

Glacier–groundwater stress gradients control alpine river biodiversity

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ABSTRACT

In alpine river networks, water source (i.e. snow, ice or groundwater) plays a major role in influencing flow regimes, benthic habitat and macro-invertebrate community structure. Across these systems, a natural stress gradient can be conceptualized, from rivers fed exclusively by meltwater (harsh habitat) to those with no melt input (relatively benign, groundwater fed). However, despite the current context of rapid glacier retreat, our understanding of linkages between meltwater contributions, physico-chemical habitat and biodiversity remains limited. To address this research gap, habitat characteristics and macro-invertebrate community structure were studied at 26 sites (five river basins) in the French Pyrénées across a meltwater gradient from 0% to 99%. A combination of generalized regression models and multivariate analyses showed that the stress gradient was associated with the following: (i) linear responses of key physico-chemical habitat variables, in particular bed stability, (ii) unimodal responses at the community level (e.g. richness and total density peaks at 40–60% meltwater contribution), and (iii) both unimodal and monotonic responses at the level of individual taxa. Sites characterized by high contributions of meltwater, although species poor, were important for beta diversity because of their specialist endemic fauna. Our findings suggest that continued glacier and snowpack retreat due to expected future climate change are likely to lead to more homogeneous alpine river habitats (i.e. reduced meltwater–groundwater stress gradient breadth). As a result, increased alpha diversity is expected as previously harsh habitats become more favourable; however, an associated decrease in beta diversity is likely as glacial stream specialists become replaced by generalists. Copyright © 2016 John Wiley & Sons, Ltd.

KEY WORDS beta diversity; climate change; glacier retreat; harsh–benign hypothesis; macro-invertebrates; stress gradients

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INTRODUCTION

Mountain environments are characterized by distinct environmental gradients (e.g. temperature, geology and vegetation cover), which occur over small spatial scales compared with lowland regions (Körner, 2007). This spatial habitat variability makes high-altitude environments particularly important for biodiversity (Grabherr *et al.*, 2000). However, these habitats are highly sensitive to climate change (Beniston, 2003), with alpine river ecosystems particularly responsive because of the strong coupling between cryospheric melt and hydrology (Khamis *et al.*, 2014b). Here, benthic communities display high species turnover along environmental stress gradients (Milner *et al.*, 2009) primarily driven by water source (i.e. snow, ice and groundwater) dynamics (Malard *et al.*, 2006; Füreder, 2007; Brown *et al.*, 2007a).

Alpine river run-off tends to be sourced from two key hydrological stores: (i) meltwater (glaciers and snowpacks)

and (ii) groundwater aquifers (Brown *et al.*, 2006), which drive habitat dynamics at two ends of a river environmental stress gradient. For example, glacier meltwater typically carries more suspended sediment (SS), and associated flow regimes are highly variable at a range of temporal scales (Hannah *et al.*, 2000; Hock *et al.* 2005; Cauvy-Fraunié *et al.*, 2014). High sediment inputs often create braided, wandering channels, with high discharge variability frequently reworking the riverbed (Moore *et al.*, 2009; Carrivick *et al.*, 2013). Groundwater-dominated flow represents the ‘benign’ end of the gradient, with typically clear water (low SS) and less variable flows leading to more stable river channels and beds (Smith *et al.*, 2001). The mixing of these water sources in different proportions creates variability in physico-chemical habitat properties, hydro-chemistry, thermal regimes and associated benthic assemblages across a range of spatial and temporal scales (Malard *et al.*, 2006; Brown *et al.*, 2015).

Studies of European glacierized basins have identified predictable patterns of macro-invertebrate diversity and species assemblages driven by changes in environmental conditions (Snook and Milner, 2001; Finn *et al.*, 2013; Khamis *et al.*, 2014a). Species-poor communities, dom-

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inated by *Diamesa* (Diptera: Chironomidae), typically prevail close to glaciers (Lods-Crozet *et al.*, 2001). As groundwater contributions increase, habitat conditions become more favourable, and environmental stress is reduced (Brown *et al.*, 2007b). The relatively benign conditions enable a more diverse benthic community to establish, including Ephemeroptera, Plecoptera and Trichoptera (EPT) and other chironomid taxa (Milner *et al.*, 2001). Large gradients in physico-chemical habitat characteristics and environmental stress can create high beta diversity across relatively small river networks (Finn *et al.*, 2013) as sites of higher meltwater contribution (stress), although species poor, are particularly important for both basin scale and regional diversity because of the presence of unique, specialist taxa (Brown *et al.*, 2007a; Jacobsen *et al.*, 2012). However, to date, no studies have explicitly tested the mechanism maintaining beta diversity in alpine river ecosystems, more specifically, whether nestedness (taxa of species poor sites are a subset of richer sites) or turnover (replacement of taxa) predominates (Baselga, 2010).

Milner *et al.* (2001) invoked an analogy between the harsh–benign concept (Peckarsky, 1983) and temporal changes in environmental conditions and macro-invertebrate community structure in glacier-fed streams. Here, the more favourable environmental conditions of spring and autumn (e.g. low turbidity and discharge variability and increased algal growth) promote increased macro-invertebrate diversity and abundance. This idea was further developed by Brown *et al.* (2007c), and a spatial, water source (meltwater–groundwater) gradient was added, which predicted richness peaks in groundwater-dominated channels. Concurrently, Füreder (2007), drawing parallels between the continuum of habitat types in alpine river ecosystems and ecological disturbance theory, suggested that alpine benthic diversity patterns may be unimodal rather than linear (cf., Brown *et al.* 2007b) depending on the specific glacier influence or ‘environmental harshness’ gradient. More recently, two studies from alpine river ecosystems have identified taxonomic richness peaks at sites with intermediate glacier influence (Jacobsen *et al.*, 2012; Brown *et al.*, 2015). However, the first study was based on a static measure of glacier influence, largely insensitive to the spatial variability of hydrological sources (e.g. snowpacks and springs) and pathways (e.g. tributary structure), which are characteristic of alpine river systems (Malard *et al.*, 1999). The second study used a multivariate habitat index (glaciation index) to represent the glacial–groundwater stress gradient. A quantitative approach for measurement of meltwater: groundwater contributions has been developed, i.e. Alpine River and Stream Ecosystems (ARISE: Brown *et al.*, 2009) tool. ARISE can account for spatial (and temporal) variability, but to date, it has only been tested in a single river basin and across a limited spectrum of meltwater contribution (Brown *et al.*, 2007a).

In this study, we characterized benthic habitat and community composition along a gradient of meltwater contribution, across five glacially influenced river systems in the French Pyrénées. The key aim was to assess the meltwater environmental stress framework as a tool for understanding alpine biodiversity patterns. Four complementary hypotheses were tested:

(H₁) environmental conditions are harshest where meltwater contribution to streamflow is highest, and vice versa;

(H₂) community diversity and abundance are unimodal across the stress gradient (meltwater), representing a shift from abiotic to biotic controls;

(H₃) invertebrate taxa display mixed responses across the meltwater gradient, e.g. specialists at the extremes and generalist more evenly distributed;

(H₄) broad meltwater gradients are important for beta diversity as turnover between high and low contribution sites is greatest (i.e. limited nestedness).

