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Runoff and the longitudinal distribution of macroinvertebrates in a glacier-fed stream: implications for the effects of global warming

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SUMMARY

1. The downstream pattern in benthic macroinvertebrate assemblages along glacier-fed streams is a result of decreasing glacial influence on environmental conditions. However, meltwater run-off shows temporal variation, reflected in differences in, for example, temperature, conductivity and turbidity. Consequently, depending on their run-off patterns, comparable environmental conditions may occur at different distances along glacier-fed streams. Our aim was to assess whether short-term variations in glacial run-off were reflected by changes in longitudinal distribution patterns of macroinvertebrates along a glacier-fed stream in the Ecuadorian Andes.

2. We measured environmental parameters, obtained continuous gauging data, measured macroinvertebrate drift rate with an hourly resolution during glacial floods and sampled benthic macroinvertebrates *c.* 3-monthly for 30 months at three sites at varying distances (0.1–4.3 km) from the glacier. For each sampling date, we fitted logarithmic equations to plots of taxon richness versus distance from the glacier, calculated similarity in assemblage composition between sites and calculated weighted averages of mid-points of taxon distributions. These data were analysed in relation to mean maximum flow over the 45 days prior to sampling.

3. Mean conductivity and temperature increased while turbidity decreased downstream. During glacial afternoon floods, conductivity decreased while temperature and turbidity increased. High flow moved maximal taxon richness downstream (reduced the slopes from logarithmic fits), while low flow made assemblages more downstream like (higher similarity with downstream assemblages). No significant relationships were found between weighted average distributions and flow. Drift rate (ind. h^{-1}) increased by an order of magnitude at the onset of afternoon floods, and the taxa that contributed most to total drift were those whose benthic densities were most reduced by increases in flow.

4. Our study provides hints as to how biological distribution patterns in glacier-fed streams might be affected by more permanent changes in run-off caused by glacial shrinkage. This study predicts a multidirectional shift in altitudinal/longitudinal species ranges, with a potential downward shift in species ranges as a consequence of global change.

Keywords: benthos, climate change, drift, elevational range shifts, glacial retreat

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Introduction

Glacier-fed streams typically originate as physically unstable, cold and nutrient-poor habitats. However, with increasing distance from the glacier, the stream environment becomes less and less influenced by the glacial source so that stream temperature, channel stability and electric conductivity of the water usually increase, while suspended solids (turbidity) decrease (Milner *et al.*, 2001). These physicochemical factors are key drivers of macroinvertebrate communities (Castella *et al.*, 2001) so that glacier-fed streams show a characteristic longitudinal succession in community composition and a rise in species richness of benthic macroinvertebrates with increasing distance from the glacier (Milner *et al.*, 2001; Jacobsen *et al.*, 2012), structured by a template of environmental filters in concert with biological traits (Ilg and Castella, 2006; Füreder, 2007), physiological tolerances (Lencioni, 2004; Lencioni *et al.*, 2008) and competitive performance of species (Flory & Milner, 1999). The rate of taxon gain along glacial streams is related to the size of the feeding glacier (Jacobsen & Dangles, 2012), a relationship probably caused by hydrology (i.e. the volume and thermal capacity of meltwater leaving the glacier) and thus the longitudinal distance required to moderate the harsh environmental stream conditions.

The flow regime in glacier-fed streams is determined primarily by glacial melting, and this varies both on a diel and seasonal basis (Jacobsen *et al.*, 2014). An increase in run-off of meltwater is therefore expected to increase environmental harshness at a given point along the stream. Therefore, not only will the environmental conditions at a given site along a stream vary in time, comparable environmental conditions would also be found at different distances along glacier-fed streams at different moments in time, partly depending on the current run-off (Fig. 1).

An increase in meltwater run-off may thus be expected to shift species downstream, further away from the glacier, tracking, for example, optimal thermal regimes or avoiding harsh environmental conditions. The downstream transport of organisms via drift is a ubiquitous phenomenon in streams, but the propensity to enter the drift varies among species and is influenced by a number of abiotic and biotic factors (Brittain & Eikeland, 1988; Giller & Malmqvist, 1998). Drift has rarely been studied in glacier-fed streams (Ilg *et al.*, 2001; Saltveit, Haug & Brittain, 2001; Hieber, Robinson & Uehlinger, 2003; Robinson, Tockner & Burgherr, 2004), but we expect it to be a highly efficient way of escaping, either actively or passively, unfavourable conditions during high glacial run-off, constituting an important downstream displacement of species.

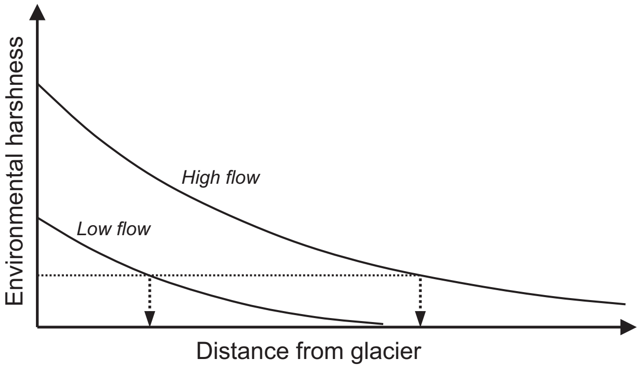

Fig. 1 Conceptual diagram illustrating how the same level of environmental harshness in glacier-fed streams will be found at different distances from the glacier, depending on actual flow (discharge), assuming that environmental harshness declines along the stream and increases with flow.

