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PRIMARY RESEARCH PAPER

Hydroclimatic and hydrochemical controls on Plecoptera diversity and distribution in northern freshwater ecosystems

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Abstract Freshwater ecosystems in the mid- to upper-latitudes of the northern hemisphere are particularly vulnerable to the impact of climate change as slight changes in air temperature can alter the form, timing, and magnitude of precipitation and consequent influence of snowmelt on streamflow dynamics. Here, we examine the effects of hydro-climate, flow regime, and hydrochemistry on Plecoptera (stonefly) alpha (α) diversity and distribution in northern freshwater ecosystems. We characterized the hydroclimatic regime of seven catchments spanning a climatic gradient across the northern temperate region and compared them with estimates of Plecoptera genera richness. By a space-for-time substitution, we assessed how warmer temperatures and altered flow regimes may influence Plecoptera alpha diversity and composition at the genus level. Our results show wide hydroclimatic variability among sites, including differences in temporal streamflow dynamics and temperature response. Principal component analysis showed that Plecoptera

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genera richness was positively correlated with catchment relief (m), mean and median annual air temperature (°C), and streamflow. These results provide a preliminary insight into how hydroclimatic change, particularly in terms of increased air temperature and altered streamflow regimes, may create future conditions more favorable to some Plecopteras in northern catchments.

Keywords Catchment inter-comparison · Northern temperate regions · Hydroclimatic · Streamflow · Plecoptera · Alpha diversity · Climate change

Introduction

Freshwater ecosystems in the mid- and upper latitudes of the Northern hemisphere are particularly vulnerable to impacts of climate change (Vincent & Pienitz, 1996). Within this circum-polar climatic region, precipitation partitioning between rain and snow, snowpack accumulation and melt are critical temperature-dependent processes with large implications for hydrologic function and annual streamflow dynamics (Helliwell et al., 1998; Barnett et al., 2005). Changes in the intensity and seasonal distribution of precipitation due to increasing temperatures are anticipated to result in alterations to flow regimes and the frequency and severity of flood and drought events (Kundzewicz, 2008). For example, climate change scenarios predict that increasing temperatures will lead to reduced snow relative to rain, higher winter stream flows, and earlier spring melt, and reduced flows in summer and autumn, with concomitant changes in stream hydrochemistry (Easterling et al., 1997; Barnett et al., 2005; Hodgkins & Dudley, 2006; IPCC, 2007; Prowse et al., 2010).

Inevitably, habitat changes resulting from such hydroclimatic change will impact upon aquatic ecosystems in general (e.g., Hrachowitz et al., 2010a) and freshwater invertebrates specifically (Dewson et al., 2007; Pastuchová et al., 2008; Prowse et al., 2009; Tierno de Figueroa et al., 2010). Species distributions in time and space are governed not only by life history strategies but also by genetic variation in niche requirements, where each species often exhibit a specific environmental tolerance to parameters such as temperature and in-stream hydraulic indices (Whittaker, 1972; Power et al., 1988; Brittain, 1990; Holt, 2003). Those species that are under the greatest threat have often been identified as having relatively narrow environmental tolerances (Foden et al., 2008). One group of aquatic insects that is of particular interest is the order Plecoptera (stonefly) due to their ability to act as bioindicators of environmental perturbation (Helešic, 2001; Fochetti & Tierno de Figueroa, 2008). Plecoptera are environmentally sensitive aquatic organisms that mainly inhabit cold, unpolluted, fast-flowing, and well-oxygenated running waters (Brittain, 1990; Fochetti & Tierno de Figueroa, 2008).

Climatically driven changes in streamflow and temperature regimes have the potential to change Plecoptera assemblages which in turn would project wider changes to the structure and function of aquatic communities (Bunn & Arthington, 2002). Plecoptera assemblages are important constituents of river and stream food web interactions, serving both as primary and secondary consumers, as well as prey for other macro-invertebrates and higher order predators such as fish and birds (Fochetti & Tierno de Figueroa, 2008). Many freshwater biomonitoring programs which underpin sustainable river management strategies are based on understanding the geographic distributions of species and how different groups of organisms respond to changing abiotic conditions (Zalewski, 2002; Roque et al., 2008). There are limited empirically based studies of the hydroclimatic controls on the biodiversity of lotic insects within the climatic-sensitive northern temperate region. Part of the problem is that only few consistent datasets are available that include long-term time-series of invertebrate abundance and composition and their related flow, thermal, and hydrochemic regimes, which would allow cross-regional site comparison.

Most empirical studies have generally been restricted to individual catchments—often nested—or single geomorphic provinces (e.g., Sheldon & Warren Jr., 2009). Thus, it is unclear how findings from individual investigations may be extrapolated to other catchments or different geographic regions (Tetzlaff et al., 2009). Comparison of catchment ecosystem functioning in different geographic regions is an obvious need that will aid catchment classification leading to a more systematic understanding of similarities and dissimilarities in catchment form and function (Burgmer et al., 2007; Tetzlaff et al., 2008; Wagener et al., 2010).