METHODS

Field location

The study was conducted across five alpine river basins in the Gave de Pau, French Pyrénées (Figure 1). All sites were located above the tree line (1670–2560 m a.s.l.) and within the Parc National des Pyrénées. Anthropogenic disturbance was minimal, although light grazing by sheep and cattle does occur. Riparian vegetation was sparse above 2200 m, with thin soils interspersed with bare rock and scree. Riparian zones were developed more at sites <2200 m, consisting of alpine grasses and scattered herbaceous plants.

Twenty-six reaches were identified across the five study basins (Table S1). In three of the river basins, seven permanent reaches were selected from hillslope springs sourced exclusively from groundwater aquifer flowpaths (ridge top and hillslope snow was absent). The other 19 study reaches were located on five glacier-fed rivers (Table S1). Additional surface run-off streams fed by seasonal melting of snow packs and episodic precipitation events (Ward, 1994) were noted, but these were intermittent, so we did not consider them in this study. The study was conducted during late summer (16 August to 30 August, 2011) after melting of the seasonally transient snowpack. Thus, the meltwater component is herein considered a mixture of (i) ‘quick flow’ sourced from ice and permanent snowpacks with minimal rock contact time and (ii) ‘distributed flow’ from slow routed meltwater that had travelled through subglacial drainage systems (Brown *et al.* 2006).

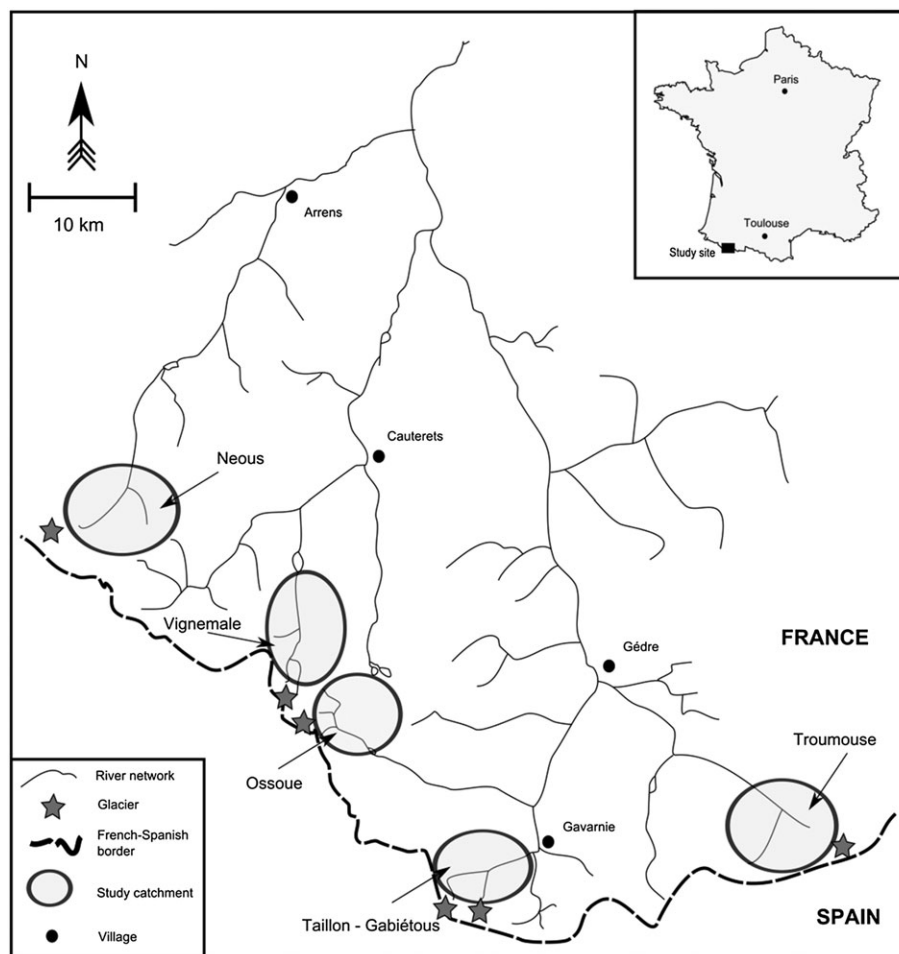


Figure 1. Map highlighting the location of study locations within the Gave de Pau drainage basin.

River water source contribution and physico-chemical data

In each basin, samples were collected from a range of potential hydrological sources or 'end members' (i.e. snow, ice and groundwater springs), and a further water sample was collected at each of the 26 study reaches. Water was filtered through cellulose nitrate filters (0.45- μm pore size) in the field, retained in pre-rinsed High-density polyethylene (HDPE) bottles (60 ml) and frozen for storage. In the laboratory, silica [Si] concentrations were determined using the molybdosilic method (ASTM D859 – 10). Si was chosen as a tracer because of its slow reaction rates and ability to identify groundwater contributions to bulk streamflow (Brown *et al.*, 2006). Basin specific, two end member mixing models (meltwater : groundwater) were then constructed and meltwater/groundwater proportions calculated for each reach using mass balance equations (Suecker *et al.*, 2000).

At each site, pH and electrical conductivity (EC) were measured using an HI 98129 handheld probe (Hannah Instruments, RI, USA). The mean and range of water temperature were calculated from records collected

continuously for 2 weeks prior to sampling using digital temperature data loggers (Tinytag Plus, Gemini, Chichester, UK; instrument error ± 0.2 °C). Water samples (500 ml) were collected at each reach to determine SS concentration. Samples were filtered through preweighed glass fibre filter papers (Whatman GF/C; pore size = 1.2 μm), dried at 95 °C for 2 h and then reweighed to the nearest milligramme. At each reach, the bottom component of the Pfankuch Index (Pfankuch, 1975) was used to estimate substrate stability. This involved a qualitative assessment of five variables (rock angularity, substrate brightness, particle packing, percentage of stable materials and scouring and aquatic vegetation) with higher scores representing channels that are more unstable. River stage (m) was averaged at 15-min intervals (from 5-s readings at sites T3, T4, G4, O3, V4 and V2 during the 2011 melt season (June to September)). Discharge was measured across the observed range of flows and stage – discharge relationships used to derive continuous discharge records.