Glacial shrinkage will usually lead to an initial increase in meltwater run-off for a few years to decades, followed by a decrease in run-off over the longer term after a critical tipping point of glacial mass has been reached (Jansson, Hock & Schneider, 2003; Barnett, Adam & Lettenmaier, 2005; Huss *et al.*, 2008; Baraer *et al.*, 2012). In conjunction with changes in run-off during glacial shrinkage, several other key environmental characteristics can be expected to change (Fig. 2). A long-term study (three decades) of a single site on an Alaskan stream until complete loss of the original source glacier revealed a temporal colonisation pattern similar to the well-known longitudinal pattern (Milner *et al.*, 2008), and similar to the upstream movement and colonisation tracking retreating glaciers (Finn, Räsänen & Robinson, 2010). It is clear that the impact of vanishing glaciers on stream environments and biotas is subject to temporal variability.

We have previously reported spatial variability in macroinvertebrate communities along and between

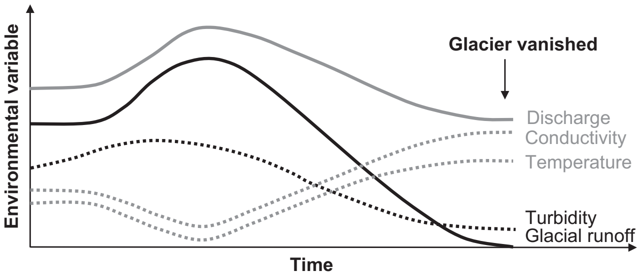

Fig. 2 Conceptual diagram illustrating the expected temporal changes in selected environmental parameters at any point along a glacier-fed stream during glacial shrinkage.

glacier-fed streams in Ecuador (Jacobsen *et al.*, 2010; Kuhn *et al.*, 2011), as well as temporal variations in relation to run-off, demonstrating that high flow reduces local faunal density and taxon richness and changes community composition (Jacobsen *et al.*, 2014). Here, our main aim was to explore whether periodic (short-term) variations in run-off of an Ecuadorian glacier produced longitudinal shifts in taxon richness, assemblage composition and distribution ranges of macroinvertebrates. Our specific objectives were (i) to elucidate the effect of glacial floods on the stream environment (water temperature, conductivity and turbidity), (ii) to explore relationships between short-term flow variations and longitudinal distribution patterns of macroinvertebrates and (iii) to determine how glacial floods affect downstream transport of macroinvertebrates through drift. Our expectations were that (i) high run-off would lead to a decrease in water temperature and conductivity, and an increase in turbidity, (ii) high run-off would drive the fauna downstream, tracking environmental conditions, and (iii) drift rate would increase with run-off and thus contribute significantly to downstream displacement of macroinvertebrates. As glacial equatorial streams do not have clear seasonality in their run-off, we regard them as convenient model systems that may allow us to infer general patterns in displacement of fauna from short-term data in the absence of other, correlated, seasonal influences. Our study is timely because it gives indications of the possible ecological consequences of future altered glacial run-off in a global warming context on longitudinal distribution patterns of macroinvertebrates in alpine streams.

Methods

Study area

Our study stream, the Río Antisana, is a headwater of the River Napo, a main tributary of the upper Amazon River (Fig. 3). It originates from the 'Crespo' glacier on Mt. Antisana in the eastern cordillera of the Andes of Ecuador (0°28′S, 78°09′W). The Crespo glacier covers an area of about 1.82 km^2 and originates at the summit of the mountain (5760 m a.s.l.), while the ablation zone extends from about 5150 m to the glacier snout at 4730 m a.s.l.

Air temperature, humidity and radiation do not vary systematically during the year, but precipitation, cloud cover and wind speed show more seasonal variability (Cadier *et al.*, 2007). Annual precipitation is about 800 mm, the majority falling as snow and hail (Maisincho *et al.*, 2007). For more information on the study area, refer to Jacobsen *et al.* (2010) and Kuhn *et al.* (2011).

We selected three sites along a stretch of the stream with no visible tributaries, providing an ideal situation for studying the effect of essentially the same hydrological regime on different communities. Site A (0.5–5 m