Here, we analyze and present data from the North-Watch (Northern Watershed Ecosystem Response to Climate Change: http://www.abdn.ac.uk/northwatch/)

international inter-comparison project that allows examination of the inter-linkages between climate, hydrology, and ecology. We combine indices based on hydroclimatic data with estimates of genera richness of Plecoptera to provide an increased regional understanding of how hydroclimatic and selected hydrochemical (alkalinity and pH) factors may impact the alpha diversity of these sensitive freshwater invertebrates. Furthermore, by means of a latitudinal gradient as a substitution for future warming (space-for-time substitution) across a hydroclimatic gradient (mean annual air temperature range 2–9°C and mean annual precipitation ranging from 650 to over 2,600 mm), we hypothesised how a warmer climate and altered flow regimes may influence future Plecoptera diversity and composition. Our specific objectives are to: (i) characterize the hydroclimatic regime of the cross-regional study sites using long term data and identify groupings among them; and (ii) investigate the relationship between hydroclimatic factors and Plecoptera alpha diversity to identify the most important controlling variables and possible sensitivity of sites to change.

Materials and methods

Study sites

The seven study sites included in the North-Watch network are among the most intensively studied long-term research catchments across the circum-boreal region, and there has been considerable research on the hydrologic functioning and biogeochemical characteristics of these catchments. The study sites span different hydroclimatic zones, including northern temperate and boreal environments, providing an inter-comparison framework across the circum-boreal region (Fig. 1). Catchment characteristics are summarized in Table 1, and have been discussed in more detail by Carey et al. (2010).

The Scottish sites range from 8 to 30 km^2 in area; at Strontian (56°45′N, 5°36′W) in the maritime northwest (Hrachowitz et al., 2010a), the Allt a' Mharcaidh (57°6′N, 3°50′W) in the subarctic Cairngorms (Soulsby et al., 2006) and the eastern Girnock (57°2′N, 3°06′W) (Tetzlaff et al., 2007). Geology is dominated by igneous and metamorphic rocks (Robins, 1990), soils range from acid peaty soils to free draining podzols, and vegetation cover ranges from forest (mainly *Pinus sylvestris*) on lower slopes to heather (*Calluna* spp.) on steeper slopes with blanket bog (*Spagnum* spp.) in poorly drained areas (Bayfield & Nolan, 1998).

Krycklan (Svartberget, 0.50 km^2) (64°14′N, 19°46′E) on the Fennoscandian shield is the most northerly site with the lowest mean annual air temperature and precipitation. It is primarily forested with Scots Pine (*P. sylvestris*) in upslope areas on podzolic soils with Norway Spruce (*Picea abies*) in wetter, low-lying areas (Buffam et al., 2007) and *Sphagnum* spp. rich wetlands dominating flatter peat-dominated areas.

The Canadian study sites are Dorset (Harp 4, 1.19 km^2, Ontario) and Catamaran Brook (Middle Reach, 28.7 km^2, New Brunswick). Harp 4 (45°23′N, 79°08′W) is an inlet stream to Harp Lake at the

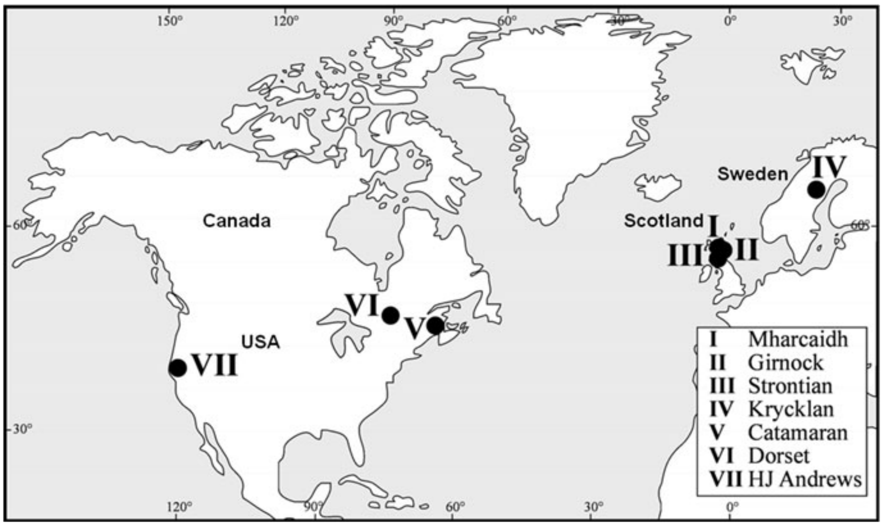

Fig. 1 Location of the North-Watch study catchments

Table 1 Site characteristics of the seven catchments and associated taxonomic data of estimated Plecoptera alpha diversity for each site

Country	Catchment	Site	Area (km^2)	Mean altitude (m)	Relief (m)	Dominant geology	Dominant land-cover	Dominant catchment soils	Estimated Plecoptera alpha diversity	No. of samples/months sampled[a]	Sampling method	Taxonomic reference
Scotland	Allt a' Mharcaidh	Site 1	9.61	704	779	Granite	Moorland	Peat, peaty podzols and gleys	6	~39/20	Kick sample/net	Evans et al. (2000)
	Girnock	Littlemill	30	405	620	Granite	Moorland/Peat (81%)	Peat, peaty podzols and gleys	8	9/~8	Collection chambers	Grant (2008)
	Strontian	Allt Coire nan con	7.97	340	740	Schist, Gneiss	Moorland	Alpine, peaty podzols and blanket peat	8	~39/20	Kick sample/net	Evans et al. (2000)
Sweden	Krycklan	Svartberget	0.5	280	72	Meta sediments	Forest (85%), wetland (15%)	Podzols	4	10/~6	Surber net	Petrin et al. (2007)
Canada	Catamaran Brook	Middle Reach	28.7	210	260	Paleozoic volcanic and sedimentary	Secondary growth mixed forest	Podzols and orthic gleysols	7	10/15	Emergence traps	Giberson & Garnett (1996)
	Dorset	Harp 4	1.19	375	91	Amphobolite/Schist/Gneiss	Forest/peat	Podzols, histosols	5	~60/6	Litter bags/muliplate/suber net	Mackay & Kersey (1985)
USA	HJ Andrews	Mack Creek	5.81	1,200	860	Igneous	Forest (100%)	Calcisols, cambisols, luvisols	11+	32/~2	Surber net	Li et al. (2001)

