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Climate change effects on upland stream macroinvertebrates over a 25-year period

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Abstract

Climate change effects on some ecosystems are still poorly known, particularly where they interact with other climatic phenomena or stressors. We used data spanning 25 years (1981–2005) from temperate headwaters at Llyn Brianne (UK) to test three hypotheses: (1) stream macroinvertebrates vary with winter climate; (2) ecological effects attributable to directional climate change and the North Atlantic Oscillation (NAO) are distinguishable and (3) climatic effects on macroinvertebrates depend on whether streams are impacted by acidification. Positive (i.e. warmer, wetter) NAO phases were accompanied by reduced interannual stability (= similarity) in macroinvertebrate assemblage in all streams, but associated variations in composition occurred only in acid moorland. The NAO and directional climate change together explained 70% of interannual variation in temperature, but forest and moorland streams warmed respectively by 1.4 and 1.7 °C ($P < 0.001$) between 1981 and 2005 after accounting for NAO effects. Significant responses among macroinvertebrates were confined to circumneutral streams, where future thermal projections (+1, +2, +3 °C) suggested considerable change. Spring macroinvertebrate abundance might decline by 21% for every 1 °C rise. Although many core species could persist if temperature gain reached 3 °C, 4–10 mostly scarce taxa (5–12% of the species pool) would risk local extinction. Temperature increase in Wales approaches this magnitude by the 2050s under the Hadley HadCM3 scenarios.

These results support all three hypotheses and illustrate how headwater stream ecosystems are sensitive to climate change. Altered composition and abundance could affect conservation and ecological function, with the NAO compounding climate change effects during positive phases. We suggest that acidification, in impacted streams, overrides climatic effects on macroinvertebrates by simplifying assemblages and reducing richness. Climatic processes might, nevertheless, exacerbate acidification or offset biological recovery.

Keywords: climate change, insects, models, NAO, rivers, streams, temperature

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Introduction

Although the ecological effects of climate change are increasingly apparent (Root *et al*., 2003), the evidence is unbalanced across ecosystems. Information from streams is scarce (e.g. Daufresne *et al*., 2004), and this is surprising for two major reasons.

First, streams are of global ecological importance. They are major conduit in the processing and downstream transport of solutes and energy from both autochthonous and terrestrial sources (Vannote *et al*., 1980). As a result, they are occupied by organisms with diverse ecological functions (Cummins & Klug, 1979). Drainage densities across landscapes mean that stream networks are extensive, while their physical complexity has led to disproportionately large biological richness per unit volume (Ormerod, 2003). As major ecotones, streams also influence many organisms in the riparian zone (Ballinger & Lake, 2006). In the face of many pressures and large risk of species' extinction, their conservation importance is increasingly recognized in legislation (e.g. European Union Directives 92/43/EEC and 2000/60/EC; Strayer, 2006).

Secondly, there is considerable speculation about how climate change effects on streams will be manifest

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(Meyer *et al*., 1999). As ecosystems characterized by ectotherms, hydrological dynamism and unidirectional flow, variations in temperature or discharge influence many stream processes. For example, through combined influences on dissolved oxygen and metabolic activity, temperature has critical effects on species' distributions (e.g. Knight & Gauffin, 1963; Rostgaard & Jacobsen, 2005). Thermal regimes regulate the growth and development of aquatic invertebrates and vertebrates so that emergence occurs in favourable periods (Vannote & Sweeney, 1980; Voelz *et al*., 1994; Chadwick & Feminella, 2001). Temperature also influences primary production, decomposition and litter processing with consequences for stream energetics (Richardson, 1992). Experiments and field data confirm that altered stream temperatures affect species' distribution and density (Hogg & Williams, 1996; Daufresne *et al*., 2004).

From a hydrological perspective, hydraulic conditions, floods, droughts and the displacement of organisms and their resources, all have direct ecological effects (Lake, 2000; Lytle & Poff, 2004). Indirect hydroecological effects arise through interactions with water quality, fluvial geomorphology, habitat structure and connectivity between water bodies. As with temperature, available data show how discharge variations can regulate taxonomic composition and abundance (Lake, 2000; Beche *et al*., 2006).

Despite the need for improved understanding, attributing changes in stream ecosystems unequivocally to directional climate change is challenging. Not only do stream temperature and discharge interact (Harper & Peckarsky, 2006), their effects must be distinguished from other stressors such as eutrophication and acidification (Root *et al*., 2003; Evans, 2005). So far, studies of interactions between climate change and other effects have been few (Wilby, 1996). The effects of directional climate change must also be separated from other large climatic variations such as El Niño or the North Atlantic Oscillation (NAO; Blenckner & Hillebrand, 2002, Hallett *et al*., 2004). By affecting temperature, precipitation and water quality, the NAO influences the growth, phenology and persistence of stream organisms in western Europe (Elliott *et al*., 2000; Bradley & Ormerod, 2001; Briers *et al*., 2004). The extent to which these effects are linked to anthropogenic climate forcing is still unclear, but some involvement of greenhouse gases in NAO trends seems increasingly likely (Osborn, 2004; Shindell, 2006). Nevertheless, better distinction between the ecological effects of the NAO and directional climate change will improve understanding and prediction (Straile & Adrian, 2000; Bradley & Ormerod, 2001).

Among the prime requirements for assessing the effects of climate change on streams are long runs of ecological data, but these are scarce globally (Jackson & Fureder, 2006). At the Llyn Brianne experimental catchments in upland Wales, stream macroinvertebrates have been sampled intensively for 25 years (Stoner *et al*., 1984). Variations in geology mean that some of the streams have been impacted by acidification, and they contrast in catchment land use (Weatherley & Ormerod, 1987). Evidence for ecological effects of the NAO at Llyn Brianne is clear, but restricted to fluctuations in community stability (Bradley & Ormerod, 2001). There has been no attempt to assess any additional effects from directional climate change.

Here, we use three pairs of Llyn Brianne streams to test three hypotheses about climate change effects: (1) the composition, abundance and stability of macroinvertebrate assemblages respond to year-to-year variations in winter climate; (2) any ecological effects attributable to directional climate change and the NAO are distinct and (3) climatic effects on macroinvertebrates vary between acidified and circumneutral streams. Hypothesis 3 makes explicit an examination of possible interactions between two long-term stressors on upland streams. To test these hypotheses, we use observations over 25 years to assess significant climatic effects to date. We then develop empirical models to project future effects under a series of heuristic thermal regimes (+1, +2, +3 °C) and broad climate scenarios for the region (UKCIP02 HadCM3). Climate change in Wales is expected to increase temperature by 2–3 °C and discharge by up to 15% by the 2050s (Table 1).

Methods

Study area

The study catchments cover ca. 300 km^2 of the central Welsh uplands (215–410 m above sea level) in the catchment of the Afon Tywi (52°8′N 3°45′W; Fig. 1). At <35 km from the nearest coast, the climate is maritime and temperate, with mean stream temperatures invariably within the range 0–16 °C and mean annual precipitation ca. 1900 mm (Weatherley & Ormerod, 1990).

The individual basins of 15–264 ha are drained by perennial hill-streams that rise either in sheep-grazed

Table 1 Climate change projections for Wales as indicated by the UKCIP02 scenario HadCM3 from the Hadley Centre (http://www.ukcip.org.uk/scenarios/)

	2020s	2050s
Change in winter temperature (°C)	0.5–1.4	0.8–2.2
Change in winter discharge (%)	6–10	7–15

The range of values indicates the variation between low- and high-emission variants.