Biological sampling and processing

Macro-invertebrates were collected in August 2011 (18–28) using a Surber sampler (0.09 m²; 250- μ m mesh). At each reach, five replicates were collected randomly in riffle habitat. Organisms were preserved in 70% ethanol prior to sorting in the laboratory. EPT and Chironomidae were identified to species where possible using a selection of identification keys (Müller-Liebenau, 1969; Tachet *et al.*, 2000; Zwick, 2004; Zwick and Vinçon, 2009). Most taxa were identified to genus except non-Chironomidae Diptera (family) and Oligochaeta, Collembola, Hydracarina and Nematoda (order/subclass). Functional feeding groups were assigned based on Tachet *et al.* (2000). Three randomly selected cobbles were also selected from each reach, surface area was calculated (following Graham *et al.* (1988)) and the epilithon was removed using a stiff brush. The resultant slurry was passed through a 0.7- μ m filter paper (Whatman GF/F) and frozen prior to chlorophyll *a* (Chl *a*) analysis. Samples were analysed within 1 month of collection using the trichromatic spectroscopy method outlined in ASTM D3731 (ASTM, 2004).

Data analysis

Standardized daily flow variability (daily discharge range/daily mean discharge) was calculated for each site with discharge records. Linear regression (ordinary least squares) was adopted to test relationships between meltwater contribution and reach-scale physico-chemical habitat variables (including standardized flow range). Reach-scale macro-invertebrate community metrics were calculated as follows: (i) total taxonomic richness, (ii) total density (ind/m²), (iii) number of EPT taxa, (iv) evenness measured as the numbers equivalent of the Shannon Index divided by total richness (Jost, 2006), (v) predator relative abundance (cf., harsh–benign concept), (vi) within-reach beta diversity (total richness/the mean richness from Surber samples) and (vii) Ephemeroptera/Trichoptera/Plecoptera/Diptera relative abundance. Further to this, abundance of the most abundant taxon from each order (E: *Baetis alpinus* (Pictet), T: *Rhyacophila evoluta* (McLachlan), P: *Protonemura* sp., D: *Diamesa latitarsis* grp.) was quantified. Generalized additive models and generalized linear models were used to investigate the relationship between meltwater contribution and the response variables outlined earlier. Because of the detection of overdispersion, negative binomial (count data) or quasibinomial (relative abundance data) distributions were used. However, as the value for the overdispersion parameter is rarely known *a priori*, it was estimated following the recursive approach outlined by Barry and Welsh (2002). For generalized additive models, the optimum smoothing was selected using a cross-validation approach outlined by (Wood, 2008). Explained deviance was used to evaluate model performance, a measure analogous to R^2 in ordinary least squares regression

(Zuur *et al.*, 2009). Model residuals were tested for spatial autocorrelation using a Mantel test (all $P > 0.05$), following methods outlined by Zuur *et al.* (2009).

Prior to multivariate analysis, taxon abundances were $\log_{10}(x+1)$ transformed and site assemblages tested for spatial autocorrelation with a Mantel test ($R=0.02$, $P > 0.05$) with 999 permutations (Lloyd *et al.*, 2005). Non-metric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity was used to examine patterns in community composition across the meltwater gradient. Standardized (mean=0, SD =1) reach-scale variables (including meltwater) were related to the NMDS ordination using a linear regression model optimized via backwards selection. To visualize patterns, meltwater contribution was fitted to the NMDS space as a smoothed surface created using a generalized additive model (Oksanen *et al.*, 2012). The relationship between taxon abundance and the NMDS scores from both axes was examined using Spearman's rank correlation, and differences in assemblage structure between basins were tested using Analysis of similarity (ANOSIM).

To explore the mechanisms that best explained variation in species composition along the meltwater stress gradient (i.e. turnover vs nestedness), we used the method outlined by Baselga (2010). Three metrics were calculated: (i) beta diversity (B_{sor}) calculated as the pairwise Sørensen dissimilarity between two reaches, (ii) species turnover (B_{sim}) calculated as the Simpson dissimilarity between two reaches and (iii) species nestedness (B_{nes}) calculated by subtracting the turnover effect from the total beta diversity (B_{nes} = B_{sor} – B_{sim}). A Euclidean environmental distance matrix was then calculated from the vector of reach-specific meltwater contribution, and the relationships between B_{sor}, B_{sim} and B_{nes} dissimilarity matrices and the meltwater environmental distance matrix were examined using Mantel tests with 999 permutations (Anderson *et al.*, 2011). Regression coefficients were calculated using a bootstrapping algorithm outlined by Baselga (2010). All analyses were carried out in R 2.14.1. using the *vegan* package (Oksanen *et al.*, 2012) for NMDS and *mgcv* package (Wood, 2006) for regression analysis.

RESULTS

Physico-chemical habitat

All recorded habitat variables, with the exception of T_w (mean and range), displayed linear relationships with meltwater contribution (Figures 2 and 3). Mean standardized daily flow range ($F_{1,4}=10.2$, $R^2=0.78$, $P < 0.05$), SS ($F_{1,24}=23.2$, $R^2=0.50$, $P < 0.001$) and bed stability (PFAN) ($F_{1,24}=56.1$, $R^2=0.69$, $P < 0.001$) were positively related, and Chl *a* ($F_{1,24}=28.1$, $R^2=0.52$, $P < 0.001$) was negatively related, to meltwater contribution (Figures 2 and 3). Weaker relationships were recorded for pH

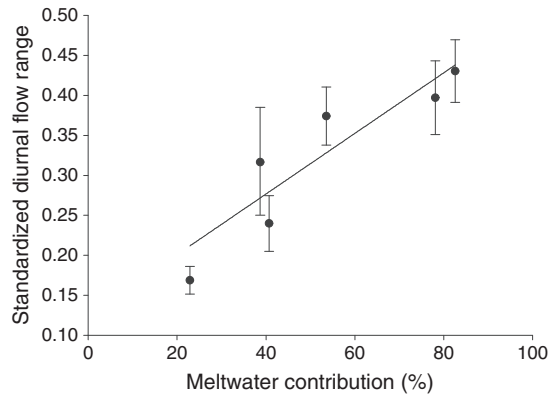


Figure 2. Relationship between mean ($\pm 95\%$ CI) standardized daily discharge range and meltwater contribution at the gauging sites during summer 2011 (29 June to 30 August).

($F_{1,24} = 10.2$, $R^2 = 0.30$, $P < 0.01$) and EC ($F_{1,24} = 4.5$, $R^2 = 0.16$, $P < 0.05$).

Taxonomic patterns and diversity

Macro-invertebrate density, taxonomic richness and EPT richness displayed unimodal relationships with meltwater contribution (Figure 4), all peaking between 40% and 60%

meltwater contribution (*intermediate* contribution) and with the lowest values recorded at sites with $>90\%$ meltwater contribution (Figure 4a–c; Table I). Predator relative abundance (Figure 4e) and within-reach beta diversity (Figure 4f) were negatively related to meltwater contribution. Community evenness displayed a parabolic relationship with meltwater, with the lowest values at *intermediate* meltwater contribution and the highest at low and high meltwater contributions (Figure 4d). Conversely, Ephemeroptera relative abundance peaked at *intermediate* meltwater contribution (Figure 5a). In contrast, the relative abundance of Plecoptera and Trichoptera decreased along the meltwater spectrum (Figure 5b and c), whereas Diptera increased (Figure 5d). Species-level responses varied, with *R. evoluta* and *D. latitarsis* gr. displaying negative and positive relationships, respectively, while *B. alpinus* and *Protonemura* spp. density peaked at intermediate meltwater contributions (Figure 5e–h; Table I).

