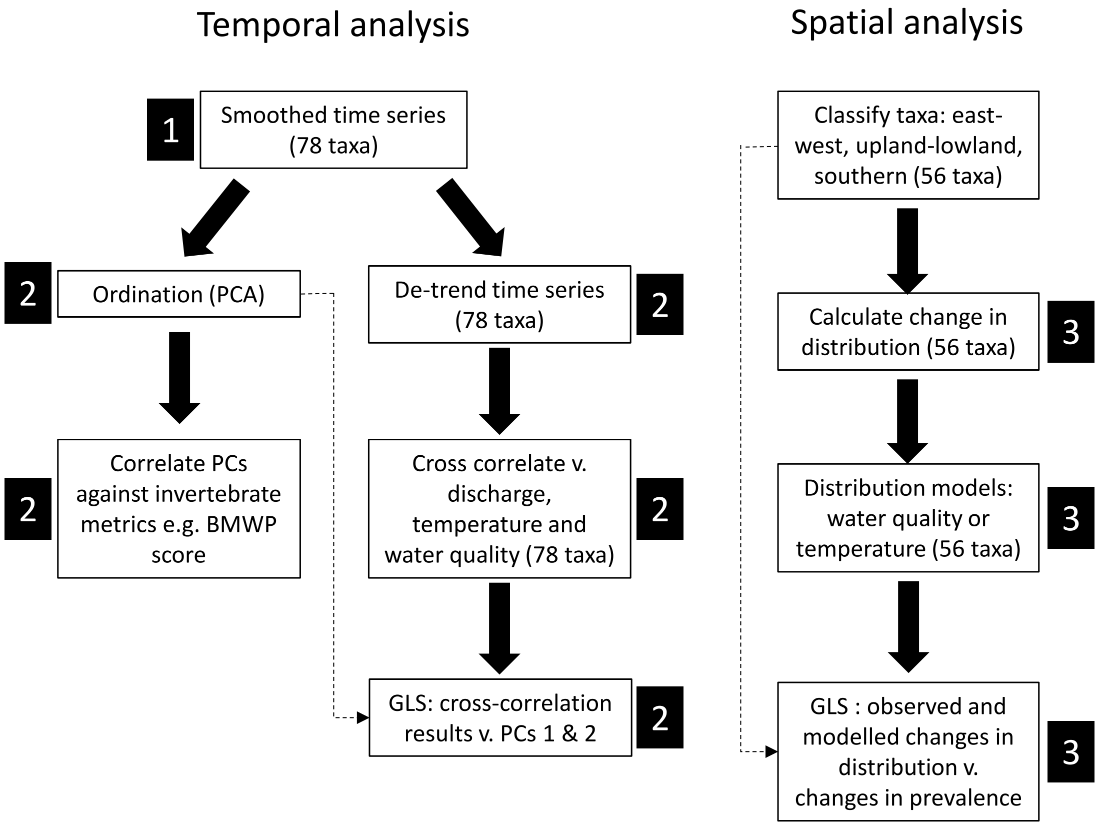

Temporal analysis
Spatial analysis
1
Smoothed time series (78 taxa)
2
Ordination (PCA)
2
De-trend time series (78 taxa)
2
Correlate PCs against invertebrate metrics e.g. BMWP score
Cross correlate v. discharge, temperature and water quality (78 taxa)
2
GLS: cross-correlation results v. PCs 1 & 2
2
Classify taxa: east-west, upland-lowland, southern (56 taxa)
Calculate change in distribution (56 taxa)
3
Distribution models: water quality or temperature (56 taxa)
3
GLS : observed and modelled changes in distribution v. changes in prevalence
3