[a] Based on estimated Plecoptera genera richness at the time of sampling

transition to the southern Boreal ecozone (Mackay & Kersey, 1985; Eimers et al., 2008). In the humid continental climate, soil frost is rare and restricted mainly to wetlands in winter. Catamaran Brook (46°53′N, 66°06′W) is a third order tributary of the Miramichi River and underlain by Paleozoic volcanic and sedimentary basement malted by coarse glaciofluvial deposits. Forest cover is mainly second-growth with white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), birch (*Betula papyrifera*), and maple (*Acer rubrum*). At both sites, podzols dominate steeper slopes with peats and gleys in valley bottom areas.

The steepest site is Mack Creek (5.8 km^2) (44°12′N, 122°09′W) in the Pacific Northwest, USA. The geology is volcanic and the catchment is covered by old growth Douglas fir (*Pseudotsuga menziesii*) forest growing on cambisols. Climate is characterized by wet mild winters and warm dry summers (Anderson, 1992); it is the warmest of the sites.

Data and inter-site comparison metrics

Hydroclimatic and hydrochemical data for each site has been collated by the North-Watch Program. This includes more than 10 years of daily time-series of air temperature, precipitation, discharge, derived evapotranspiration, and selected stream chemistry (pH and alkalinity). To standardize comparisons, all data for the same 10 years (1998–2008), except for the Allt a' Mharcaidh (4 years) and Catamaran Brook (6 years), have been used (Table 2). Annual runoff ratio (Q/P) describes the relationship between mean annual runoff (Q) to mean annual precipitation (P). Area normalized streamflow statistics Q_5 (equaled or exceeded 5% of the time), Q_{50}, and Q_{95} were used to describe the variability between high and low flows and have been described as biologically meaningful descriptors of flow variability (Puckridge et al., 1998; Monk et al., 2006). The median flow, Q_{50}, expresses the central tendency (Clausen & Biggs, 2000). Similarly, T_5, T_{95}, and T_{50} were used as extreme and average descriptors of temperature variability.

Seventeen variables related to catchment physiography, hydroclimate, hydrochemistry, and Plecoptera alpha diversity were examined for each site (Tables 1, 2). Initially, seasonal variables were analyzed, but were later rejected from the analyses due to differences in the timing of Plecoptera sampling and lack of statistical correlation.

Table 2 Mean annual climate, discharge and hydro-chemical (alkalinity and pH) characteristics for the study sites. (95, 50, and 5% exceedance (temperature; T_5, T_{50}, and T_{95}, and runoff; Q_5, Q_{50}, Q_{95}, respectively)

Catchment	Air temp. (°C)[a]	T_5 (°C)[a]	T_{50} (°C)[a]	T_{95} (°C)[a]	Precipitation (mm)[a]	Discharge (mm)[a]	Q_5 (mm/day)[a]	Q_{50} (mm/day)[a]	Q_{95} (mm/day)[a]	Runoff ratio[a]	Alkalinity (μeq/l)[b]	pH[b]
Mharcaidh	5.70	15.27	4.99	−2.19	1,222	873	10.56	1.83	0.39	0.72	44.2	6.45
Girnock	6.73	16.65	6.47	−4.74	1,059	603	8.96	0.82	0.02	0.57	205.1	7.3
Strontian	9.08	17.95	9.09	1.42	2,632	2,213	30.08	2.87	0.10	0.84	21.6	5.85
Krycklan	2.41	18.34	2.09	−22.76	651	327	6.42	0.33	0.00	0.49	−50.38	5.02
Catamaran	5.01	21.60	4.74	−19.58	990	534	10.37	0.87	0.09	0.54	419.4	7.36
Dorset	4.94	22.63	5.74	−19.87	980	507	9.13	0.68	0.00	0.52	123.9	6.26
HJ Andrews	9.22	23.79	7.96	−1.44	2,158	1,744	26.54	3.11	0.29	0.80	62.65	7.2

[a] Mean data based on all available data from the 1998–2008 period—Carey et al. (2010)

[b] Mean data based on the specific dates/duration of Plecoptera sampling period, where possible

Ecological data

Data on aquatic insect richness were collated from all available literature for each site for published taxa lists, species assemblages, and estimated richness. Considering the difficulties of taxonomic identification and the limited number of studies that have made complete invertebrate surveys, we focused our efforts on the insect order, Plecoptera, and quantitative estimates of genera found. Zoogeographically, the North-Watch sites lie within the Palaearctic region (Canada and America) with 108 described genera of Plecoptera, whereas the Nearctic region (including Scotland AND Sweden) has 102. At species level, Europe is estimated to have 426 Plecopterans, whereas northern America has 650 (Fochetti & Tierno de Figueroa, 2008).