The NMDS ordination (two-dimensional solution, stress=0.14) stress plot indicated a negligible amount of the variation in the original data set was lost ($R^2 = 0.98$; Figure 5). *Post hoc* regression analysis identified that meltwater contribution, water temperature and Chl *a*

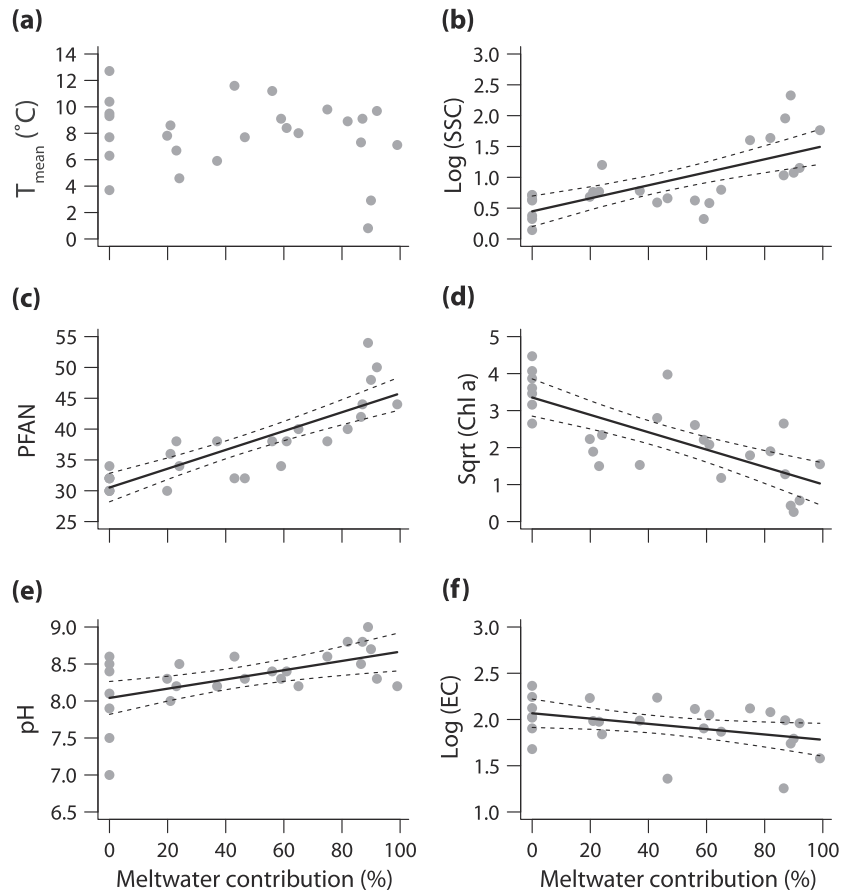


Figure 3. Meltwater–habitat relationships for (a) mean water temperature, (b) suspended sediment concentration, (c) bed stability (PFAN), (d) chlorophyll *a*, (e) pH and (f) electrical conductivity. Solid line is ordinary least squares regression fit, and dashed lines represent 95% confidence intervals.

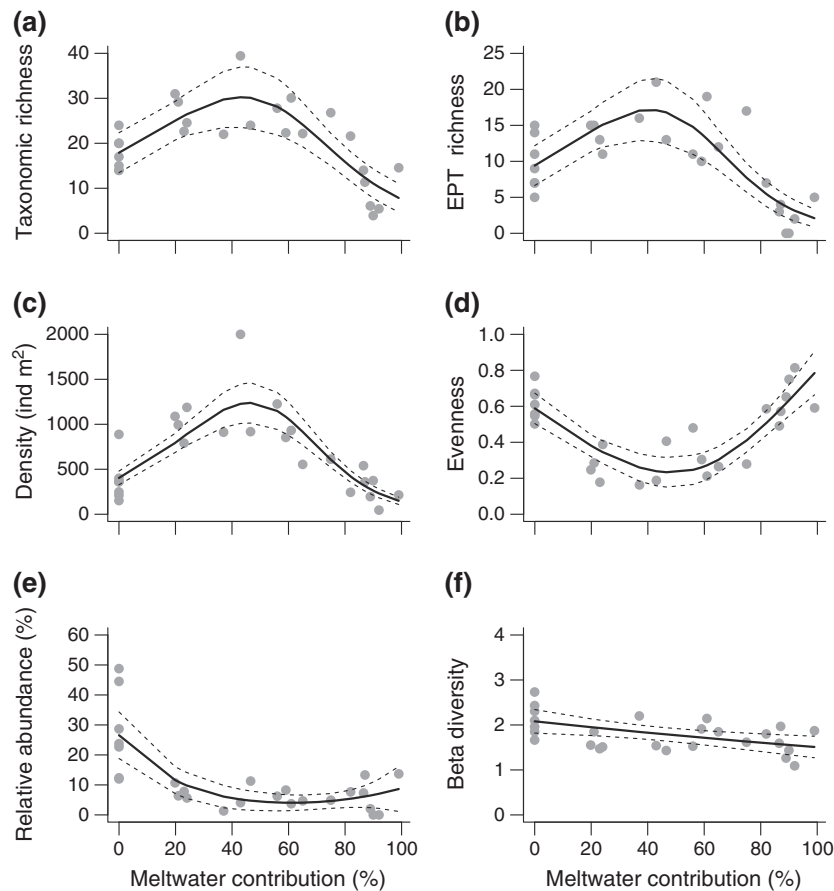


Figure 4. Generalized additive models for the relationship between meltwater contribution to streamflow and (a) taxonomic richness, (b) total density, (c) Ephemeroptera, Plecoptera and Trichoptera (EPT) richness, (d) evenness and (e) predator relative abundance. (f) Generalized linear model of reach scale beta diversity in response to meltwater contribution. Dashed lines represent 95% confidence intervals.

Table I. Summary of the GAM and GLM models for the relationship between meltwater (dependant variable) and community/ population level responses.