Figure 2

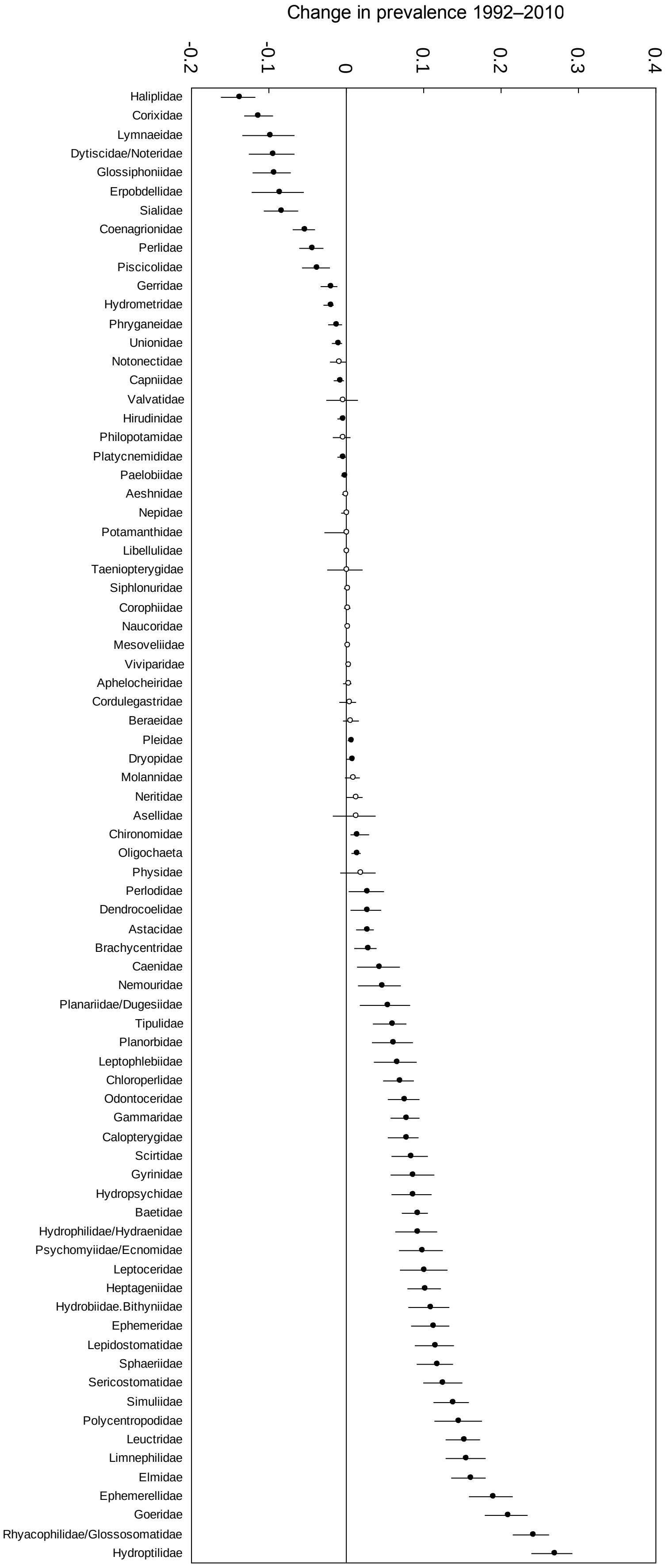

Change in prevalence 1992–2010
-0.2
-0.1
0
0.1
0.2
0.3
0.4
Haliplidae
Corixidae
Lymnaeidae
Dytiscidae/Noteridae
Glossiphoniidae
Erpobdellidae
Sialidae
Coenagrionidae
Perlidae
Piscicolidae
Gerridae
Hydrometridae
Phryganeidae
Unionidae
Notonectidae
Capniidae
Valvatidae
Hirudinidae
Philopotamidae
Platycnemididae
Paelobiidae
Aeshnidae
Nepidae
Potamanthidae
Libellulidae
Taeniopterygidae
Siphlonuridae
Corophiidae
Naucoridae
Mesoveliidae
Viviparidae
Aphelocheiridae
Cordulegastridae
Beraeidae
Pleidae
Dryopidae
Molannidae
Neritidae
Asellidae
Chironomidae
Oligochaeta
Physidae
Perlodidae
Dendrocoelidae
Astacidae
Brachycentridae
Caenidae
Nemouridae
Planariidae/Dugesiidae
Tipulidae
Planorbidae
Leptophlebiidae
Chloroperlidae
Odontoceridae
Gammaridae
Calopterygidae
Scirtidae
Gyrinidae
Hydropsychidae
Baetidae
Hydrophilidae/Hydraenidae
Psychomyiidae/Ecnomidae
Leptoceridae
Heptageniidae
Hydrobiidae.Bithyniidae
Ephemeridae
Lepidostomatidae
Sphaeriidae
Sericostomatidae
Simuliidae
Polycentropodidae
Leuctridae
Limnephilidae
Elmidae
Ephemerellidae
Goeridae
Rhyacophilidae/Glossosomatidae
Hydroptilidae