In its broadest sense, we define Plecoptera alpha diversity as the estimated number of different genera that have been found within a study site. Raw datasets for HJ Andrews (Mack Creek) and Krycklan (Svartberget) were obtained due to limitations in published data. A summary of the taxonomic data obtained and associated sampling methodology is presented in Table 1. Criteria for inclusion were: (i) a regular methodological sampling effort between the years 1981–2006 that represented all but the rarest genera at a site; and (ii) studies that captured the flow dynamics of the stream by focusing on sampling that had predominantly been conducted within the riffles, a common microhabitat for many benthic invertebrates (Carter & Fend, 2001).

Statistical analyses

Normalized mean daily flow (mm) and air temperature (°C) data were used to examine the temporal hydroclimatic variability among sites through time-exceedance curves. In addition, a principal component analysis (PCA) was conducted to examine the spatial heterogeneity in hydroclimate for the study catchments and to assess whether distinct hydroclimatic-hydroecological groupings of catchments could be identified. The PCA used 15 independent variables: number of Plecoptera genera, catchment area (km^2), altitude (m), relief (defined as maximum minus minimum elevation) (m), annual temperature (°C), T_5, T_{50}, T_{95}, precipitation (mm), discharge (mm), Q_5, Q_{50}, Q_{95}, runoff ratio, alkalinity (µeq/l), and pH.

Associations among hydroclimatic variables, catchment characteristics and Plecoptera genera richness were examined by Pearson's product moment correlation (r_p) before development of stepwise multiple linear regression modeling. Scatterplots were analyzed to assess the nature of hydro-ecological associations and the presence of outliers. Forward and backward stepwise multiple linear regression analysis was used to seek out the most important predictor(s) governing Plecoptera alpha diversity. The entry and removal criterion was set at an alpha probability of 0.05 ($n = 7$). For all regression and correlation analyses, the variables' altitude and Q_5 were normalized by logarithmic transformation. All other variables were normally distributed. All analyses were performed using MINITAB (Minitab Inc., USA). Significance levels were taken at $P \leq 0.05$.

Results

Hydroclimatic and hydrochemical characterization of the study sites

Scatterplots of mean annual air temperature against mean annual precipitation and mean annual discharge showed that both precipitation and discharge increased with temperature within the climatic gradient examined (Fig. 2). Differences in the long-term temperature and area-normalized discharge of the sites were evident from time exceedance curves (Fig. 3). Steeper curves indicated greater variability in temperature regimes—thus, stronger seasonality (including prolonged stream freezing)—in Dorset, Catamaran, and Krycklan. In contrast, the other sites, and particularly the Scottish sites, had a moderate temperature response with lower maximum values and higher minimum values.

The convex character of most of the time exceedance curves reflected the highly responsive nature of most of the streams, with low baseflows compared with storm runoff and flows ranging over four orders of magnitude. The Allt a' Mharcaidh showed the most subdued curve—an indication of the importance of groundwater contributions (Soulsby et al., 2006). Median discharge (Q_{50}) was greatest at HJ Andrews and smallest at Krycklan (Table 2), consistent with differences in mean annual precipitation.

In terms of the hydro-chemical properties, stream alkalinity (mean values based on the specific duration

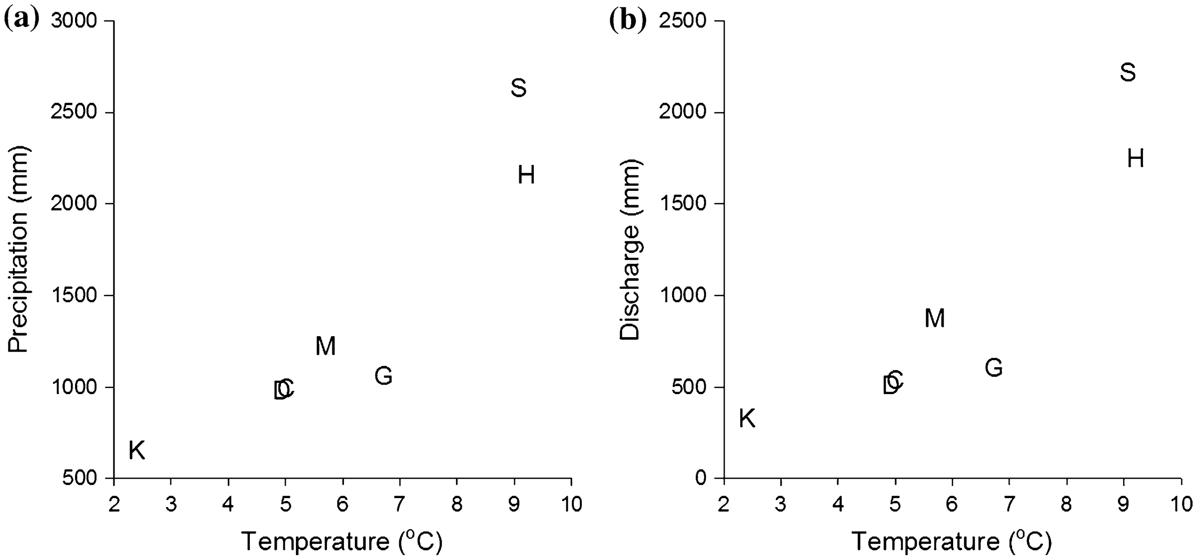

Fig. 2 Scatterplot of mean annual air temperature (°C) versus **a** mean annual precipitation (mm) and **b** mean annual discharge (mm) for the study sites. Key for sites: *M* Allt a' Mharcaidh, *G* Girnock, *S* Strontian, *K* Krycklan, *C* Catamaran Brook, *D* Dorset, *H* HJ Andrews

of Plecoptera sampling period from which estimate is derived) ranged from −50 to 419 µeq/l and pH ranged from 5.0 to 7.3 (Table 2). Most sites are acidic, reflecting the dominance of peaty soils; the strongly acidic character of Krycklan is noteworthy, where the low pH is caused by natural organic acidity from extensive peat bogs (Bishop et al., 2000), which does not adversely affect invertebrate diversity in the region (Dangles et al., 2004). Catamaran and Girnock were the least acidic sites with a mean annual pH of >7.3 reflecting the more base-rich geology.