Response variable	Method (distribution)	Significance of meltwater term		Deviance explained
		χ^2 (F)	P	(%)
Total density	GAM (negative binomial)	130.2	<0.001	61.5
Taxonomic richness	GAM (negative binomial)	26.3	<0.001	58.7
EPT richness	GAM (negative binomial)	33.9	<0.001	55.4
Predator proportion	GAM (negative binomial)	24.8	<0.001	75.3
Evenness	GAM (poisson)	24.2	<0.001	65.3
Beta diversity	GLM (gaussian)	7.1*	<0.05 ^{ns}	22.9
Trichoptera proportion	GAM (quasibinomial)	12.0*	<0.001	55.7
Ephemeroptera proportion	GAM (quasibinomial)	16.6*	<0.001	66.7
Plecoptera proportion	GAM (quasibinomial)	5.6*	<0.01	34.6
Diptera proportion	GAM (quasibinomial)	7.7*	<0.01	44.4
<i>Rhyacophila evoluta</i> density	GLM (gaussian)	5.4*	<0.05 ^{ns}	15.4
<i>Baetis alpinus</i> density	GAM (negative binomial)	9.8	<0.001	47.9
<i>Protonemura</i> density	GAM (negative binomial)	11.1	<0.001	65.6
<i>Diamesa latitarsis</i> density	GAM (negative binomial)	10	<0.001	44.2

^{ns} No significant relationship between meltwater and the response variable after controlling the false discovery rate associated with multiple tests (Benjamini & Hochberg 1995).

GAM, generalized additive model; EPT, Ephemeroptera, Plecoptera and Trichoptera; GLM, generalized linear model.

* Denotes models for which F - values are reported rather than χ^2 .

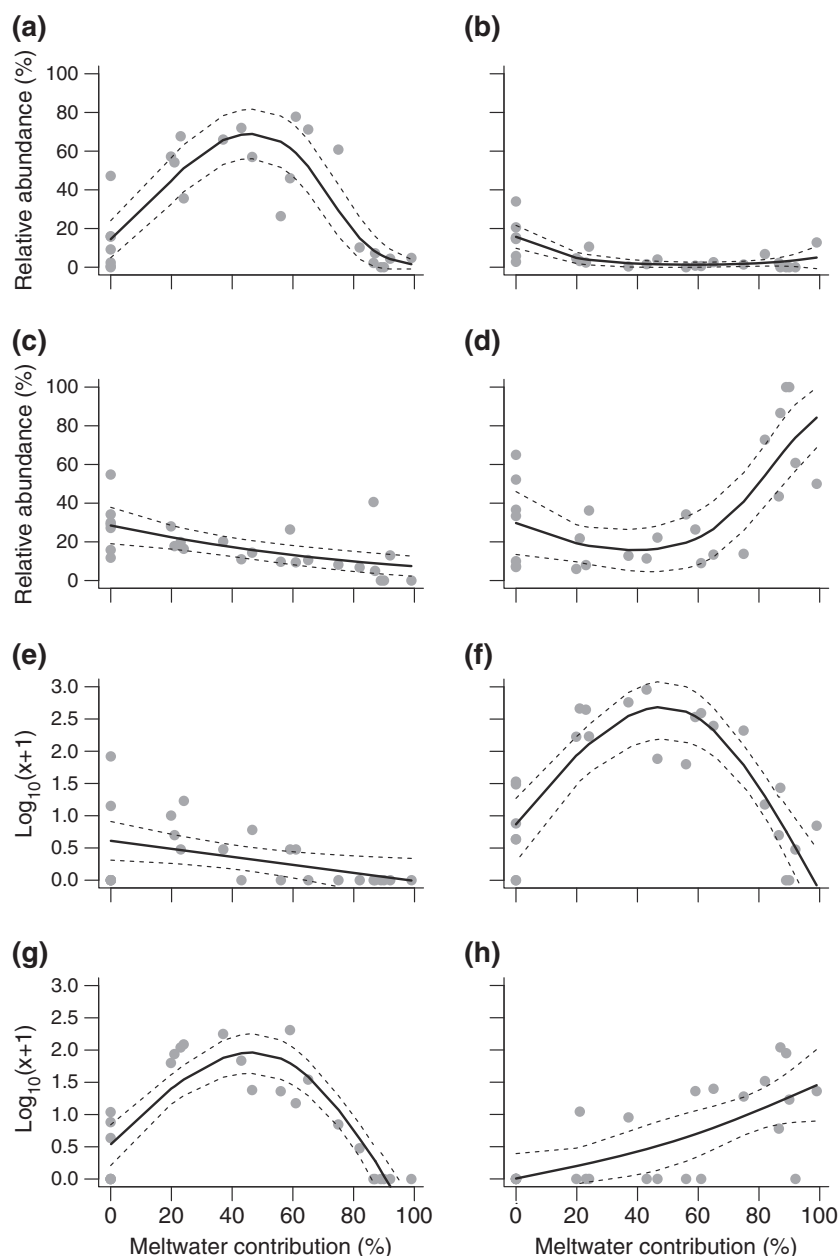


Figure 5. Relationship between meltwater contribution to streamflow and (a) Ephemeroptera relative abundance, (b) Trichoptera relative abundance, (c) Plecoptera relative abundance, (d) Diptera relative abundance, (e) *Rhyacophila evoluta* density ($\log_{10}(x+1)$), (f) *Baetis alpinus* density ($\log_{10}(x+1)$), (g) *Protonemura* spp. density ($\log_{10}(x+1)$) and (h) *Diamesa latitarsis* grp. density ($\log_{10}(x+1)$). All lines of best fit represent generalized additive models except (c) and (e), which are generalized linear models. Dashed lines represent 95% confidence intervals.

were significantly related to NMDS axis 1, whereas for NMDS axis 2 meltwater contribution, EC and PFAN were the significant predictors (Table II). A smoothed surface fit for meltwater contribution highlighted that site variation in macro-invertebrate composition followed the meltwater gradient along axis 1; however, axis 2 appeared to separate groundwater sites in the Vignemale basin (see Table S1 for details) from intermediate meltwater sites (Figure 5). One significant difference in community composition was identified between basins

(ANOSIM: $R=0.01$, $P>0.05$). *Diamesa* spp. and Empididae displayed the strongest negative correlation to axis 1, while *Agapetus fuscipes* (Curtis), *Leuctra fusca* gr., *Polycelis* spp. and *Isoperla* sp. displayed the strongest positive correlation. *Perla grandis* (Rambur), *Micropsectra* sp. Simuliidae, *B. alpinus* and *Rhithrogena* spp. were correlated negatively to axis 2, whereas *Arcynopteryx compacta* (McLachlan) and *Crenobia alpina* (Dana) were correlated positively (Table III) (Figure 6).

Table II. Results from linear regression models (backwards selection) testing the relationship between NMDS axes and reach scale variables.

	NMDS 1	NMDS 2
Meltwater	-3.79***	-4.21**
Chl <i>a</i>	1.41*	
T _w mean	2.95***	
EC		-1.89*
PFAN		1.93*
<i>F</i>	62.9	4.24
<i>R</i> ²	0.88	0.36

For each axis standardised beta coefficients (mean = 0, SD = 1) are presented to enable comparison of variable contribution to the final model. *F*-values and *R*² of the final models are also displayed. NMDS, non-metric multidimensional scaling; T_w, water temperature; Chl *a*, chlorophyll *a*; EC, electrical conductivity; PFAN, bed stability. **P* < 0.05, ***P* < 0.01 and ****P* < 0.001.