Figure 3

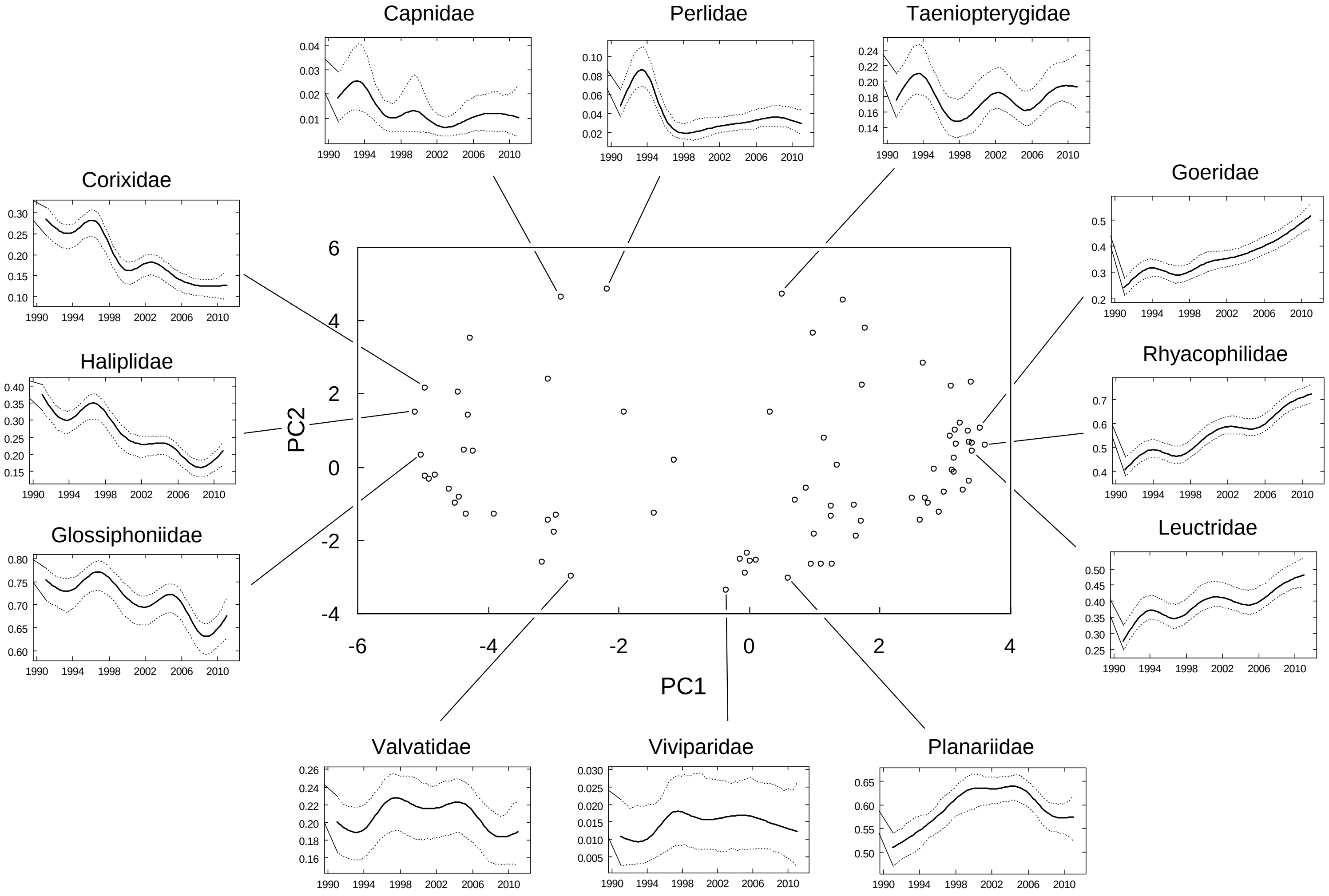

Capnidae
Perlidae
Taeniopterygidae
Corixidae
Goeridae
Haliplidae
Rhyacophilidae
Glossiphoniidae
Leuctridae
Valvatidae
Viviparidae
Planariidae
PC1
PC2
6
4
2
0
-2
-4
-6
-4
-2
0
2
4
1990
1994
1998
2002
2006
2010