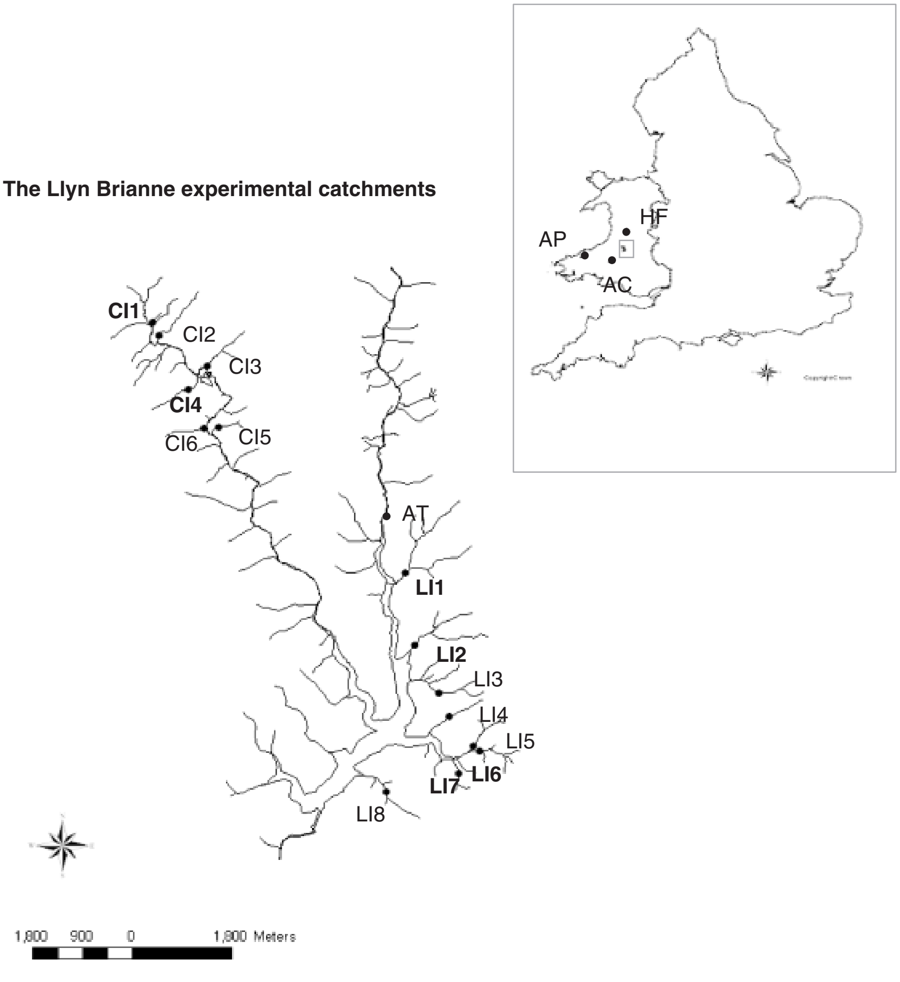

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Fig. 1 The location of the Llyn Brianne experimental catchments in upland Wales. LI and CI sites in bold were involved in this study. Other points shown include the Hafren Flume (HF), Upper Cothi flow gauge (UC), Aberporth (AP) and Afon Tywi stream temperature site (AT).

acid grasslands or coniferous plantations. The underlying rocks are base-poor, and combined with brown podzolic soils, stagnopdzols and peats yield soft-water runoff (mean total hardness 3.9–7.9 mg $CaCO_3$ L^{-1}) that is chronically or episodically acid (Kowalik & Ormerod, 2006). Local calcite veins buffer some streams at circumneutral pH and 15–19 mg $CaCO_3$ L^{-1}. Macroinvertebrates vary with increasing pH from species-poor streams dominated by plecopterans and dipterans to richer, circumneutral streams occupied also by ephemeropterans and trichopterans (Weatherley & Ormerod, 1987; Bradley & Ormerod, 2002a).

From 14 streams available, we selected three replicate pairs that represented a gradient in acid–base status, had the longest sampling runs and avoided the confounding effects of previous experimental manipulations (e.g. catchment liming). These were the acid forest streams, LI1 and LI2 (pH 4.9–5.4); the acid moorland streams CI1 and CI4 (pH 5.2–6) and the circumneutral moorland streams LI6, LI7 (pH >6.9; see Bradley & Ormerod, 2001). Acid forest streams and acid moorland streams were considered separately because their acid–base chemistry, hydrology, thermal regime, habitat structure and macroinvertebrate assemblage composition at Llyn Brianne are distinct (Weatherley & Ormerod, 1987, 1990; Rutt *et al*., 1989).

Stream macroinvertebrates and chemistry

The streams were first sampled for macroinvertebrates in 1981–1982 by Stoner *et al.* (1984) and from 1985 to 2005 (except 1991) by Cardiff University using identical, quality-assured methods (Bradley & Ormerod, 2002b). Samples were collected at each site in spring (April) annually using standardized kick-samples of 3 min total duration aggregated between riffles (2 min) and marginal habitats (1 min) using a hand-net (0.9 mm mesh; 230 mm × 255 mm) (Weatherley & Ormerod, 1987; Bradley & Ormerod, 2002a). Individual animals were identified where practicable to species (i.e. except for Diptera and Oligochaeta), and absolute abundances for each recorded. The level of taxonomic resolution achieved was standardized as far as possible throughout the data run by combining taxa at lowest minium level of identification achieved in any single year. For example, 'Large' Limnephilidae represented *Halesus* spp., *Potamophylax* spp. and other species in which early instars were not easily differentiated in some years. In total, 102 species or species-group formed the data set after eliminating singletons. We averaged abundances and pooled assemblages across replicate pairs of streams (i.e. LI1/LI2; CI1/CI4; LI6/LI7) to reduce the risk of sampling error. Equivalent sampling effort during validation exercises in both 1990 and 2001 on average collected over 90% of all but the rarest taxa present in Llyn Brianne streams (see Fig. 1 in Bradley & Ormerod, 2002b). Results were consistent between different samplers.

pH and aluminium have been monitored weekly–monthly at Llyn Brianne since 1981 using standardized procedures (Weatherley & Ormerod, 1987). We calculated mean pH and aluminium concentrations during each winter (October to March) before macroinvertebrate sampling ($n = 6$–12 samples per site yr^{-1}). These data were used to ensure that macroinvertebrate trends ascribed to climate were not confounded by recovery from acidification, and we report on these investigations elsewhere (S. J. Ormerod *et al*., unpublished data).

Climatic data

We focussed on the winter conditions before April biological sampling for three reasons. First, macroinvertebrate assemblages in April were expected to reflect climatic conditions over the antecedent period because of potential discharge and temperature effects during larval development. Secondly, the NAO affects the UK climate in winter with consequences for stream organisms (Elliott *et al*., 2000; Bradley & Ormerod, 2001; Briers *et al*., 2004). Thirdly, chronic or episodic acid conditions are most likely during increased winter discharge and have marked effects on macroinvertebrates (Kowalik & Ormerod, 2006).