Meltwater contribution differences accounted for a significant proportion of the variability in between-reach beta diversity (*B*_{sor}: *r* = 0.49, *P* < 0.001). Community dissimilarity increased with increasing meltwater difference (*coeff.*; $\beta = 0.003 \pm 0.0002$). That is, for a 10% difference in meltwater, a 3% increase in dissimilarity was apparent (Figure 7a). Similarity, pairwise difference in meltwater contribution was significantly correlated to community turnover (*B*_{sim}: *r* = 0.41, *P* < 0.001) and increased with the magnitude of difference (*coeff.*; $\beta = 0.003 \pm 0.0003$; Figure 7b). Conversely, community dissimilarity due to nestedness was not significantly related to between site differences in meltwater contribution (Figure 7c).

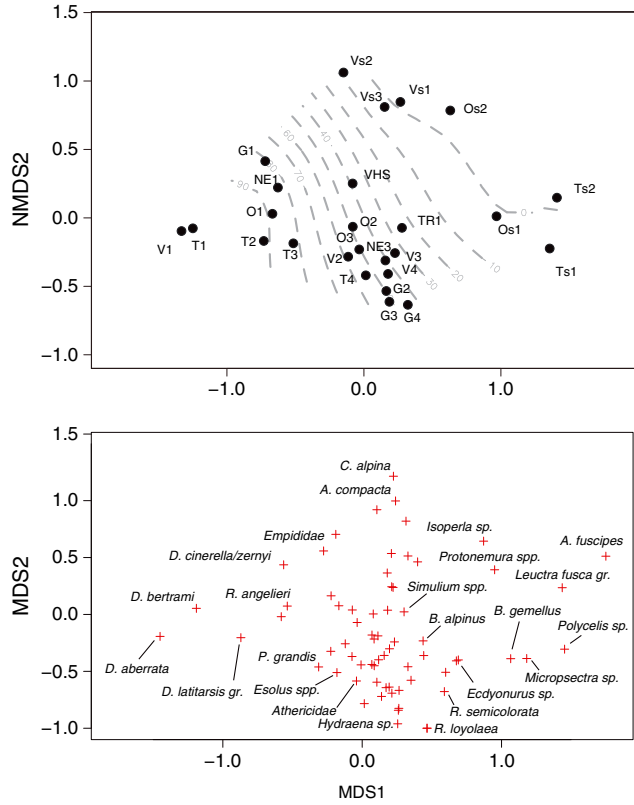


Figure 6. Upper panel is non-metric multidimensional scaling (NMDS) ordination biplot, sites in species space, for the log₁₀(*x* + 1) transformed community data. Filled circles are sites (T, Taillon; G, Tourettes; O, Ossoue; V, Vignemale; Tr, Tromouse; Ne, Néous). Grey dashed lines represent smoothed, meltwater contribution contours fitted via thin-plate regression. The lower panel is the species biplot with taxa significantly correlated to the axes highlighted.

Table III. Spearman rank correlations between taxa abundances and non-metric multidimensional scaling axis scores.

Axis 1		Axis 2	
Taxa	<i>R</i>	Taxa	<i>r</i>
<i>Diamesa cinerella/zernyi</i>	-0.73	<i>Micropsectra</i> sp.	-0.82
<i>Diamesa bertrami</i> (Edwards)	-0.71	<i>Perla grandis</i> (Rambur)	-0.78
<i>Diamesa latitarsis</i> spp.	-0.67	<i>Prosimulium</i> spp.	-0.75
<i>Diamesa aberrata</i> (Lundb.)	-0.52	<i>Simulium</i> sp.	-0.69
Empididae	-0.51	<i>Baetis alpinus</i> (Pictet)	-0.68
<i>Agapetus fuscipes</i> (Curtis)	0.65	<i>Rhithrogena semicolorata</i> (Curtis)	-0.68
<i>Leuctra fusca</i> gr.	0.64	<i>Rhithrogena loyolaea</i> (Navás)	-0.65
<i>Polycelis</i> sp.	0.58	<i>Hydraena</i> sp.	-0.63
<i>Isoperla</i> spp.	0.58	Athericidae	-0.60
<i>Ecdyonurus</i> sp.	0.56	<i>Protonemura</i> spp.	-0.59
<i>Pentaneuriini</i> spp.	0.53	<i>Esolus</i> spp.	-0.59
<i>Baetis gemellus</i> (Eaton)	0.49	<i>Parametricnemus stylatus</i> (Kieffer)	-0.51
<i>Simulium</i> spp.	0.49	<i>Tvetenia bavarica</i> (Goetghebuer)	-0.50
<i>Siphonoperla torrentium</i> (Pictet)	0.43	<i>Crenobia alpina</i> (Dana)	0.53
<i>Plectrocnemia</i> sp.	0.42	<i>Arcynopteryx compacta</i> (McLachlan)	0.56

All correlations are significant at *P* < 0.05 after Holm correction for multiple tests.

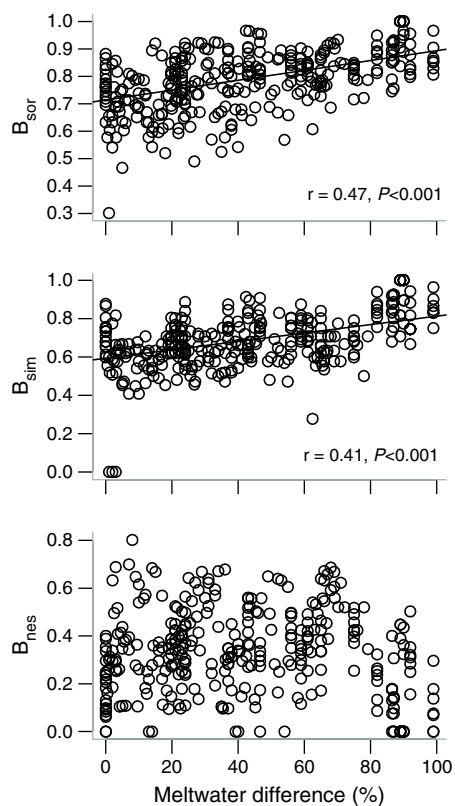


Figure 7. Relationships between differences in meltwater contribution between sites and (a) beta diversity (B_{sor}), (b) turnover (B_{sim}) and (c) nestedness (B_{nes}). Solid lines represent the coefficients derived from a bootstrapping procedure (1000 replicates).