Plecoptera distribution and spatial heterogeneity of the study sites

Estimated Plecoptera alpha diversity ranged from four genera in Krycklan to approximately eleven or greater at Mack Creek, HJ Andrews (Table 3). Most families were widely distributed in all four countries. The genera richness exhibited a strong correlation with mean annual air temperature ($r^2 = 0.79$, $P < 0.05$). Although the specific genera distribution was unknown for Harp 4 (Dorset), Mackay & Kersey (1985) noted that the majority of genera found at these sites were within the families Perlodidae and Chloroperlidae. The genus *Leuctra* was the most frequently represented genus found at all the study sites. The Scottish sites were uniquely characterized by *Amphinemura* genera, even though they occur in our study regions of northern Sweden, Canada and USA [Catalogue of Life: 2007 Annual Checklist, Species 2000 & ITIS Catalogue of Life Hierarchy, Edition 1 (2007) (accessed through GBIF data portal, http://data.gbif.org/datasets/resource/1542, 26/9/2011].

PCA analysis of catchment groupings indicated that the first two principal components explained 78% of the variance in catchment characteristics (Fig. 4). The first principal component explained 59% of the variance and largely reflected Q_{50}, runoff ratio, and mean annual air temperature (Web Appendix 1—Electronic supplementery material). The second principal component explained 18% of the variance and reflected stream water alkalinity, pH and to a lesser extent catchment area. Warmer and wetter catchments with higher runoff ratios were situated in the right PCA quadrant, as were catchments associated with greater Plecoptera genera richness. Cooler and drier catchments with reduced Plecoptera genera richness were plotted to the left of the PCA quadrant. Catchments with greater pH and alkalinity generally plotted lower than catchments situated higher on the PCA. Although geographically distant, HJ Andrews and Strontian plotted closely together highlighting similarities in their hydroclimatic characteristics and higher Plecoptera genera diversity.

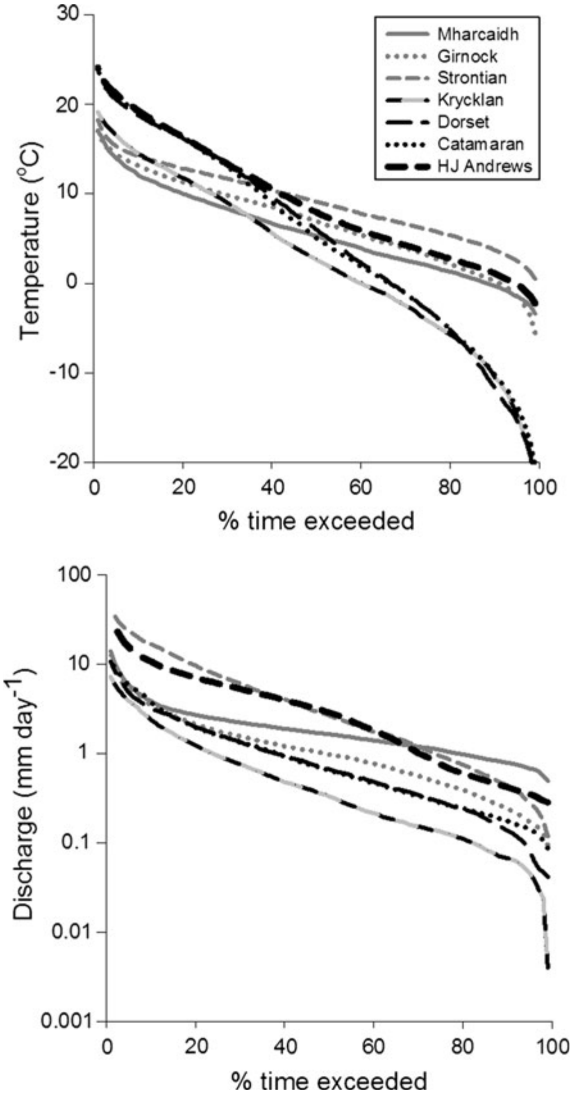

Fig. 3 Daily mean air temperature (°C) and discharge (mm/day) time exceedance curves for the study sites

Hydroclimatic relationships

Catchment relief, air temperature (T_{50}), and some streamflow statistics (Q_5 and Q_{50}) exhibited significant and positive correlations with Plecoptera genera richness and yielded coefficients greater than 0.70 (Web Appendix 2—Electronic supplementery material). Although not statistically significant, mean annual precipitation, discharge, and runoff ratio also showed moderate correlations with Plecoptera genera richness ($r = 0.72$, 0.70, 0.69, respectively). There was no correlation found between number of samples, sampling duration and estimated Plecoptera genera richness ($r = -0.05$, -0.14, respectively; not shown here).