Measured stream temperature data were not available throughout the study, although there were considerable runs of continuous measurements. We, thus, estimated stream temperatures closely as follows. First, monthly mean air temperatures for each catchment at Llyn Brianne were derived from continuous air temperatures at Aberporth (52°07:55′N, 4°32:44′W) after allowing for altitudinal differences using the environmental lapse rate. These data closely followed continuous air temperatures from an automatic weather station deployed at Llyn Brianne between March 1985 and April 1989 ($r^2 = 0.93$; slope $= 0.97$). Next, we used linear regression to calibrate relationships between stream temperature and derived air temperature using 16 months of continuously logged (i.e. 15 min) data from LI1 (forest; 1985–1986), 25 months from CI6 (moorland; 1985–1987) and 59 months from the Afon Tywi (AT) upstream of Llyn Brianne (mixed forest/moorland; 1980–1984) (Weatherley & Ormerod, 1990). Mean monthly air temperatures $<0\,^{\circ}\mathrm{C}$ were rare, and assumed to represent 0.5 °C in the streams. Monthly air temperature explained 85–95% of the variation in stream temperature, with slopes of 0.94–0.97 and intercepts 0.5–0.67 °C in CI6 and AT (Table 2), typical for non-groundwater-dominated headwaters at monthly timesteps (Caissie, 2006). A lower slope (0.78) and greater intercept (1.6 °C) in the afforested LI1 reflects well-known shading and heat-exchange effects under forest (Weatherley & Ormerod, 1990; Caissie, 2006). All monthly stream temperatures throughout the 25 years of the study were finally adjusted from the derived monthly air temperature in each catchment using these

Table 2 Regression relationships ($y = a + bx$) between actual monthly stream temperature and monthly air temperature (estimated from Aberporth; see 'Methods') for three streams at Llyn Brianne over the period 1980–1986

Stream type	Dependent variable	Independent variables	a (±SE)	b (±SE)	$100 \times r^2$ (%)	F	df
Moorland (CI6)	Mean winter temperature	Air temperature	0.67 (0.33)	0.944 (0.041)	96.0***	526.23	1, 22
Moorland/forest (AT)	Mean winter temperature	Air temperature	0.51 (0.34)	0.971 (0.041)	90.6***	558.22	1, 58
Forest (LI1)	Mean winter temperature	Air temperature	1.56 (0.69)	0.778 (0.089)	84.6***	76.82	1, 14

***$P < 0.001$.

calibrating relationships, respectively, for moorland and forest streams. We calculated mean winter temperatures for the 4 months preceding macroinvertebrate sampling (December–March inclusive).

Hydrological data were not available from Llyn Brianne streams, but discharge was measured continuously by the Centre for Ecology and Hydrology at the Hafren flume, <40 km to the North, on streams of identical order and similar altitude (52°27:26′N, 3°47:46′W). The assumption that interannual trends reflected those at Llyn Brianne was validated by comparison with discharge at a second gauged site on the Afon Cothi (51°51:37′N, 4°11:00′W), also in the Tywi system ($r = 0.89$, $n = 289$ monthly mean values, $P < 0.0001$). Most year-to-year variations occurred among higher discharges (i.e. those flows exceeded on average for 5% of the time, denoted Q5), and these were calculated in cubic metres per second for the period from October–March inclusive for each year.

We parameterized the NAO using the winter index (December–March inclusive; provided by the Climate Analysis Section, NCAR, Boulder, CO, USA; Hurrell, 1995). The index is calculated from the difference is sea surface pressure between the Azores and Iceland (Hurrell *et al*., 2003), with positive values associated with mild, wet winters in NW Europe and negative values with cold, dry winters (Hurrell, 1995). This synoptic, climatic indicator captures many ecological effects (Blenckner & Hillebrand, 2002; Stenseth *et al*., 2002; Hallett *et al*., 2004). In addition to considering how stream macroinvertebrates at Llyn Brianne tracked annual NAO values, we investigated a longer-term smoothed NAO index, corresponding to mean values over the three preceding winters. Cumulative NAO effects across years might arise if there were prolonged positive or negative phases over several years; if effects on runoff quality or quantity were cumulative across years; or if macroinvertebrate survival or emergence patterns in 1 year affected recruitment and assemblage composition in subsequent years.

Data analysis

We used multiple regression to assess whether year-to-year variations in stream temperature or discharge could be explained independently by the NAO or by linear trends through time. This was a requirement of hypothesis 2.

Testing hypothesis 1 required macroinvertebrate abundance, assemblage composition and stability for each stream pair be reduced to continuous variates. This was straightforward for total abundances (i.e. numbers of organisms per sample). Stability from year-to-year in assemblage composition was assessed using the Jaccard similarity index ($J = c/(a + b - c)$), in which a is richness (i.e. numbers of taxa) in the preceding year, b is richness in the current year and c is the number of taxa in common (Bradley & Ormerod, 2001). Larger values are taken to indicate assemblages that are more similar, and hence more stable, from year-to-year. Jaccard values for each current year were related to climatic conditions for the previous winter (or winters in the case of the smoothed NAO).

We parameterized assemblage composition using Detrended Correspondence Analysis (DCA), a simple and flexible method of unconstrained ordination (Van Der Maarel, 1969). DCA uses reciprocal averaging to order samples objectively according to the frequency of co-occurrence among their constituent taxa. Sample scores reflect turnover in composition along orthogonal axes such that 4 SD $\equiv$ 100% change on any one axis. Scores can be related quantitatively to sample attributes or conditions, in this case climatic variables. The resulting relationships allow the prediction of ordination score under new conditions. Because species are ordinated simultaneously with samples, changes in their occurrence and tolerance to the presumed driving variable(s) can be quantified. In our case, DCA was performed for each stream type using CANOCO 1.4, with rare species downweighted and abundances log transformed.

Invertebrate variables were related to potential climatic predictors using Pearson' correlations and stepwise regression. Statistical assumptions were checked carefully. We also assessed whether polynomial or logarithmic functions improved fits to the data. Analyses were performed separately for acid forest, acid moorland and circumneutral streams thereby testing hypothesis 3.

Projecting future climatic effects

To project the effects of climate change at Llyn Brianne, we used a modelling approach similar to that used in appraising the long-term effects of acidification (Ormerod *et al*., 1988). This requires transfer functions that link stream ecological response to climatic conditions, and for this we used the regression and ordination models described above. Named *CLIO* (climate invertebrate optima), these empirically derived functions projected macroinvertebrate abundance, stability and assemblage composition using mean winter temperature, discharge or the NAO as input variables. Tolerance ranges indicated the climatic conditions under which individual species could be retained or lost from the assemblage.The heuristic scenarios modelled included winter temperatures increased by +1, +2 and +3 °C over current means, winter discharge by +10%, +20%, and values for the smoothed NAO of −1, +1, and +3. We also specifically projected the effects on stream macroinvertebrates of the UKCIP02 HadCM3 scenario for upland Wales for the 2020s and the 2050s as derived by the UK Hadley Centre (see Hulme & Jenkins, 1998 for original methods). These scenarios, with high- and low-emission variants, envisage temperatures and discharge increasing in Wales by the 2020s–2050s (Table 1).

Results

Climatic variations at Llyn Brianne

Mean stream temperatures during winter at Llyn Brianne ranged from 1.45 to 4.45 °C over the 1981–2005 period, with the NAO and linear long-term trends together explaining 70% of interannual variation (Table 3; Fig. 2). Temperatures increased on average by 2.4 °C in moorland streams and 2.0 °C in forest streams between NAO index values of −4 and +6. After accounting for NAO effects, stream temperature increased over the study period by 1.7 and 1.4 °C in moorland and forest streams, respectively.

High flows (Q5 on percentiles) in the adjacent Hafren ranged between years from 1.15 to 3.88 $m^3 s^{-1}$, but there were no trends through time. The NAO explained just under 10% of the variation in Q5, with discharge tending to be greater in positive NAO years, but effects were not significant ($P = 0.13$).

Invertebrate assemblages and climate

Annual mean richness varied strongly between stream types from just 18 taxa in acid forest streams to 39 in circumneutral streams, reflecting total pools of 39–84 taxa. Mean abundances and numerically dominant species also varied (Table 4).