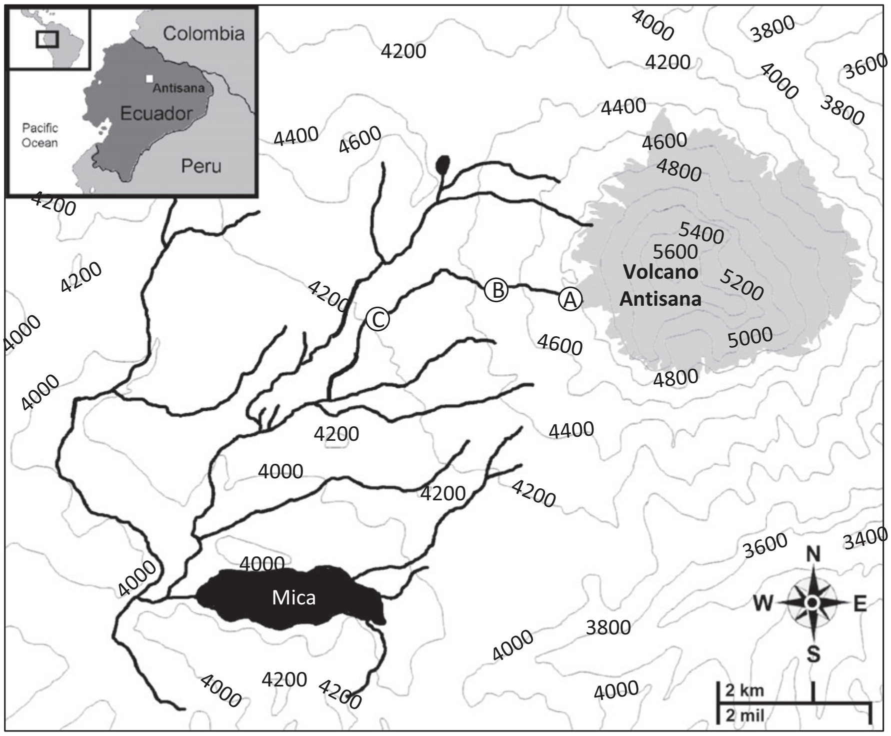

Fig. 3 Map of the Antisana stream system. Letters A, B and C indicate the locations of the three study sites along the stream draining the Crespo glacier.

wide) at 4730 m a.s.l. was located about 100 m from the glacier, on a wide plain with wandering, braided threads of water. It was fed directly from the glacier snout, but the stream regularly froze and ceased flowing at night. The site conformed well to the model proposed by Smith *et al.* (2001) for a high-altitude stream controlled by sediment regime and fed by a rapidly retreating glacier. Site B (1–2 m wide) was located at 4490 m a.s.l. and 1.62 km from the glacier, and site C (1–2 m wide) at 4225 m a.s.l. and 4.30 km from the glacier. Sites B and C were located in a confined, but eroding flood valley. Glacial cover is *c.* 100, 67 and 42% of the catchment areas of sites A, B and C, respectively (Maisincho *et al.*, 2007).

Environmental conditions

Data on hydrological regime were obtained through continuous recording of discharge during 2008–2010 at a gauging station established at site B, providing us with daily minimum, maximum and mean discharge [Institut de Recherche pour le Développement (IRD), Instituto Nacional de Hidrología y Metereología (INAMHI), Empresa Municipal de Ancantarillado y Agua Potable de Quito (EMAAP-Q)]. Precipitation had negligible effects on short-term variability in stream discharge, as neither minimum, maximum nor mean discharge was significantly correlated with daily precipitation records, either from the same day or the day before (Jacobsen *et al.*, 2014).

To verify that environmental conditions change along the stream, and with glacial run-off, a number of physicochemical parameters were measured on various occasions. Water depth and temperature were continuously recorded (30 min intervals) by Hobo loggers (Onset Computer Corporation, Cape Cod, MA, U.S.A.) at all sites over different periods during the study. Water pressure loggers, placed in protective plastic tubes, were attached vertically to boulders along the stream. One more logger was left in the air at 4100 m a.s.l. to correct for atmospheric pressure variations. Water level and height between the stream bottom and the Hobo sensor were measured twice, when the loggers were installed and removed. Conductivity (at 25 °C) was measured with a portable WTW Cond 315i meter (Weilheim, Germany) on every visit to the study sites (10–12 measurements). Water turbidity was measured 5–6 times at each site with a Eutech TN-100 Turbidimeter. As part of a previous study performed in January 2008, we had data from site B of water depth, suspended solids, water temperature and conductivity measured at *c.* 2-h intervals during an entire 48-h period.

Benthic macroinvertebrate sampling

Sampling of benthic macroinvertebrates was carried out between April 2008 and September 2010 at intervals from 2 to 5 months. Nine samplings were performed at sites B and C, and one less at site A (due to bad weather conditions). At each site, five quantitative Surber samples (500 cm^2; mesh size 200 μm) were collected randomly from pebble–cobble substratum within a stream reach of *c.* 20 m. All samples were collected during the day and preserved in the field in 70% ethanol. In the laboratory, samples were rinsed through a 200-μm sieve and sorted without use of magnification. Subsampling was applied to samples with large numbers of chironomids. Complete species analysis of the Ecuadorian stream fauna is not possible, as only a few groups can be identified to a taxonomic level lower than family. Invertebrates other than Chironomidae were identified mostly to family according to Roldán (1996), Merritt and Cummins (1996), Fernández and Domínguez (2001) and separated into morphospecies. Larvae of Chironomidae were sorted under a stereoscopic microscope at 10× magnification, dehydrated in 96 and 99% ethanol and mounted in Euparal. Larvae were identified to subfamily under a compound microscope at maximum 400× magnification using current taxonomic literature (Wiederholm 1983, Ruiz-Moreno *et al.* 2000, Epler 2001). Larvae of Orthocladiinae were not identified further.

Drift sampling

At the beginning of the study (23–25 February 2008), a 48-h drift sampling was performed at site B. Two replicate drift nets (mouth: 15 × 35 cm; bag length: 1.3 m; mesh size 500 μm) were placed a few cm above the bottom substratum at two sites about 6 m apart in the study reach. Water flow through each net was estimated from three corresponding measurements of water depth and current velocity (using a Höenstch anemometer) at the mouth of the net at the time of introduction and again before it was emptied. The volume of water filtered by each net was calculated as the average between initial and final flow multiplied by the length of the sampling period, and this was used to calculate drift density (ind. m^{-3}). The mean water depth at the mouth of the net was 3–15 cm, and the mean current velocity 0.02–0.94 ms^{-1}. As the sampling sites were shallow, drift nets collected most of the water column drift as well as surface drift. Nets were left to collect for 47–74 min (except for the last five samples which covered 93–181 min). To minimise the time that the nets were out of the water, they were emptied as quickly as possible (4–43 min; mean 10 min) and relocated in the stream. In total, eighty-two individual drift samples were collected. The content of the nets was preserved in 70% ethanol. As drift density is not necessarily related to discharge (Elliott, 1970), and our focus was to explore the downstream export of macroinvertebrates, we calculated drift rates as the mean number of individuals collected net^{-1} h^{-1}.