Although statistically limited by low degrees of freedom ($n = 7$), a stepwise multiple linear regression incorporating all 15 variables indicated that approximately 75% of the variance in the total number of Plecoptera genera was explained by mean annual air temperature alone, which emerged as the single and most important factor governing their distribution (Plecoptera genera $= 1.79 + 0.846$ Temp, $r^2 = 0.75$; $P = 0.007$). However, over the hydroclimatic gradient investigated temperature also exerts an obvious influence on stream flow as increasing temperatures reduces the seasonality of snowmelt on streamflows, resulting in more variable and higher flow regimes.

Discussion

We characterized the hydroclimatic regime of cross-regional study sites and found that it was possible to informally differentiate the sites into four groups along gradients characterized by air temperature and precipitation/streamflow (Figs. 2, 4). Krycklan is the coldest and driest; Catamaran and Dorest are wetter and have cold winters but warmer summers; Girnock and Mharcaidh are also wetter but have cool winters and summers; while Strontian and Andrews are clearly wettest and warmest, though the latter has colder winters and warmer summers.

Plecoptera genera richness was largely ordinated with mean annual temperature and streamflow (Q_{50}), indicating a strong correlation with alpha diversity which was greatest in streams with higher temperatures and greater flow variability (Fig. 5). Stepwise multiple linear regression modeling indicated that a significant proportion of the variance in Plecoptera diversity among the sites can be explained by air temperature alone. Consequently, it is reasonable to hypothesise that such changes in air temperatures and associated changes in water temperature and flow regimes are likely to affect Plecoptera. With warmer conditions and projected changes from snowmelt regimes, we can hypothesise that habitat conditions in many such northern catchments are likely to become more favorable for many Plectopterans in future. Although geographically distant, some of the sites had similar hydroclimatic characteristics and associated Plecopteran genera richness (e.g., Strontian and Andrews). Such association

Table 3 Distribution and composition of Plecoptera genera within the study sites

Family	Genus	Mharcaidh	Girnock	Strontian	Krycklan	Catamaran Brook	HJ Andrews
Capniidae	*Capnia*		+				
Chloroperlidae	*Alloperla*					+	
	Chloroperla	+	+	+			
	Siphonoperla			+			
	Sweltsa					+	+
Leuctridae	*Despaxia*						+
	Leuctra	+	+	+	+	+	
Nemouridae	*Amphinemura*	+	+	+			
	Malenka						+
	Nemoura			+	+		
	Nemurella		+		+		
	Paranemoura					+	
	Protonemura	+		+	+		
	Zapada					+	+
Perlidae	*Calineuria*						+
	Dinocras		+				
	Doroneuria						+
	Perla		+				
Perlodidae	*Helopicus*					+	
	Isoperla	+	+	+			+
	Megarcys						+
	Skwala						+
Peltoperlidae	*Yoraperla*						+
Pteronarcyiidae	*Pteronarcys*					+	+
Taeniopterygidae	*Brachyptera*	+		+			

Based on published data as shown in Table 1, excluding Harp 4, Dorset, where no data available

links to similar characteristics in terms of catchment hydroclimate and hydrologic function. Earlier work on the North-Watch sites by Carey et al. (2010) described this in terms of the hydrologic resistance of catchments (i.e., the strength of coupling between precipitation and discharge) and their resilience (i.e., the degree to which a catchment can sustain its precipitation-runoff relationships under change).

Clearly, these associations are likely to have significant influences on biotic communities. Temperature is one of the most important abiotic drivers governing invertebrate assemblages (e.g., Brittain, 1990; Petts, 2000) due to its strong influence on physiological, reproductive, and evolutionary processes (Clarke, 1996; Voelz & McArthur, 2000; Burgmer et al., 2007). Likewise, streamflow plays a key role in regulating biodiversity and assemblage structure in aquatic systems of varied size (Poff & Allan, 1995; Clausen & Biggs, 2000; Monk et al., 2006). Flow regimes not only maintain and structure the physical habitat of streams, but also influences life history strategies of aquatic species which in turn drives biotic composition (Puckridge et al., 1998; Bunn & Arthington, 2002). Early work showed that Plecoptera have a clear preference for colder streams and lakes; their distribution in warmer streams is much more restricted (Baumann, 1979). Similarly, Plecoptera have often been identified as having specific hydraulic flow preferences, with a general preference for higher flows (rheobiont), but ability to tolerate standing waters (limnobiont) in some groups so long as temperatures are low (Mérigoux et al., 2009; Korte, 2010; Tierno de Figueroa et al., 2010).

Thus, based on previous research examining the ecological tolerance of Plecoptera (Baumann, 1979; Houseman & Baumann, 1997), it is possible to hypothesize how changes in some of the abiotic