In no stream type did richness correlate with climatic indicators, and no ecological effects of winter discharge

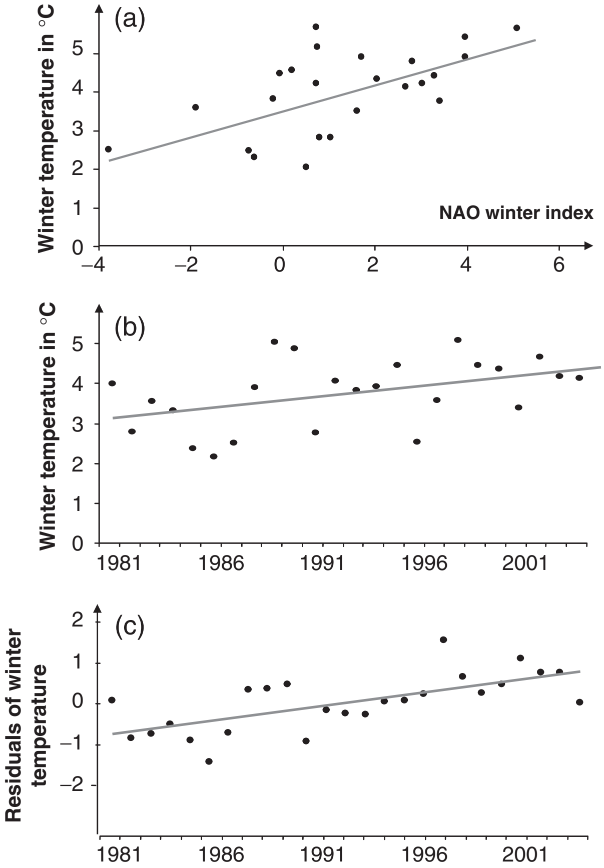

Fig. 2 Variations in the mean winter temperature (December–March) in moorland streams at Llyn Brianne during 1981–2005: (a) in relation to the winter North Atlantic Oscillation (NAO) index; (b) as trends through time and (c) as residual temperature variations through time after accounting for NAO effects. See Table 3 for regression parameters.

Table 3 Regression relationships ($y = a + bx$) between winter stream temperature, winter NAO and sampling year in moorland and forest streams at Llyn Brianne over the period 1981–2005

Stream type	Dependent variable	Independent variables	a (±SE)	b (±SE)	100.r^2 (%)	F	df
Moorland	Mean winter temperature	NAO	3.448 (0.168)	0.244 (0.07)	35.2**	11.98	1, 22
Forest	Mean winter temperature	NAO	3.930 (0.138)	0.201 (0.058)	35.2**	11.98	1, 22
Moorland	Mean winter temperature	NAO	−139.9 (29.0)	0.301 (0.05)	70.1***	24.62	2, 21
		Year		0.072 (0.014)			
Forest	Mean winter temperature	NAO	−114.2 (23.9)	0.248 (0.041)	70.1***	24.62	2, 21
		Year		0.059 (0.011)			
Moorland	Residual winter temperature/NAO	Year	−136.7 (23.4)	0.068 (0.014)	51.0***	22.88	1, 22
Forest	Residual winter temperature/NAO	Year	−111.8 (23.4)	0.056 (0.012)	51.0***	22.88	1, 22

See text for calculation 'Methods', which used a combination of real stream temperatures and air temperature data.
**$P < 0.01$; ***$P < 0.001$.
Example plots are shown in Fig. 2.

Table 4 Attributes of the macroinvertebrate assemblage in each major stream type at Llyn Brianne

	Mean annual richness (±SD)	Total richness (i.e. total pool of taxa)	Mean abundance (±SD)	Most abundant taxa
Circumneutral moorland	39.4 (±5.3)	84	1713 (±661)	*Baetis rhodani* *Leuctra inermis* *Rhithrogena semicolorata*
Acid moorland	23.3 (±4.0)	62	511 (±251)	*Chloroperla torrentium* *Isoperla grammatica* *Leuctra hippopus*
Acid forest	18.2 (±4.0)	39	1234 (±668)	*Amphinemura sulcicollis* Simuliidae *Leuctra nigra*

Values were averaged or pooled across all years of the study (1981–2005).

Table 5 Significant relationships ($y = a + bx$) between macroinvertebrate assemblages in each stream type and climatic variables

Stream type	Dependent variable	Independent variable	a (±SE)	b (±SE)	$100 \times r^2$ (%)
Circumneutral moorland	Abundance	Temperature	3057 (576)	−358 (153)	23.3*
Circumneutral moorland	DCA3 scores	Temperature	−0.493 (0.88)	0.527 (0.23)	22.0*
Circumneutral moorland	Jaccard index	Smoothed NAO	0.70 (0.03)	−0.05 (0.02)	35.5**
Acid moorland	DCA1 scores	Smoothed NAO	0.78 (0.27)	0.54 (0.16)	37.7**
Acid moorland	Jaccard index	Smoothed NAO	0.62 (0.03)	−0.05 (0.02)	25.3*
Acid forest	Jaccard index	Smoothed NAO	0.72 (0.04)	−0.05 (0.02)	21.7*

Degrees of freedom reflected variation in the numbers of years of available data from 18 df for acid moorland streams to 20 df for acid forest streams.
*$P < 0.05$; **$P < 0.01$.

were detectable. However, interannual stability in macroinvertebrate composition in all streams tracked the smoothed NAO, which explained 21–36% of the variation in Jaccard indices between years (Table 5). Jaccard values fell in all streams by 0.2 as the smoothed NAO shifted from −1 to +3. In acid moorland streams only, assemblage composition tracked the NAO due to significant effects on DCA axis 1. Species associated with positive NAO years included *Perlodes microcephala*, *Elmis aenea*, *Psychomyia pusilla*, and *Esolus parallelepipedus*, whereas Wormaldia sp. and *Oulimnius tuberculatus* characterized negative NAO phases (Fig. 3).

Only in circumneutral streams were macroinvertebrates related to winter temperature, but effects were pronounced. Total abundances fell on average by 21% of the mean value (1713 animals per sample) for every 1 °C rise, with temperature explaining 23% of the variance (Table 5). Consistent with this effect, total macroinvertebrate abundance tended to decline in circumneutral streams over the investigation at $P < 0.1$ (Fig. 4).

Assemblage composition varied with temperature in circumneutral streams due to significant effects on DCA axis 3 (Table 5). Species characteristic of cooler years included *Rhyacophila munda*, *Drusus annulatus*, *O. tuberculatus* and *Limnius volckmari* while *Baetis niger*, *Leuctra moselyi* and *Hydropsyche instabilis* were typical of warmer years (Fig. 5). However, *Brachyptera risi*, *Amphinemura sulcicollis* and *Isoperla grammatica* were among 'core' species present over a wide temperature range.

Projecting future effects

With temperature-dependent variations among macroinvertebrates confined to circumneutral streams, we used these to project potential climatic effects using *CLIO*. Future increase of +1, +2 and +3 °C would progressively reduce total macroinvertebrate abundance by up to 60% of current mean values if climate change replicated observed effects (Fig. 4). Temperature change under the HadCM3 scenarios approach this magnitude by the 2020–2050s, and could reduce macroinvertebrate abundance in circumneutral streams by 10–43% (Fig. 6a and b).