Data treatment

As a standardised measure of flow, we extracted mean maximum discharge from the last 45 days prior to each sampling. We have previously compared relationships of mean, maximum and mean maximum discharge from the last 3, 6, 9, 21 and 45 days prior to sampling in the Crespo stream and found that mean maximum discharge generally had the highest explanatory power for temporal variations in the macroinvertebrate community, but that the length of the period used to extract this flow metric had little effect on the obtained relationships (Jacobsen *et al.*, 2014).

As a measure of taxon richness at a site on a specific date, we used the mean number of taxa per Surber sample from the set of five replicate samples per date. We have previously reported that the taxon richness of macroinvertebrates in this time series data set is temporally independent at all sample lag periods at all three study sites (Jacobsen *et al.*, 2014). To describe the pattern in taxon richness along the stream, we plotted taxon richness versus distance from the glacier and fitted a logarithmic function for each sampling date, and the slope of these logarithmic fits was used as a measure of taxon gain rate in relation to flow prior to sampling.

To explore flow-related changes in longitudinal patterns in community composition, we calculated Bray–Curtis similarities (on log-transformed data to downweight the effect of very abundant taxa) of each sample from site B with the mean composition at site A and site C, respectively, and regressed this against mean maximum flow during the last 45 day prior to sampling. In this way, we compared the fauna that is 'left' at site B with those at the two other sites. We expected the fauna at site B to be more 'downstream-like' (i.e. higher similarity with site C) after periods of low flow, and more 'upstream like' (i.e. higher similarity with site A) after periods of high flow.

To quantify longitudinal movement of taxa, we calculated weighted averages (WA) of distance mid-points of taxon distributions as:

$$\mathrm{WA} = \frac{\sum_{i=1-3} (n_i \cdot D_i)}{N}$$

where n_i is the number of individuals found at a site, D_i is the distance along the stream from the glacier of the site, and N is the sum of the number of individuals of the taxon found at all three sites in the stream. The weighted averages were used in regressions against mean maximum flow.

Results

Environmental conditions

Environmental parameters varied systematically in both space and time. Overall, mean water temperature and conductivity increased, while turbidity decreased downstream along the Crespo stream (Fig. 4a). However, these parameters were temporally dynamic and showed a close relationship with short-term, diel fluctuations in discharge; suspended solids (≈ turbidity) and temperature increased, while conductivity decreased during the typical afternoon peak in meltwater run-off (Fig. 4b). Water temperature was positively related to flow at peak daily run-off, and this relationship became steeper moving along the stream (Fig. 4c).

Macroinvertebrate benthos

In total, we identified 51 taxa from all Surber samples, of which 22 were found only at site C. In addition, many taxa occurred rather sporadically; just 10 taxa were found on every sampling date. The mean number of macroinvertebrate taxa increased with distance from the glacier, closely following a logarithmic function (Fig. 5a). The rate of this taxon gain along the stream (the slope of the logarithmic fit) decreased with increased mean maximum flow during the last 45 days prior to sampling ($R^2 = 0.529$; $P = 0.040$), so high flow tended to displace richness downstream (Fig. 5b).

Analyses of weighted average longitudinal mid-points of taxa distributions were only performed on taxa occurring on all sampling dates at two or three sites. Eight taxa fulfilled these requirements; none of them showed significant correlations with mean maximum flow ($P > 0.05$).

The similarity between macroinvertebrate communities at each sampling date at site B and the 'average' reference community found at upstream site A was unrelated to previous flow, in contrast to our expectations (Fig. 6a). However, in accordance with our expectations, similarity between site B and site C was negatively related to flow