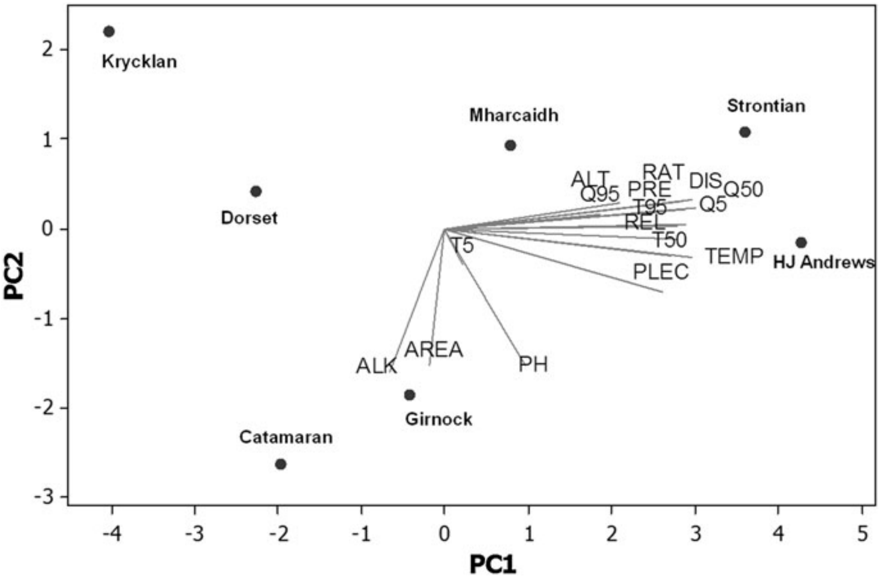

Fig. 4 Principal component analysis (PCA) for the study sites. Each catchment was characterized using the following indices: Plecoptera alpha diversity (PLEC), catchment area (km^2) (AREA), altitude (m) (ALT), relief (m) (REL), air temperature (°C) (TEMP), T_5 (°C), T_{50} (°C), T_{95} (°C), precipitation (mm) (PRE), discharge (mm) (DIS), Q_5 (mm), Q_{50} (mm), Q_{95} (mm), runoff ratio (RAT), alkalinity (μeq/l) (ALK), and pH

drivers may affect Plecoptera at different North-Watch sites and which groups may be more susceptible to change, and which may be more resilient. Variability in habitat diversity can also be related to levels of disturbance, with intermediate levels of disturbance promoting greater diversity by maintaining habitat heterogeneity (Townsend et al., 1997; Voelz & Mcarthur, 2000; Lepori & Hjerdt, 2006). When habitats are intensely and frequently disturbed, the ability of species to colonize these disturbances is greatly reduced (e.g., due to physiologic stress), while low intensity of disturbance increases the likelihood that fewer numbers of competitively superior taxa (Poff et al., 1997; Townsend et al., 1997) will dominate. Thus, "intermediate" variations in environmental hydrologic conditions are an important component in shaping evolutionary and ecological processes in these ecosystems (Poff & Ward, 1989, 1990; Lake, 2000; Poff et al., 2007). As climate warming reduces the influence of snow and snowmelt on northern catchments, the disturbance regimes is likely to change, though the exact impacts will differ from site to site. High proportions of winter precipitation falling as rain, may increase winter peak flows and reduce the frequency of icing events in streams (e.g., Herbst & Cooper, 2010). Spring melt events are likely to become less pronounced with an earlier onset and completion. The frequency and magnitude of ice flows in streams may also decline. Similarly, summer flows may decline both because summer snowpack influence declines, and in many areas, rainfall declines and evapotranspiration increases. Such shifts are likely to be most pronounced at sites with the strongest snow regimes like Krycklan, Catamaran, and Dorest, and less pronounced where snow is already a relatively minor input but increases in stream temperature have already been observed (e.g., Girnock and Strontian) (Langan et al., 2001).

Obviously, it is difficult to make any precise projections using the available data at the family level, but it is possible to hypothesize which groups may be more susceptible to the effects of such change at the North-Watch sites. For example, Nemouridae are a widespread cold water family, but a genus like *Zapada* has endemic species identified that may be vulnerable to the effects of warming in some areas (e.g., Newell et al., 2006). Conversely, members of the Peltoperlidae found at HJ Andrews are more geographically more restricted among the North-Watch sites to the Cascades Mountains, but they are also found in low altitude coastal streams and hence likely to be able to tolerate projected increased temperatures. Other families like Chloroperlidae and Leuctridae may be more susceptible to warming temperatures and they are adapted to cold water streams, though some genera, such as *Leuctra* have adapted to warmer streams (Baumann, 1979). Similarly, the Perlodidae are large carnivores and numbers tend to be small in colder, less productive