A rise of +3 °C would also change scores on DCA axis 3 by 1.58 units (± 0.7), leading to the local

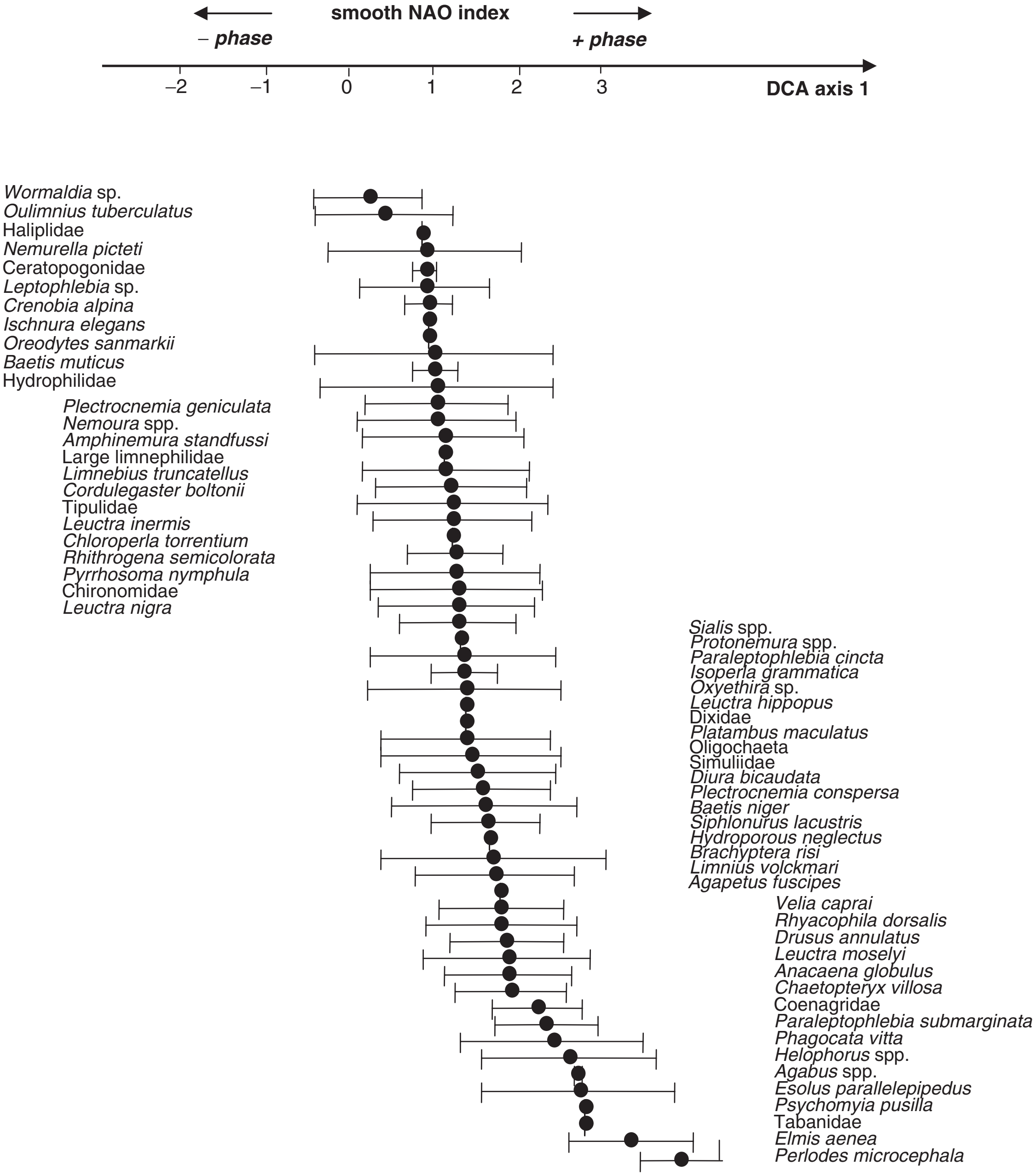

Fig. 3 The optimum and amplitude of each macroinvertebrate taxon in acid moorland streams at Llyn Brianne (1991–2005) in relation to the smoothed North Atlantic Oscillation (NAO) index as indicated by Detrended Correspondence Analysis (DCA) axis 1 (see Table 5).

extinction at Llyn Brianne of four taxa (*Cordulegaster boltonii*, Ceratopogonidae, *R. munda* and *Pisidium* sp.). Variation around this estimate suggests that up to 10 taxa might be at risk (Fig. 6d), representing 25% of typical mean richness or 12% of the total species pool. Projections under HadCM3 were of similar magnitude, with 4–6 taxa at risk by the 2050s. Rank abundance patterns show that mostly scarce taxa were at risk from increased temperature due to small ecological amplitudes. However, one species at risk, *D. annulatus,* was among the most abundant (Fig. 7).

Variations in the NAO are a source of uncertainty in modelling the consequences of climate change at Llyn Brianne and might mask effects, or exacerbate future temperatures variation. In acid moorland streams, average NAO index values >3 for successive winters would be unfavourable for taxa with low DCA axis 1 scores (e.g. Haliplidae, *Wormaldia* sp., *Ischnura*

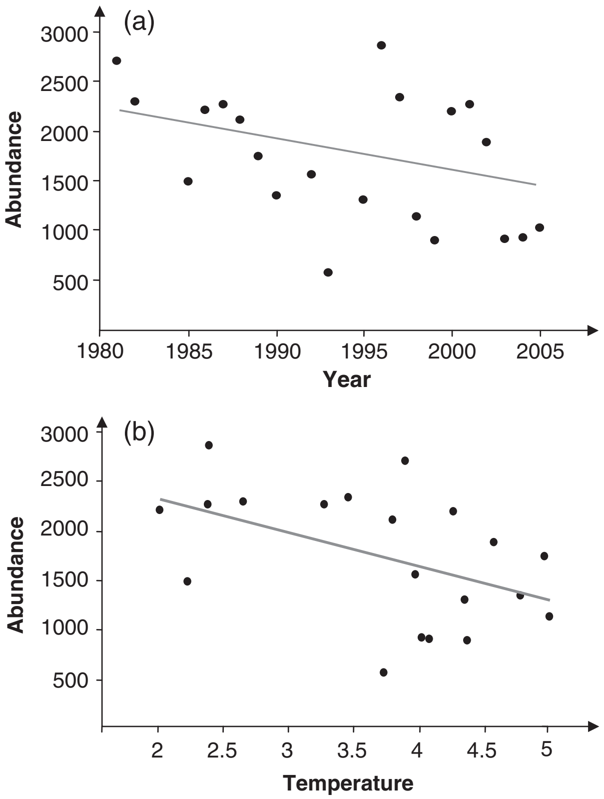

Fig. 4 Trends in the total abundance of aquatic macroinvertebrates in circumneutral streams at Llyn Brianne during 1981–2005 (a) in relation to sampling year ($y = 72\,811 - 35.6\ (\pm 20.1)$ year; $F_{1,18} = 3.15$, $P = 0.09$; $r^2 = 14.9$) and (b) in relation to the antecedent winter temperature (see Table 5 for regression).

elegans, *Oreodytes sanmarkii*, *Limnebius truncatellus*, *O. tuberculatus*, *Crenobia alpina*, *Rhithrogena semicolorata*, *Paraleptophlebia cincta*, Dixidae, *Platambus maculatus*; Figs 3 and 6e). The effects of the NAO on year-to-year stability could further complicate macroinvertebrate responses to climate during strong positive phases (Fig. 6f).

Discussion

The effects of directional climate change at Llyn Brianne over the last 25 years have been distinguishable from the NAO but depend on whether streams are acidified. Whereas interannual stability (i.e. similarity in composition) among macroinvertebrates tracked the NAO in all streams, longer-term variations in temperature appeared to affect macroinvertebrates only in circumneutral streams. Here, abundance fell and assemblage composition changed significantly as temperature increased. The data support all three hypotheses and illustrate that headwaters are sensitive ecologically to climate. If future effects are consistent with these observed trends, progressive temperature increase could remove some scarcer taxa while reducing springtime abundance in the most diverse and productive – i.e. circumneutral – upland stream ecosystems.