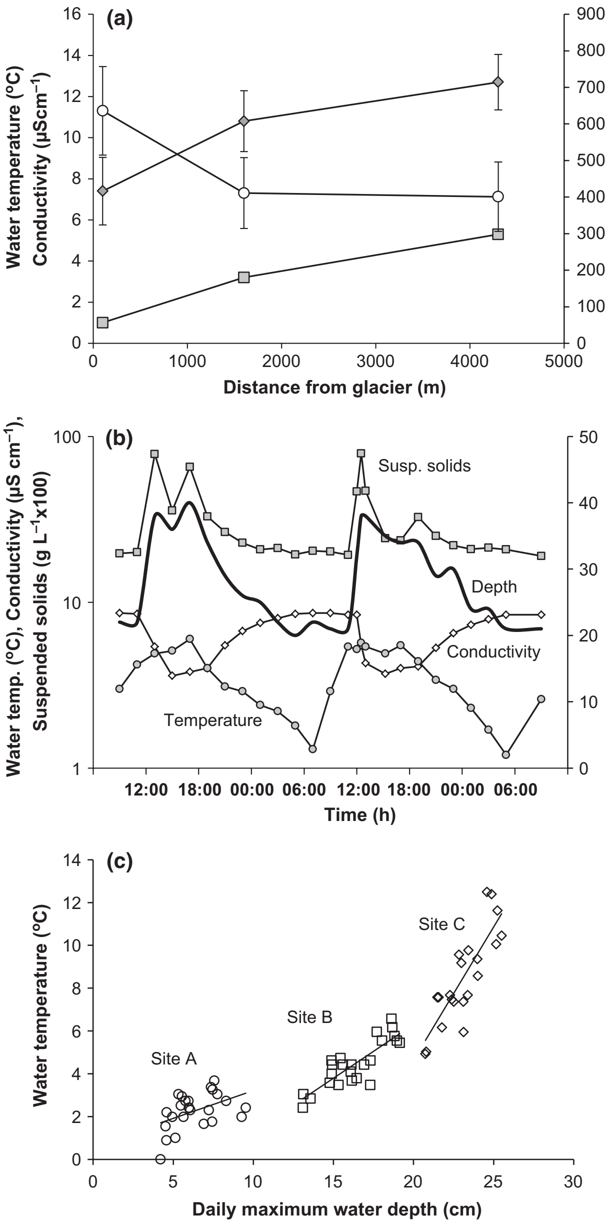

Fig. 4 Spatiotemporal variability in environmental parameters in the Ecuadorian, glacier-fed Crespo stream. (a) Mean water temperature, turbidity and conductivity at the three study sites versus distance from the glacier. (b) Water depth (thick line), suspended solids (filled squares), conductivity (open diamonds) and water temperature (filled circles) measured approximately every 2 h during a 48-h period at site B. Note the logarithmic *y*-axis. (c) Water temperature versus water depth at peak afternoon flow at each of the three study sites during April 2008. Linear regressions are Site A, $y = 0.261x + 0.612$, $R^2 = 0.210$, $P = 0.024$; site B, $y = 0.502x + 3.731$, $R^2 = 0.710$, $P < 0.001$; site C, $y = 1.243x - 20.210$, $R^2 = 0.704$, $P < 0.001$.

($R^2 = 0.492$; $P = 0.035$). So, after a short (45 days) low-run-off period, the community at site B had a more 'downstream-like character' (Fig. 6b).

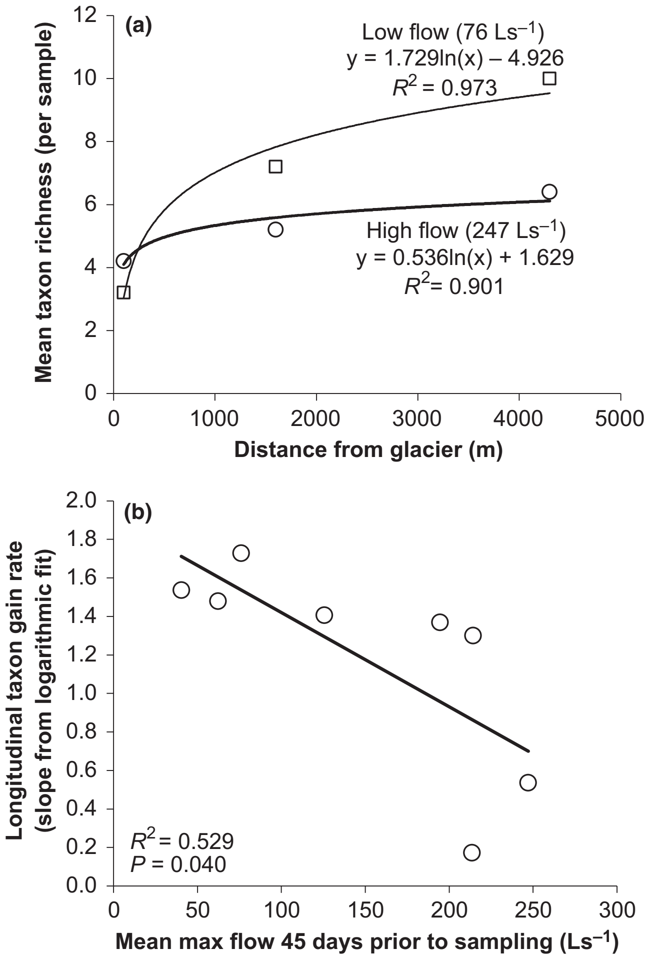

Fig. 5 Taxon gain along the Ecuadorian Crespo stream and its relation to flow. (a) Taxon richness as a function of distance from the glacier. Data from two sampling occasions with different mean maximum flow during the 45 days prior to sampling are shown. A logarithmic function is fitted to the data. (b) The slopes from logarithmic fits of taxon richness against distance from specific sampling occasions as a function of mean maximum flow (measured at site B) 45 days prior to sampling. Linear regression line: $y = -0.005x + 1.909$, $R^2 = 0.529$, $P = 0.040$.

Macroinvertebrate drift

A total of 32 taxa were collected from drift samples at site B. Chironomidae accounted for about 60% of total drift (Podonominae sp. 1, 20.3%; Diamesinae sp. 1, 13.4%; Podonominae sp. 3, 12.5%; Orthocladiinae 11.1%). Other important taxa in the drift were Limnophora sp. 1 (11.2%), *Cailloma* sp.1 (6.5%) and Tipulidae sp.1 (6.3%). Mean drift density during the 2-days drift study (1.46 ind. m^{-3} ± 1.29 SD) did not vary systematically, either with the day/night cycle or with discharge (data not shown).

Total drift rate (ind. h^{-1}), in contrast, clearly reflected diel variations in flow. Compared with the background level, drift rate increased momentarily at the onset of the afternoon glacial flood by approximately an order of magnitude, but rapidly returned to pre-flood levels within <1 h, while discharge was still high (Fig. 7).