DISCUSSION

Physico-chemical characteristics of the meltwater–groundwater stress gradient

Findings identified a steep environmental stress gradient, with glacier melt-dominated streams (harsh) and groundwater streams (benign) at the two poles, thereby supporting H_1 and a number of previous studies in alpine systems (Brown *et al.*, 2007a; Füreder, 2007). Here, SS and channel stability (PFAN) were positively related to meltwater as predicted by the ARISE habitat template (Brown *et al.*, 2009) because of the strong linkages between climate-cryospheric water generation–hydrology–benthic habitat. Chl *a* biomass was greatest in groundwater streams because of a combination of high bed stability and low turbidity (Uehlinger *et al.*, 2010). At higher meltwater contribution, reduced periphyton cover was potentially due to more frequent hydrological disturbance and bed movement combined with higher SS increasing possible abrasion and turbidity (Uehlinger *et al.*, 2010).

Mean water temperature showed no clear relationship with meltwater contribution, likely because of variability in geomorphic and stream habitat characteristics between and within basins (i.e. aquifer depth, stream azimuth and depth: width ratios), which can interact with meltwater to

influence temperature (Isaak and Hubert, 2001; Brown and Hannah, 2008). However, using meltwater contribution as a predictor of community structure still captures numerous facets of environmental stress in alpine river systems (e.g. SS and food limitation, i.e. Chl *a*). Furthermore, diurnal flow variability, which can act as major control on biodiversity (Cauvy-Fraunié *et al.*, 2014), was also strongly related to meltwater contribution. Thus, from an organismal perspective, both physiological stress (conditions outside the tolerance range) and physical stress (mechanical forces) are represented when examining the meltwater stress gradient (Menge and Sutherland, 1987).

Diversity and abundance patterns along the meltwater stress gradient

In support of H_2 , unimodal responses of community-level metrics (e.g. taxonomic richness and total density) were observed across the meltwater gradient. Despite some studies alluding to variability regarding the shape and magnitude of stress-related diversity responses (Stendera *et al.*, 2012), this study demonstrates agreement with traditional stress-related concepts such as the harsh–benign concept (cf., Menge and Sutherland, 1987) and Intermediate Disturbance Hypothesis (Connell, 1978). Furthermore, our findings are supported by Gutiérrez-Cánovas *et al.* (2013) in a study that highlighted unimodal macro-invertebrate richness responses to natural stress gradients. Recent analyses that examined species richness along continuums of glacier influence identified diversity peaks at intermediate glaciality influence (Jacobsen *et al.*, 2012; Brown *et al.*, 2015), comparable with those observed in this study between 40% and 60% meltwater contribution. This is likely due to the highly adapted regional species pool in alpine environments with all taxa displaying, to varying degrees, resistance or resilience to environmental stress (Füreder, 2007).

High meltwater sites have a unique stress regime as a diurnal flow disturbance pulse, interspersed by flood events, occurs within the context of an underlying harsh physico-chemical habitat (Malard *et al.*, 2006; Jacobsen and Dangles, 2012). Hence, the low number of species able to colonize high meltwater sites is due to stressors such as low water temperature and channel stability and limited food availability (Clitherow *et al.*, 2013) that are exacerbated further by frequent flow and SS pulses (Milner and Petts, 1994). This suggests that deterministic, niche-controlled community assembly processes predominate (Brown and Milner, 2012). Additionally, minimal refugia, upstream/tributary recolonization potential (Cauvy-Fraunié *et al.*, 2015) and short ecological ‘windows of opportunity’ (Milner *et al.*, 2001; Füreder *et al.*, 2005) could also limit density and richness close to the glacier during mid to high meltwater phases.

Taxonomic richness/diversity is generally lower at stable, less stressed sites because of negative biotic

interactions (e.g. predation and competition), which reduces abundance and excludes inferior competitors (Connell, 1978; Townsend *et al.*, 1997). In this study, groundwater streams supported low diversity and density, despite having the highest Chl *a*. Although environmental harshness was lowest in these sites, it is likely that this was offset by an increase in biotic stress; hence, total stress was greater than at mid meltwater sites (Ewel, 1999; Hobbs *et al.*, 2006). A higher abundance of predatory Plecoptera, and Trichoptera (Figure 4), along with large predatory amphibians (*Calotriton asper* (Dugs) and *Rana* spp.) in groundwater-dominated environments (Parc National des Pyrénées, 2005), suggests that negative biotic interactions (i.e. predation) may have limited community diversity in this study (Peckarsky *et al.*, 1990). Furthermore, recent streamside experiments have demonstrated that prey taxon densities were reduced in the presence of a predatory plecopteran through a combination of drift and direct consumption (Khamis *et al.*, 2015).

The unimodal responses for macro-invertebrate richness and total density are likely due to a trade-off between abiotic (environmental harshness) and biotic stresses. At high meltwater sites, we presume abiotic stress to be highest, as outlined earlier, but biotic stress may also be an important limiting factor as recent studies have highlighted that low food availability creates dense food webs with high connectance and frequent cannibalism (Clitherow *et al.*, 2013). At groundwater sites, abiotic stress is low, but biotic stress, in the form of top-down predation, also promotes lower diversity and abundance (Khamis *et al.*, 2015). Hence, total stress (biotic + abiotic) is expected to be greatest at the extremes of the meltwater gradient (Ewel, 1999) and either lowest at intermediate sites or dynamically switching between the two states based on meltwater dynamics, thus enabling high diversity to be maintained.

In support of H₃ (the most abundant invertebrate taxa would display mixed responses across the meltwater spectrum), varied responses to meltwater stress among individual taxa were observed. At *intermediate* (i.e. 40–60% contribution) meltwater sites, a higher density of smaller-bodied Ephemeroptera (*B. alpinus*) and Plecoptera (*Protonemura* spp.) was evident. Many alpine Ephemeroptera and Plecoptera display flexible and resistant life history traits, making them successful in reaches with temporally dynamic environmental conditions (Knispel *et al.*, 2006). However, other traits possessed by *Baetis/Protonemura* such as swimming/crawling and gill respiration may limit colonization of high meltwater sites. Here, high flows would inhibit the locomotive strategy, and high SS would reduce gill efficiency (Larsen *et al.*, 2011). Furthermore, because of conspicuous swimming and feeding behaviour, *Baetis* are particularly susceptible to invertebrate predation at low meltwater sites (Peckarsky and Penton, 1989; Khamis *et al.*, 2015). Two abundant taxa, *D. latitarsis* grp. and *R. evoluta*,

displayed positive and negative responses along the gradient, respectively (Figure 5). *R. evoluta* is a relatively large-bodied invertebrate predator, which will be more sensitive to environmental fluctuations because of longer generation times and lower fecundity (Menge and Sutherland, 1987; Trexler *et al.*, 2005). *D. latitarsis* is a glacial stream specialist that is adapted to low water temperature, high variability in flows and limited food availability (Clitherow *et al.*, 2013) and thus reaches higher density at high meltwater sites. However, it is probably competitively inferior under more benign conditions, when interspecific biotic interactions are more likely (Flory and Milner, 1999).