Assumptions and caveats

A fundamental assumption in this work was that linear correlations among macroinvertebrates and climate represent mechanistic links that provide a basis for projection. There are parallels in terrestrial ecosystems, where climate-change effects are increasingly predicted from intercorrelations in space among climate, species distribution and population processes (e.g. Huntley *et al*., 2004; Thuiller *et al*., 2006). Such approaches are simple, and can generate hypotheses about processes testable at other scales. They also have the ability to inform management. Research into another long-term aquatic problem, acidification, illustrates these strengths: when combined with catchment-scale experiments, long-term data and process studies, empirical models increased understanding while guiding mitigation (Ormerod *et al*., 1988; Hindar & Wright, 2006). Similar outcomes are likely in climate change research.

Despite basing our projections on data collected over 25 years, uncertainties in extrapolating future climatic effects on streams are real. The future frequency or magnitude of extreme floods or droughts will differ from current regimes (Huntington, 2006). Additionally, change in stream temperatures over the next 20–50 years will be more sustained than the interannual variations assessed here. In addition to direct effects on existing species, such changes could promote invasion by exotic or lowland species to result in gains, as well as losses. Our ecological projections could, thus, be conservative. Conversely, however, projected rates of climatic adjustment among macroinvertebrates at Llyn Brianne might be considered typical because they reflect real long-term data.

A further uncertainty in projecting climate change effects at Llyn Brianne is that no variable explained more than 37% of the interannual variance among macroinvertebrates (Table 5; Fig. 4). Neither multiple predictors nor alternative procedures improved model fit. Unavoidable sources of nonclimatic variation included sampling effects and variations in stream chemistry. The first of these was reduced by examining trends averaged between paired streams, effectively doubling sampling effort. The second was minimized by examining trends separately in acidic and circumneutral streams. pH in acid forest, acid moorland and circumneutral streams at Llyn Brianne increased between 1981 and 2005, respectively, by 0.3, 0.8 and 0.4

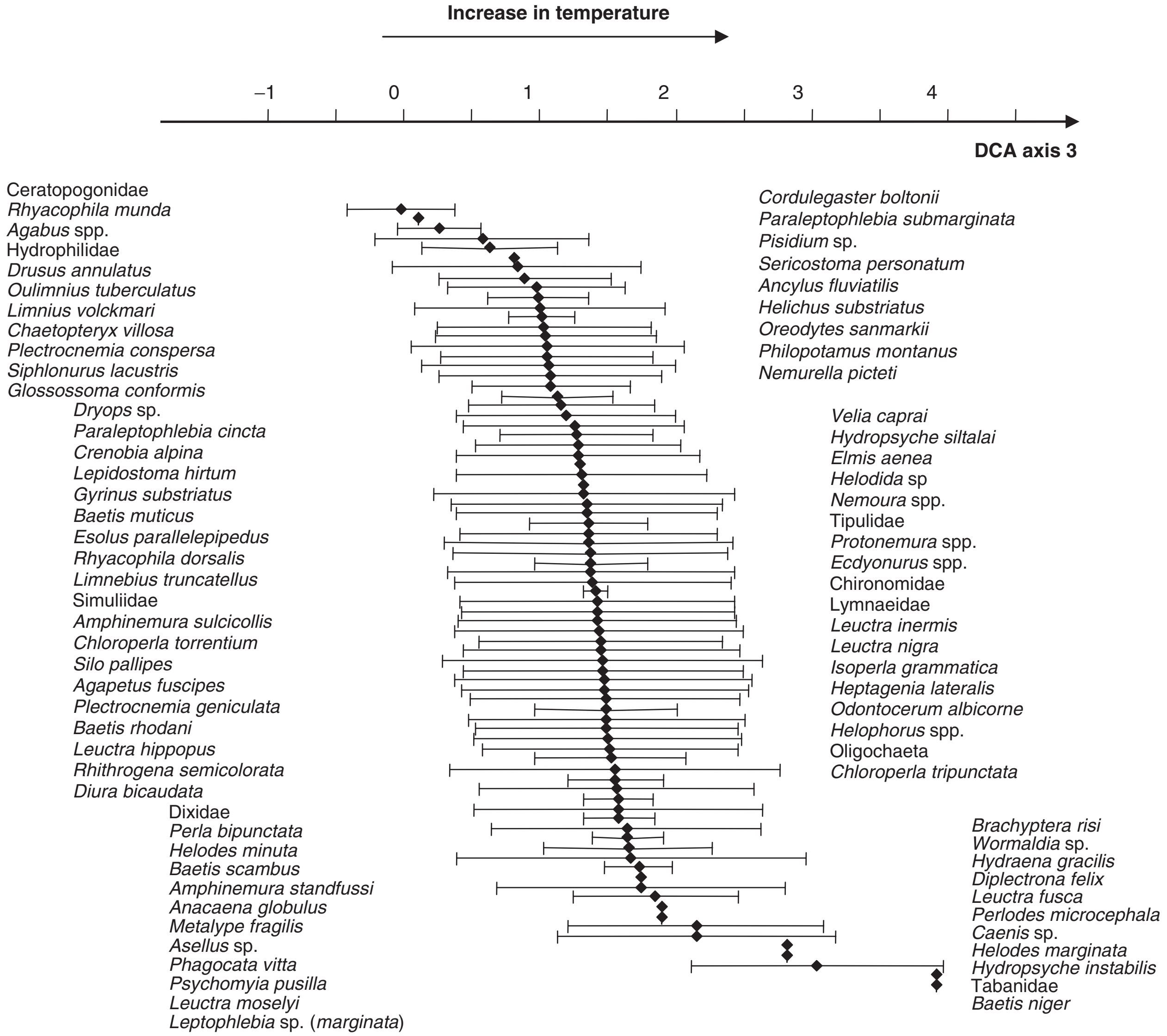

Fig. 5 The optimum and amplitude of each macroinvertebrate taxon in circumneutral streams at Llyn Brianne along Detrended Correspondence Analysis (DCA) 3. See Table 5 for regression relationship with temperature.

units (S. J. Ormerod *et al.*, unpublished data), but in no case did acid–base status explain variation additional to that explained by climate. Nevertheless, potential interactions between the NAO, climate change and acid–base variations may be important. Effects include short-term episodic events that would be undetected at the annual resolution of this study (Kowalik & Ormerod, 2006).

Effects of the NAO

Positive phases of the NAO at Llyn Brianne apparently reduced stability among macroinvertebrates across streams and habitats, as shown from a shorter data run (Bradley & Ormerod, 2001). There were also systematic variations in assemblage composition in acid moorland streams (see Fig. 3). The exact mechanisms are unclear, but thermal, hydrological and hydrochemical processes are possibilities. Available data indicate consistent NAO effects over larger areas of western Britain. For example, relationships between stream temperature and the NAO at Llyn Brianne ($b = 0.20$–0.24; $r^2 = 0.35$) were similar to both Plynlimon in central Wales ($b = 0.32$–$0.34x$; $n = 7$ years; $r^2 = 0.51$–0.57) and Black Brows Beck in NW England ($b = 0.285x$; $n = 29$ years; $r^2 = 0.42$) (Elliott *et al.*, 2000; Briers *et al.*, 2004). Effects also reach eastwards in central Europe (Webb & Nobilis, 2007). As well as affecting stability, tempera-