Only one common taxon from the benthos (>1%) was not found in the drift as well (*Limnophora* sp.1), while several taxa contributed more to drift than to benthos (Fig 8a). The taxa that contributed most to total drift (>3%) were those whose benthic densities were generally most negatively correlated with run-off during the last 45 days prior to sampling ($R = -0.458$; $P = 0.021$); in other words, the taxa that were most affected by increases in run-off (Fig. 8b).

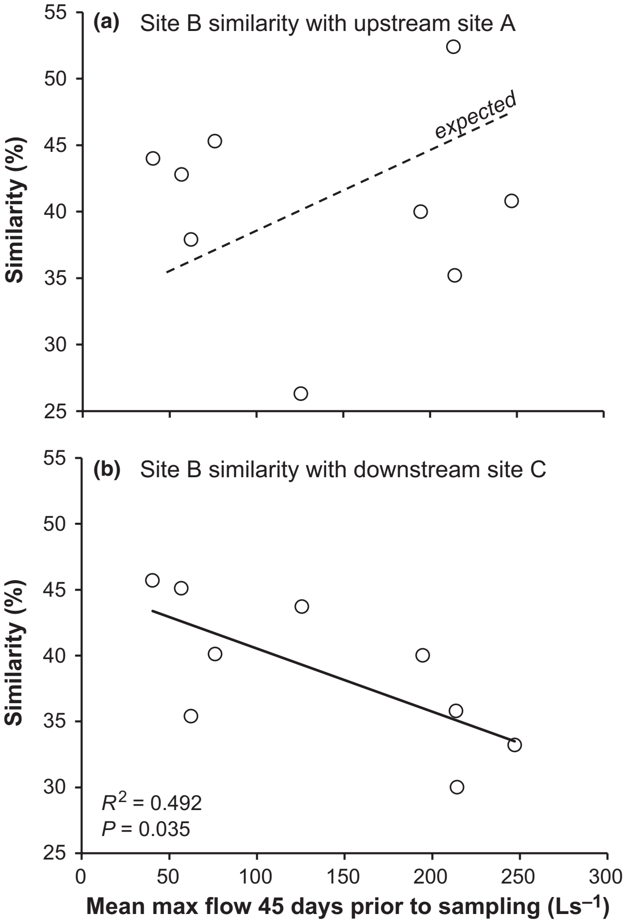

Fig. 6 (a) Similarity (Bray–Curtis on log x + 1-transformed data) between benthic macroinvertebrate assemblages at site B on each sampling occasion and the 'mean assemblage' at site A (all dates from site A pooled) versus mean maximum flow (measured at site B) 45 days prior to sampling. The expected relationship is indicated as a dashed line. (b) As above, but in relation to the 'mean assemblage' at site C (all dates from site C pooled). A linear regression line is included.

Discussion

Flow and environmental conditions

As expected according to the general model for glacier-fed streams (Milner *et al.*, 2001), as well as our previous studies in this system (Jacobsen *et al.*, 2010; Kuhn *et al.*, 2011), the physicochemical environment changed systematically along the course of the stream; mean turbidity decreased, while mean conductivity and water temperature increased with distance from the glacier. Suspended solids (turbidity) and conductivity also showed the expected pattern following variations in run-off, at least in the short term in connection with afternoon peaks in glacial melting (Smith *et al.*, 2001).

One of our *a priori* expectations was that water temperature would decrease with an increase of cold meltwater run-off, based primarily on the general assumption of decreasing temperature with increasing

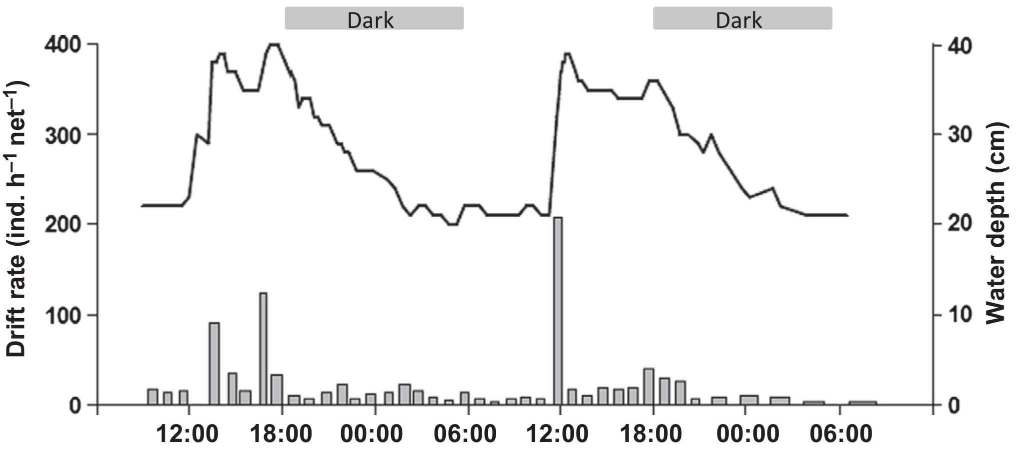

Fig. 7 Mean drift rate (from two nets) measured approximately hourly together with continuous data on water depth during a 48-h period at site B.