Figure 4

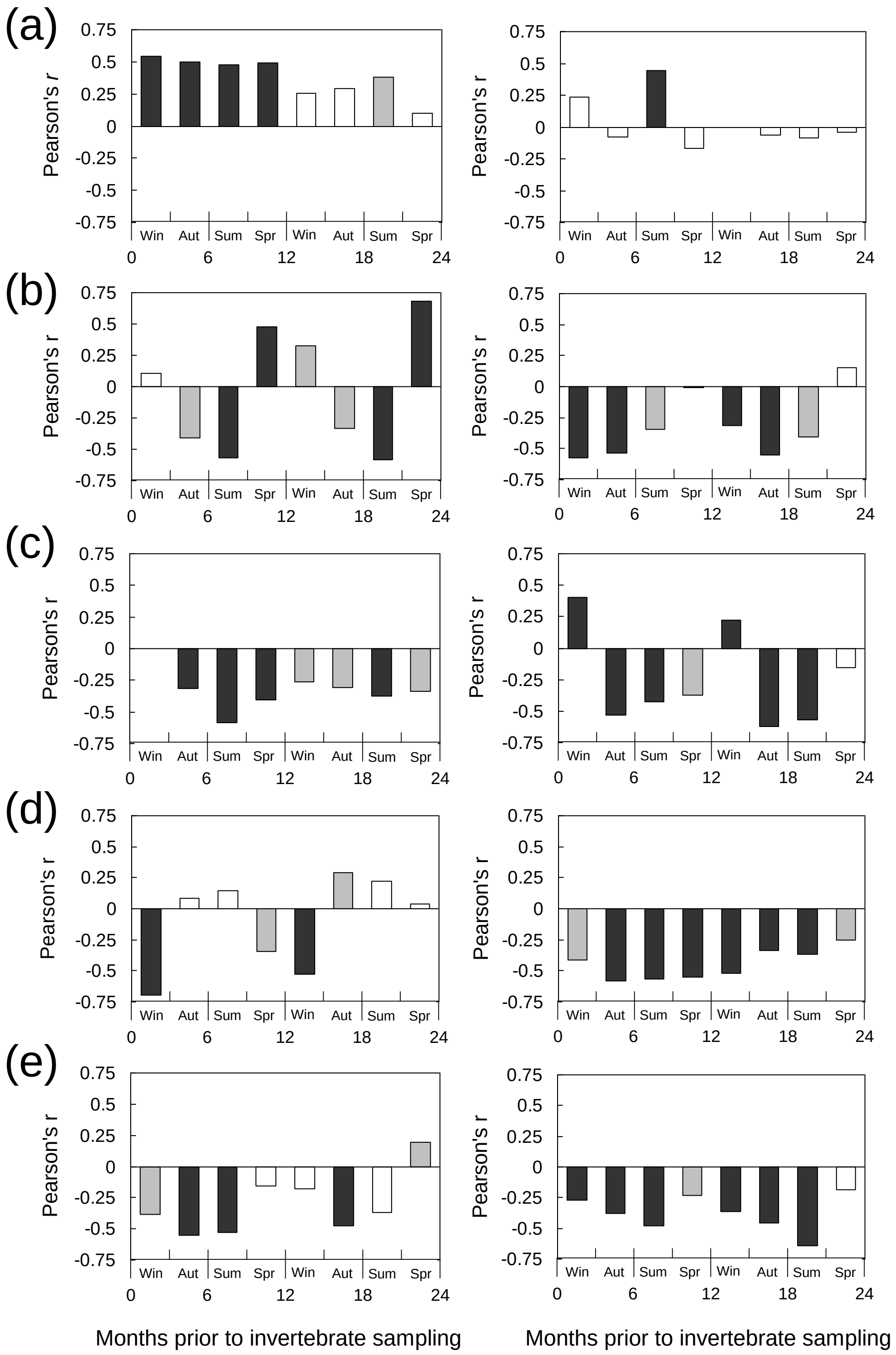