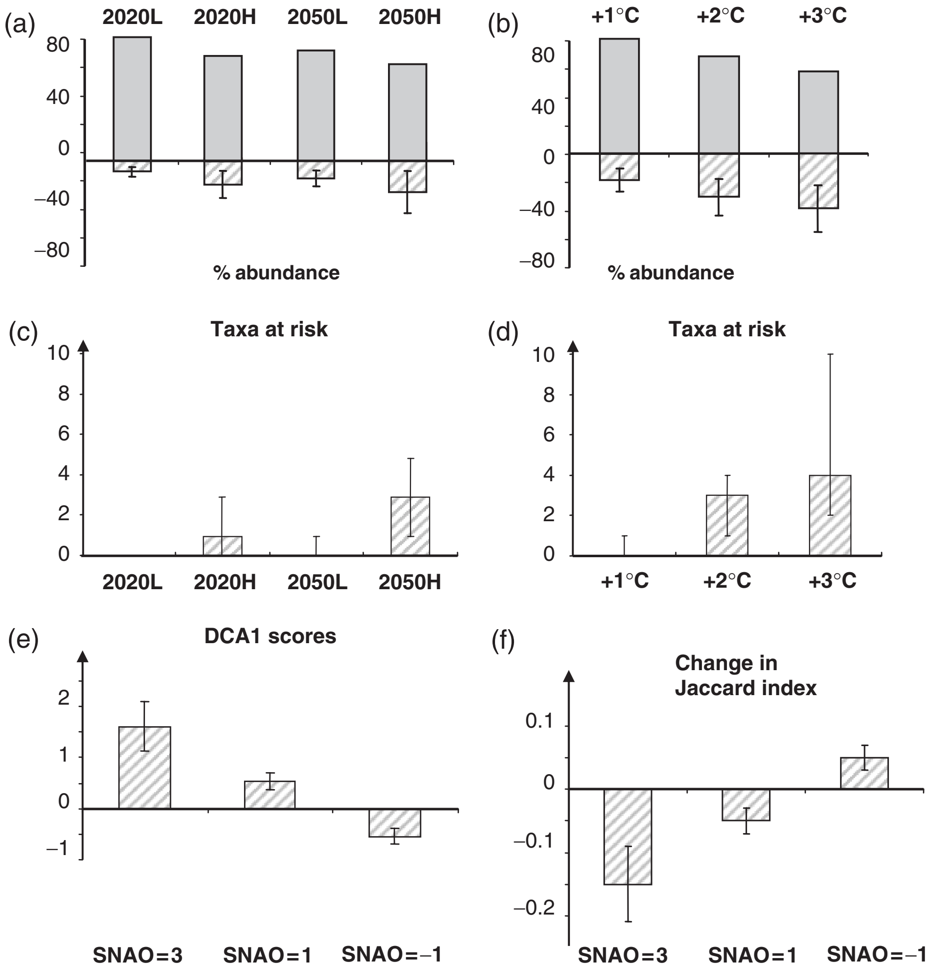

Fig. 6 Projected mean changes (with range) among stream macroinvertebrates in Llyn Brianne according to *CLIO* under various climatic scenarios: (a) percentage change in total macroinvertebrate abundance in circumneutral streams with incremental temperature (+1, +2 and +3 °C) or (b) under the HadCM3 scenario for Wales (see Table 1); (c) and (d) numbers of taxa at risk of local extinction in circumneutral streams under the same temperature scenarios; (e) changes in ordination score or (f) Jaccard index in acid moorland streams with varying smoothed NAO index scores.

ture change linked to the NAO alters the development of salmonid fishes and insects, with potentially large consequences for phenology and assemblage composition (Elliott *et al*., 2000; Briers *et al*., 2004).

NAO effects on estimated winter discharge at Llyn Brianne were barely detectable over the duration of the study, although flows increase markedly elsewhere in NW Europe during positive phases (Bouwer *et al*., 2006). Over shorter timescales, links between discharge at adjacent Plynlimon sites and the NAO were clear (Bradley & Ormerod, 2001). The NAO also causes flow-dependent variations in the chemistry of base-poor streams on Plynlimon, reducing base-cations and increasing aluminium during positive phases (Ness *et al*., 2004). These effects are further complicated by increased sea-salt deposition on organic acids and H^+ (Evans, 2005). In acid streams at Llyn Brianne, winter mean pH in acid moorland streams declines following sustained positive phases of the NAO on average by ca. 0.29 pH units, sufficient to offset almost 10 years of recovery from acidification at current rates (S. J. Ormerod *et al*., unpublished data). Five of the species least likely to occur during positive NAO phases were acid-sensitive taxa such as *Wormaldia* sp., *Baetis muticus* and *O. sanmarkii*. Such species are probably lost from acid-sensitive streams at Llyn Brianne due to low pH events (Kowalik & Ormerod, 2006).

Composite thermal and hydrochemical effects on stream organisms would support suggestions that the NAO predicts climatic effects synoptically on organisms more effectively than individual variables (Stenseth *et al*., 2002). Using the NAO as such a predictor at Llyn

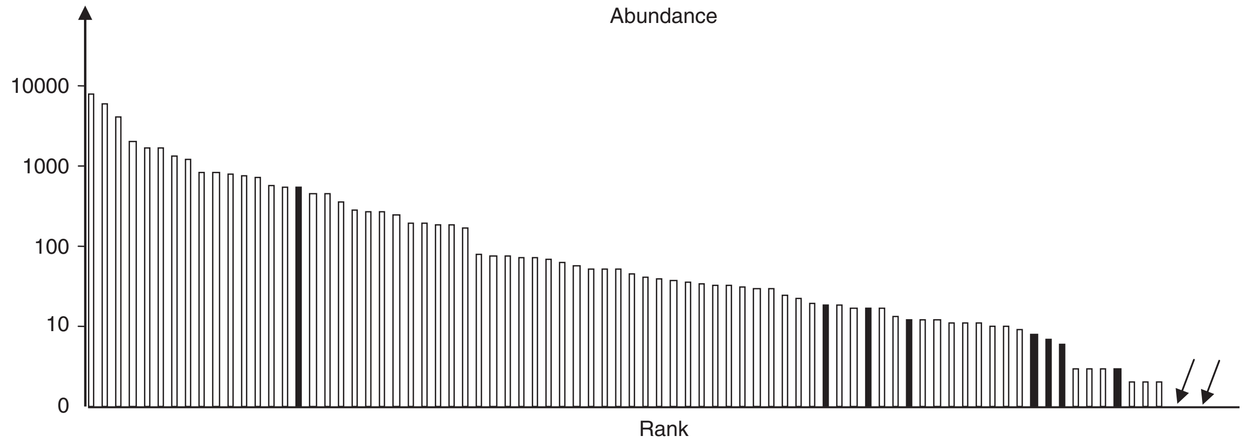

Fig. 7 Logarithmic rank-abundance curves for 84 taxa recorded in circumneutral streams at Llyn Brianne, 1981–2005. Solid bars and arrows indicate taxa at risk of local extinction following increased temperature by 2050 according to Figs 5 and 6.

Brianne showed how future climatic change effects might be compounded during positive NAO phases by reduced interannual stability or altered assemblage composition (Fig. 6).

Effects of long-term climatic change

There were no long-term trends in discharge at the study sites, implying that directional climate change did not alter winter runoff during the study. This accords with current analysis of the duration required for climate change effects on discharge to become clear (Wilby, 2006). Nor did interannual variations in winter discharge affect macroinvertebrates. Discharge effects on stream macroinvertebrates elsewhere can be pronounced, but depend on refuge availability and bed sensitivity to disturbance (Townsend *et al.*, 1997). Organisms are most affected in finer sediments, unlike the stony headwaters at Llyn Brianne. Other possible explanations for the lack of discharge effect are that (i) macroinvertebrates in these headwaters are resilient against naturally large flow variations; (ii) effects were masked by the effects of temperature or (iii) discharge parameterization (as winter Q5) was insufficient to capture ecological effects either at other times of the year (e.g. summer drought) or through flow effects that are threshold- or duration-dependent.