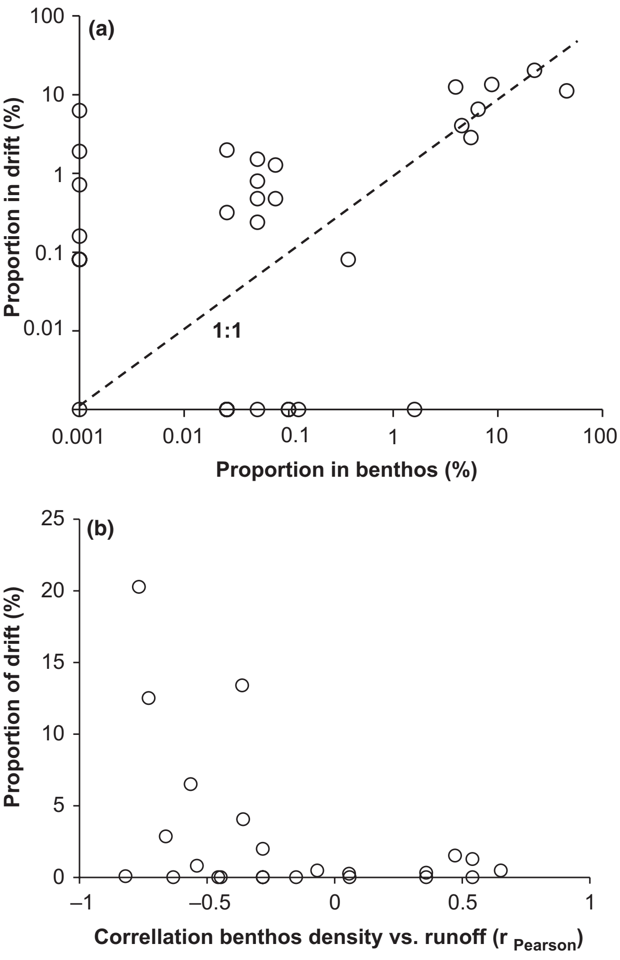

Fig. 8 Drift in relation to benthos. (a) Overall proportion of each taxon in drift versus benthos, all samples pooled. (b) Overall proportion in drift versus the effect of flow on the density of the taxon in benthos (Pearson's correlation coefficient). Only taxa occurring on at least two sampling dates in the benthos are included.

glacial influence (e.g. Ilg and Castella, 2006; Milner *et al.*, 2008). In contrast to our expectation, the temporal variability caused by the high afternoon flow was followed by an increase in water temperature, and the generality of this pattern was confirmed at all three sites, showing positive relationships between the magnitude of daily peak flow and corresponding water temperature. Even though the source of the afternoon glacial flood is ice-cold meltwater, the afternoon melting is the result of a rise in air temperature and/or solar radiation, and this warms up the water along the course of the stream, as clearly demonstrated by the rising slopes of the regressions at greater distances from the glacier. The balance between the thermal capacity of the meltwater and heat budget components is, however, stream specific and varies with channel morphology, orientation and surrounding topography (Webb *et al.*, 2008). Both convective and radiative warming (Webb *et al.*, 2008) is probably particularly accentuated along the Crespo stream due to the intense equatorial sun and the stream's relatively low discharge, and because the stream is shallow (mean depth 3–19 cm) and wide (mean width 39–204 cm). Mean daily run-off and stream temperature were also positively correlated over an annual cycle in Swiss glacier-fed rivers (Uehlinger, Malard & Ward, 2003). However, such relationships probably depend on the temporal scale, and it is important to note that other studies covering only the summer period in temperate glacier-fed steams have, indeed, found water temperature to decrease during high run-off (Lods-Crozet *et al.*, 2001).

Flow and longitudinal patterns in macroinvertebrates

We have previously demonstrated that density and taxon richness of macroinvertebrates were inversely related to preceding flow at all three study sites (Jacobsen *et al.*, 2014). Here, we show that 'short-term' periods of high flow reduce the taxon gain rate along the stream. This is in line with the results of Jacobsen & Dangles (2012) who compared glacial streams worldwide and found that the taxon gain rate was inversely related to glacier size, and presumably therefore to run-off. The implication of this is that at high flow, the ecological gradient along the stream is less steep, while it is compressed and steeper at low flow. High flow particularly affects the taxon gain close to the glacier; that is, where there is a particularly steep diversity gradient (Milner *et al.*, 2001).

In our system, no taxa were found exclusively at upstream sites A or B. This means that downward shifts of taxa would not mean introducing any new taxa to the downstream site C, but rather a contraction of upper altitudinal distribution limits. However, we could not demonstrate this from the data on weighted averages of distribution mid-points. This may be because our spatial resolution with only three study sites was insufficient, because macroinvertebrate samples were not large enough or because most taxa occurred rather sporadically. Thus, we were not able to identify the taxa responsible for the less steep taxon gain rates after high flow, and local stochastic depletion of different taxa seems to be important. Nevertheless, further downstream and outside our study reach, as well as in other systems/regions where streams may have other distribution patterns of macroinvertebrates, increased meltwater run-off may introduce new taxa into downstream reaches.

We have previously reported that assemblage composition is influenced by preceding run-off in this stream (Jacobsen *et al.*, 2014). Here, we show, as expected, that assemblages at site B at low flow tended to be more similar to those found further downstream at site C. Finn *et al.* (2010) found a quite similar result comparing macroinvertebrate assemblages along a glacier-fed stream in the Swiss Val Roseg, where community types seemed to move up the gradient in low run-off seasons (spring and autumn) and down the gradient in high run-off seasons (summer), regardless of stream site. In contrast, we did not observe the anticipated higher similarity with site A after high flow periods. We attribute this to the highly stochastic composition of the taxon-poor assemblages at site A, a pattern that is not mainly driven by hydrological regime, but rather by stochastic catastrophic events occurring in the extremely unstable environment close to the glacier snout (Jacobsen *et al.*, 2014).