In support of H₄, we observed a distinct succession of benthic assemblages along the meltwater contribution gradient. The pattern was consistent with studies investigating the deterministic trajectories of community succession in glacier-fed rivers (Milner *et al.*, 2001) with a high meltwater assemblage dominated by *Diamesa* spp. and a mid meltwater community characterized by Ephemeroptera (*Baetis* spp. and *Rhithrogena* spp.) and Plecoptera (*Protonemura* spp.). Groundwater spring/stream assemblages with moderate alpha diversity and abundance were dominated by Perlodidae (*A. compacta* and *Perlodes* sp.); the net spinning trichopterans, *Hydropsyche* sp. and *Plectrocnemia* sp.; and the flatworm *C. alpina*. These taxa tend to have more specialized habitat requirements, such as specific flow velocities for net spinning caddis (Edington and Hildrew, 1995) and constant (cool) water temperature for *C. alpina* (Wright, 1974), thus limiting the distribution to stable conditions of groundwater-fed channels (Bottazzi *et al.*, 2011).

Meltwater gradients and beta diversity

In this study, we have highlighted the importance of glacier meltwater for maintaining high beta diversity in alpine river basins. A number of studies in glacierized river systems, undertaken at a range of spatial scales, have reported similar findings suggesting a consensus is emerging (Brown *et al.*, 2007a; Jacobsen *et al.*, 2012; Finn *et al.*, 2013; Cauvy-Fraunié *et al.*, 2015). However, here, we have adopted a method that has unravelled turnover from nestedness, thus quantifying the importance of unique taxa at high meltwater sites for beta diversity (Figure 7). It appears likely a number of factors contributed to observed patterns of species turnover along the meltwater contribution gradient. First, the absence of *Diamesa aberrata* (Lundb.) and *Diamesa dampfyi* (Kieffer), cold-adapted glacier stream specialists (Rossaro *et al.*, 2006), at sites with lower meltwater contribution increased the dissimilarity between high and low meltwater sites. Second, the loss of heterogeneous distributions of certain taxa (e.g. *Rhyacophila angelieri* (Decamps) and *Pseudokiefferiella* spp.) as meltwater contributions decreased contributed to greater similarity between sites (Jacobsen *et al.*, 2012).

Third, the dominance of ephemeropteran taxa (e.g. *B. alpinus* and *Rhyacophila loyolaea*) also contributed to increased similarity between reaches of intermediate meltwater contribution (Finn *et al.*, 2013).

The strong relationship between meltwater difference and community dissimilarity has important implications for future biodiversity patterns as small alpine glaciers are expected to disappear in the coming century (Zemp *et al.*, 2006), altering the current stress gradient and likely reducing beta diversity (Jacobsen *et al.*, 2012). The identification of species turnover, rather than nestedness, as the key mechanism driving beta diversity across the continuum of meltwater contribution is similar to recent findings exploring links between natural stress gradients (altitude and salinity) and macro-invertebrate diversity (Gutiérrez-Cánovas *et al.*, 2013). As natural stressors exist across geological time, the evolution of stress specialists from a generalist pool is likely (Gray, 1989). In the case of temperate glacier-fed stream systems, these stress specialists are represented by *Diamesa* species. Hence, a unique set of species is found at environmentally harsh, high meltwater sites.

CONCLUSIONS

In this study, mixed responses to a natural environmental stress gradient were observed at different levels of biological organization (community–population) and between different taxa. At the community level, a reduction in both biotic/abiotic stresses may have led to the unimodal richness and density peaks. While at the extremes of the gradient, strong niche filtering (high meltwater stress) and competitive interactions (low meltwater contributions) contributed to the

presence of specialists (e.g. *Diamesa* and *R. evoluta*) and excluded generalists (e.g. *B. alpinus*). Hence, the linear response of various diversity-based and density-based metrics to meltwater contribution demonstrated by Brown *et al.* (2007c) was likely an artefact of the absence of samples from exclusively groundwater-fed rivers.

Based on the framework presented here (i.e. meltwater stress gradient), we suggest that future glacier and snowpack retreat/loss will lead to more homogeneous alpine river ecosystems because of a truncated environmental stress gradients as the meltwater end of the spectrum is reduced. An increase in mean diversity at the reach scale is predicted as habitats become more benign (Brown *et al.*, 2007a; Jacobsen *et al.*, 2012). However, loss of higher meltwater habitats will likely lead to extinction of specialist taxa and a reduction in beta diversity, emphasizing the importance of these high glacial-influenced habitats for regional diversity (Figure 8; Brown *et al.*, 2007a). As the current trend of glacier retreat in temperate regions is predicted to continue (Khamis *et al.*, 2014b), conservation efforts should focus on limiting additional anthropogenic stressors such as flow regulation, tourist infrastructure and intensive grazing. Finally, these findings further emphasize concerns regarding the potential for substantial changes in aquatic biodiversity as glaciers retreat and meltwater contributions decrease.

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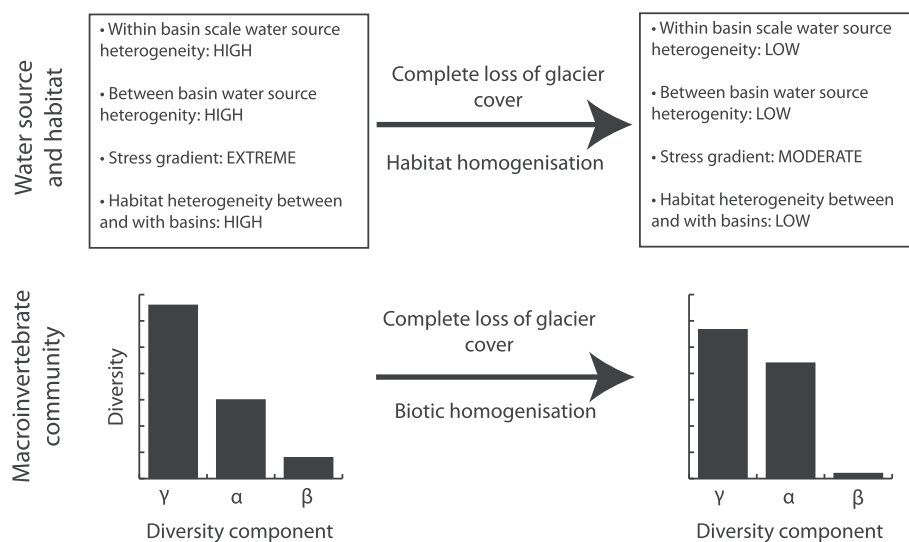


Figure 8. Conceptual representation of the changes in water source, habitat heterogeneity and biodiversity as glaciers retreat and disappear. The loss of high meltwater habitats and associated specialist taxa leads to reduced gamma diversity (γ). Habitat conditions become more benign and homogenous leading to increased reach scale diversity (α), but a reduction in beta diversity (β) is apparent.

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