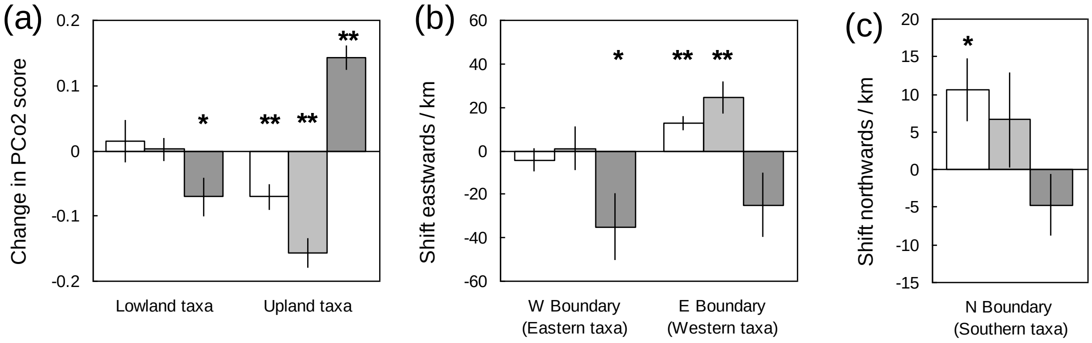
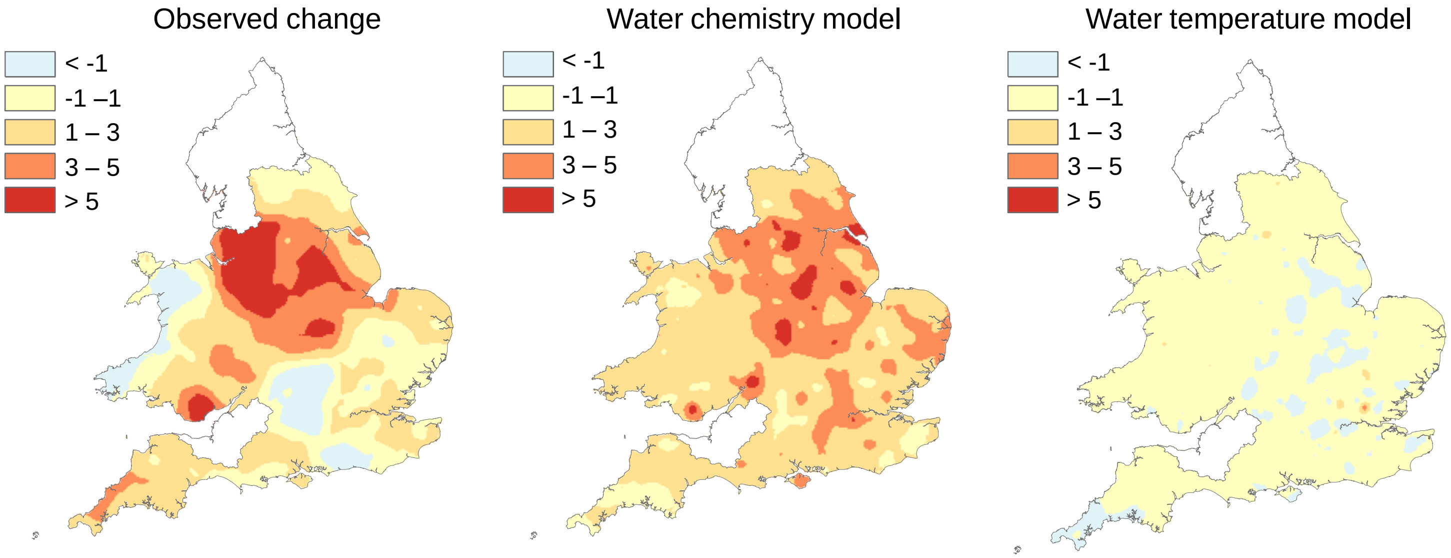