In contrast to discharge, long-term and directional variations in estimated stream temperature were distinct from the NAO, and associated with detectable ecological effects. Directional winter warming in these headwaters is apparently bigger than can be explained by the effects of progressive positive NAO amplification between the 1960s and 1990s (Hurrell *et al.*, 2003).

Reliable long-term data on stream temperature are scarce, but the recent increase at Llyn Brianne is reflected elsewhere. In the upper Danube, temperatures have increased by 1.4–1.7 °C since 1901, with much of this increase occurring form 1950–1970 onwards (Webb & Nobilis, 2007). Temperature in the upper Rhone increased by ca. 1.5 °C between the late 1970s and 1990s (Daufresne *et al.*, 2004), while spring temperature in the Girnock (NE Scotland) increased by 1.45 °C between 1968 and 1997 (Langan *et al.*, 2001). January temperatures in the River Pulham on Exmoor, within 120 km of Llyn Brianne, increased by 1.5 °C between 1977 and 2004 (B. W. Webb, unpublished data). At Llyn Brianne, trends contrasted between forest and moorland streams, with the latter following air temperature most closely (Table 2). In larger streams, evaporative cooling, thermal mass and groundwater moderate temperature variations so that slopes linking air to water temperature are <1.0 (Caissie, 2006). In smaller glacially fed streams, meltwater effects also damp temperature variations with air temperature (Webb & Nobilis, 2007). In the small, cooler and dominantly rainfed moorland streams at Llyn Brianne, however, these effects are negligible, implying that sensitivity to atmospheric warming will be marked. By contrast, month-to-month and interannual temperature variations were damped in forest streams (Tables 2 and 3). Increasing riparian tree cover is an option for local mitigation of future heating effects on headwaters, a notion supported by extensive data (Caissie, 2006). Summer maxima might be reduced, but winter minima elevated.

The apparent effects of increasing stream temperature were twofold, with assemblage composition changing moderately while macroinvertebrate abundances during April declined. Both effects occurred only in circumneutral streams, where macroinvertebrate abundances and richness were greatest. One possibility is that acidification, in impacted streams, overrides climatic effects by simplifying assemblages and reducing richness (see Table 4; Bradley & Ormerod, 2002a; Kowalik & Ormerod, 2006). Warmer, wetter climates, in turn, might exacerbate acidification effects by altering N release, increasing organic acidity, diluting base-cations and offsetting recovery (e.g. Wright *et al*., 2006). Additionally, circumneutral streams are dominated numerically by Ephemeroptera, while acid streams are dominated by Plecoptera. These groups contrast in developmental sensitivity to temperature (Weatherley & Ormerod, 1990; Briers *et al*., 2004). Circumneutral streams contrast further from acidic streams in supporting salmonids and other predators such as riparian birds, with potential consequences for food-web function (Ormerod & Tyler, 1991).

Consideration of thermal effects on macroinvertebrate numbers requires caution since good abundance estimates depend notoriously on large samples (Needham & Usinger, 1956). The variations with temperature identified here reflected 25 years of samples in paired streams, and so are difficult to dismiss as sampling error. Moreover, trends through time were consistent with the effects of increasing temperature, albeit at $P<0.1$. Reductions in density also parallel those detected during experimental stream warming (Hogg & Williams, 1996) or following periods of extreme weather (Mouthon & Daufresne, 2006). However, recent quantitative sampling of macroinvertebrates in LI6 suggests that year-round densities (geometric mean 2067 m^{-2}; 2002/2003) are not dissimilar from the 1980s (geometric means 629–1374 m^{-2}; 1985–1988) (Weatherley *et al*., 1989; Kowalik & Ormerod, 2006; S. J. Ormerod *et al*., unpublished data). Reductions in abundance over the 25 years of the study therefore appear to be restricted to the spring period represented by April sampling.

Candidate mechanisms likely to reduce spring macroinvertebrate abundance at higher temperatures include alterations in emergence phenology or energy flow. Directional climate change over the period 1981–2005 has altered detectably the emergence phenology of amphibians in adjacent ponds (Chadwick *et al*., 2006), and effects on stream macroinvertebrates are likely (Briers *et al*., 2004). For example, a 1.7 °C rise in mean winter temperatures between ca. 3.1 and 4.8 °C over 25 years at Llyn Brianne could increase the average specific growth-rate of overwintering *Baetis rhodani*, the most abundant insect in circumneutral streams, from 0.78% to 1.02% day^{-1} (Elliott *et al*., 1988). Critically, any nymphs already at 1 mm or larger by 1 October in the preceding year would then attain sufficient size (ca. 9 mm) to emerge as adults before 1 April. Effects on abundance would depend on complex interactions among these losses through emergence, as well as any thermal effects on the hatching, development, survival and detectability of the subsequent spring–summer cohort (Elliott *et al*., 1988). Thermally mediated energetic effects in streams are also complex, but include increased predation by fish as temperatures increase (Kishi *et al*., 2005), as well as increased loss rates of litter to decomposition (e.g. Lepori *et al*., 2005). Both can reduce macroinvertebrate numbers demonstrably. Experimental evidence from Llyn Brianne shows how shredder numbers depend on litter supplies (Dobson *et al*., 1995).

Variations with temperature in the macroinvertebrate composition of circumneutral streams mostly affected less common species that occurred under warm or cool extremes (Fig. 5). One exception was *D. annulatus*, a relatively abundant trichopteran that was also sensitive to elevated temperature in a German stream (Wagner, 2005). The occurrence of *B. niger* and *H. instabilis* at higher temperatures is consistent with their more typical downstream distribution in warmer waters and implies some potential for invasion from other basins (Hildrew & Edington, 1979; Masters *et al*., 2007). However, larger numbers of commoner ‘core’ species had wider temperature amplitudes, and persisted through interannual variations. This pattern might be expected in a relatively high-latitude location such as western Britain, where many species have larges latitudinal and thermal ranges than at lower latitudes (Addo-Bediako *et al*., 2000).

When projected under future climates, trends with temperature in the abundance and composition of macroinvertebrates at Llyn Brianne were substantial. While many core species would persist even if gains reached 3 °C, a net loss of four to 10 taxa might occur through local extinction. This is equivalent to 10–25% of typical mean richness, or 5–12% of the species pool in circumneutral streams. Outcomes from such modelling exercises can be variable (e.g. Thuiller *et al*., 2005), but these values from Llyn Brianne are remarkably similar to the potential loss of 6–11% of 1200 plant species from a theoretical portfolio of European protected areas over the next 50 years (Araújo *et al*., 2004). Reduced richness in river macroinvertebrates at increasing temperature also follows trends detected elsewhere (Mouthon & Daufrense, 2006). Such losses would have major conservation significance, particularly if obligate cooler-water species were lost from their limited, higher altitude range (Daufresne *et al*., 2004). Reduced macroinvertebrate abundance in streams will also affect energy transfer to predators during critical periods of annual reproduction (e.g. Ormerod & Tyler, 1991), while potential functional consequences associated with energy processing are being assessed (I. Durance *et al*., unpublished data).

Overall, these data suggest that the ecological consequence of climate change for upland streams could be far reaching, with effects greatest in the most species-rich locations. Our strongest recommendations are, therefore, for (i) an increased commitment to the longer-term assessment of climate change effects on headwater organisms and the processes affecting them and (ii) increased research into measures for adaptation and mitigation with specific focus on stream ecosystems.

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