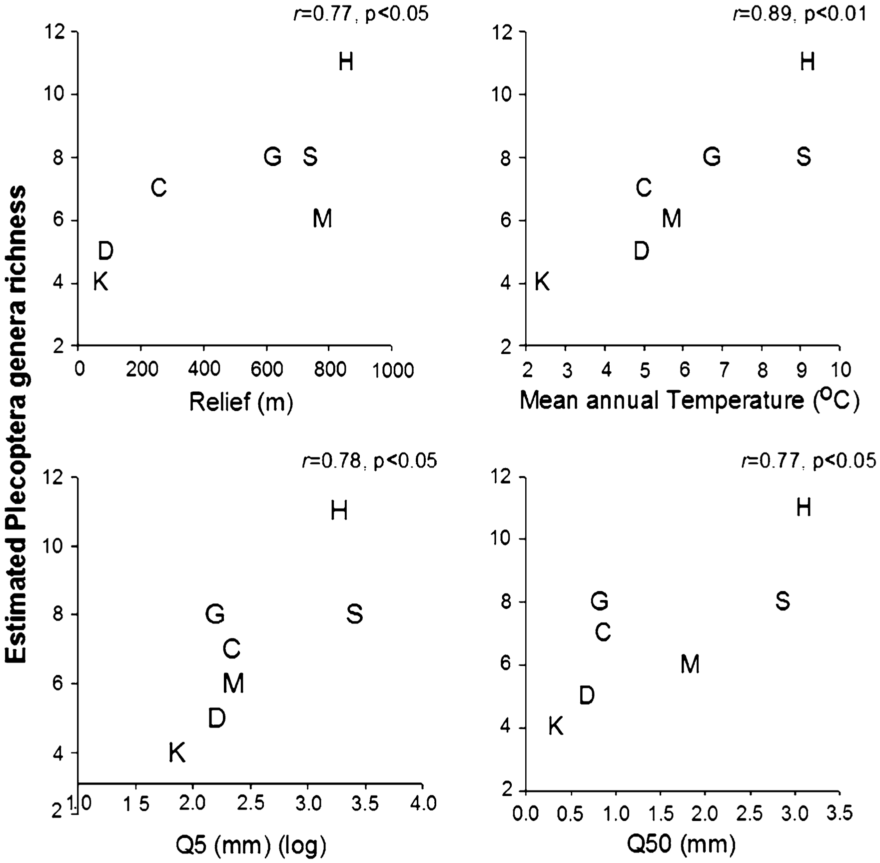

Fig. 5 Relationship between catchment relief (m), mean annual air temperature (°C), area normalized stream flow statistics (Q_5, Q_{50}, mm), and estimated Plecoptera alpha diversity for the study sites. Key for sites: *M* Allt a' Mharcaidh, *G* Girnock, *S* Strontian, *K* Krycklan, *C* Catamaran Brook, *D* Dorset, *H* HJ Andrews. *r* represents Pearson's product moment correlation coefficient

streams, though species of genera like *Isoperla* are also found in warmer streams. However, the nature of adaptation of some groups is not related to temperature in a straightforward sense. For example, while the *Capnia* genus of the Capniidae family can tolerate warm lotic conditions, some species require ice-cover and break-up to trigger various life stages (Baumann, 1979). Conversely, many genera of Perlidae are widespread in warmer streams and rivers and may have extended ranges as climate change effects progress.

In addition to temperature and flow regimes, hydrochemistry also exerts a major influence on benthic invertebrate communities, in terms of both density and diversity of species (Rosemond et al., 1992; Soulsby et al., 1997). Although no significant relationships were observed between Plecoptera alpha diversity and pH or alkalinity, many field studies reveal significant relationships between benthic invertebrates and these parameters (Økland & Økland, 1986; Rosemond et al., 1992; Vrba et al., 2003; Tixier & Guérold, 2005). Indeed, the more alkaline conditions of Catamaran and the Girnock, are likely to help explain their higher Plectoptera diversity compared with Dorest and the Mharcaidh sites (Fig. 4). Chemical recovery of many acidified freshwaters has seen not only an increased trend toward more acid-sensitive macroinvertebrate assemblages in some places (Malcolm et al., 2012), but also in some cases, an increased abundance of macroinvertebrate predators in several lakes and streams, (Monteith et al., 2005). Despite *Perlodidae* being prevalent in northern Swedish streams (Malmqvist & Mäki, 1994), their absence in the Krycklan catchment may also be a response to low pH values within this catchment, as has been noted in other studies (e.g., Mackay & Kersey, 1985).

These results, although preliminary in nature, provide a valuable insight into how hydroclimatic variability and potential changes may influence the biodiversity and composition of freshwater invertebrates within northern freshwater ecosystems in the future. Although difficult to predict, alterations in composition and a reduction in taxa with specific thermal and flow tolerances are likely. This is particularly true for invertebrates with limited dispersal ability and that show a high rate of endemism, like Plecoptera, where migration to more favorable environments may not be possible (Briers et al., 2002; Fochetti & Tierno de Figueroa, 2008). A major research challenge in the future is not only to understand past ecological systems and their composition (Landres et al., 1999) but also how biota within climate-sensitive regions may alter with time and how more complex interactions such as food webs evolve in a changed environment (Stenseth et al. 2002). Moreover, the potential for adaptive management to mitigate changes is further unknown. For example, in catchments without extensive riparian tree cover (e.g., the Girnock and Mharcaidh), tree planting could significantly mitigate projected temperature increases by moderating net radiation inputs (Hrachowitz et al., 2010b). Though, such land use change would also alter the quantity and quality of nutrient inputs from allochthonous sources, with further impacts on species assemblages and interactions (Malcolm et al., 2008).

Given the lack of long-term data, the use of space-for-time substitution has become an increasingly important methodological approach to project the likely consequences of environmental change on ecosystems along environmental gradients at the supra-regional scale (Fukami & Wardle, 2005). Although this study selected a relatively narrow habitat niche (i.e., riffles) in which to observe Plecoptera genera distribution, such scales has the advantage of standardizing the influence of habitat type on the invertebrate fauna (Carter & Fend, 2001). Despite this, although riffles are a common microhabitat for many benthic invertebrates, various studies have shown that macroinvertebrate species composition can vary among habitat types (e.g., riffle, pool, and run), and thus habitat type is an important element to consider when comparing ecologic dynamics, even at larger spatial scales (Giberson & Garnett, 1996; Pastuchová et al., 2008) and will undoubtedly influence and buffer the response of invertebrate groups to environmental change. Clearly, integrated long-term monitoring at experimental sites like those in the North-Watch project in conjunction with an increased emphasis on standardized ecological data will be key to provide evidence-based approaches to understanding and managing the effects of climate change on freshwater ecosystems.

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