(a)
(b)
(c)
(d)
(e)
Pearson's *r*
Pearson's r
0.75
0.5
0.25
0
-0.25
-0.5
-0.75
Win
Aut
Sum
Spr
Win
Aut
Sum
Spr
0
6
12
18
24
Months prior to invertebrate sampling
Months prior to invertebrate sampling

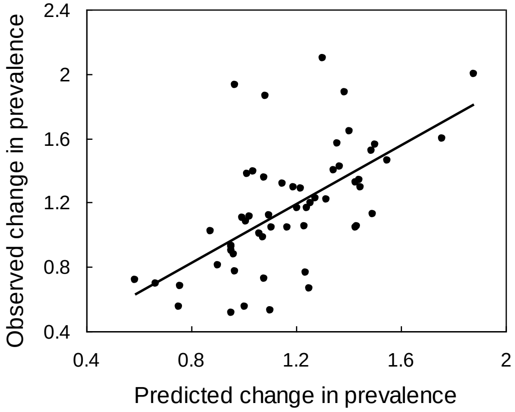
Figure 5


(a)
Change in PCo2 score
0.2
0.1
0
-0.1
-0.2
*
**
**
**
Lowland taxa
Upland taxa
(b)
Shift eastwards / km
60
40
20
0
-20
-40
-60
*
**
**
W Boundary
(Eastern taxa)
E Boundary
(Western taxa)
(c)
Shift northwards / km
20
15
10
5
0
-5
-10
-15
*
N Boundary
(Southern taxa)

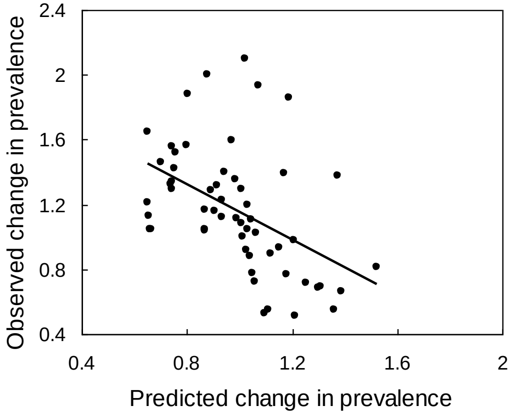
(a)


Observed change
Water chemistry model
Water temperature model
< -1
-1 –1
1 – 3
3 – 5
> 5

(b)


Observed change in prevalence
Predicted change in prevalence
0.4
0.8
1.2
1.6
2
2.4

(c)


Observed change in prevalence
Predicted change in prevalence
0.4
0.8
1.2
1.6
2
2.4