Flow and macroinvertebrate drift

Drift densities in the Crespo stream were slightly higher than those measured in an earlier study on Ecuadorian non-glacial high-altitude streams (0.3–0.7 ind. m^{-3}; Jacobsen & Bojsen, 2002), but considerably lower than monthly averages found in temperate glacier-fed streams in Norway (23–185 ind. m^{-3}, Saltveit *et al.*, 2001) and Switzerland (3–280 ind. m^{-3}, Robinson, Tockner & Burgherr, 2002; 2–140 ind. m^{-3}, Hieber *et al.*, 2003). These quantitative differences between our results and densities found in the European streams may be due to the use of different mesh sizes, 500 μm here as opposed to 100–250 μm in the European studies. None of these European studies showed a clear pattern in drift with respect to meltwater run-off, neither on a diel nor seasonal basis. This may be due to the fact that all studies reported drift density instead of drift rate (i.e. the number of individuals transported downstream per unit time).

In our stream, macroinvertebrate drift rate increased by approximately an order of magnitude during the afternoon glacial flood, compared with the background level. This form of catastrophic drift would occur in any stream subject to increase in discharge and current (Water, 1972; Brittain & Eikeland, 1988). Interestingly, it occurred even though the fauna in our equatorial stream is exposed to such daily glacial floods year-round and therefore should be well adapted to this disturbance. However, peaks in drift rate were rather short term, and drift did not remain high during the entire glacial flood. Unfortunately, our drift data from only two glacial floods of almost similar magnitude do not allow us to explore in more detail the resistance of the fauna to floods.

The fact that the taxa that contributed most to total drift were those whose benthic densities were most negatively affected by run-off strongly indicates that downstream export of organisms via drift is, at least partly, responsible for the changes that we observed in benthic assemblages in relation to run-off. Previous work in this stream has shown that low-stress areas persist in benthic habitats even during daily glacial floods that increase overall hydraulic stress (Cauvy-Fraunié *et al.*, 2014). This study indicates, however, that the temporal variability in the benthos is due to a longitudinal spatial displacement and not just caused by taxa seeking hyporheic or other types of flow refugia (Lancaster & Hildrew, 1993; Malard *et al.*, 2003; Dole-Olivier, 2011).

We observed an increase in water temperature during high flow, so if we suppose that species are tracking their optimal thermal regime, and temperature is assumed to be the driving factor, we should expect species to move upstream during high flow. We did not observe this. Of course, temperature may not be the overriding factor; turbidity or conductivity could be equally or more important (Miserendino, 2001). However, we imagine that downstream drift of organisms during high run-off is an efficient and important way of downstream dispersal and a general phenomenon in glacier-fed streams, even though, as in this study, this might take organisms further away from their usual temperature environment. Thus, the fauna may not enter into catastrophic drift as an active response to changes in temperature, turbidity or conductivity, but could instead simply be transported downstream as passive or accidental dislodgements caused by the increased shear stress during high flow (Water, 1972; Brittain & Eikeland, 1988). Whether populations establish themselves downstream, and downwards range shifts take place, will depend on the stream-specific environmental gradients.

Implications and perspectives of global warming

In contrast to the terrestrial environment (e.g. Lenoir *et al.*, 2008; Moritz *et al.*, 2008; Chen *et al.*, 2011), surprisingly few studies have dealt with range shifts in aquatic organisms, in particular along altitudinal gradients (Heino, Virkkala & Toivonen, 2009). Altitudinal range shifts of stream macroinvertebrates have been mostly indirectly predicted or inferred from polewards expansions of distribution ranges (Hickling *et al.*, 2006), space-for-time studies (Brown, Hannah & Milner, 2007), species distribution models (Domisch, Jähnig & Haase,

2011) and by estimating future isotherm shifts (Isaak & Rieman, 2013).

If we assume that environmental changes are similar during short-term and long-term changes in run-off and that the fauna responds in a similar manner to these environmental changes, then our study may provide hints to how biological distribution patterns in glacier-fed streams could be affected by more permanent changes in run-off caused by climate change. Our study predicts that an increase in meltwater run-off will lead to a downward shift and general reduction in taxon richness, while the opposite would be the outcome of a decrease in run-off. A downward shift of macroinvertebrate communities contrasts with previous predictions made in other stream types fed by surface run-off of rain/snowmelt or ground water where fish (Hari *et al.*, 2006; Buisson *et al.*, 2008) and stream macroinvertebrates (Bálint *et al.*, 2011; Sheldon, 2012) are expected to move upwards. Our findings therefore extend to altitudinal migration the view recently proposed by Van der Wal *et al.* (2013) that niche tracking under warming conditions will result in multidirectional distribution shifts. Such multidirectional shifts may have several potential implications for the alpine stream fauna.

Firstly, populations in glacier-fed streams might become increasingly isolated by distance from sister populations in non-glacial streams, with possible effects on metapopulation dynamics (Heino, 2005; Anderson *et al.*, 2009; Brown *et al.*, 2011). Secondly, altered water temperature could affect growth rates and phenology of aquatic organisms, and insects emerging later from cold water to an increasingly warmer terrestrial environment could lead to reduced interbreeding with populations from non-glacial streams, and thus a higher degree of phenological isolation of populations from glacier-fed streams and eventually genetic drift (Finn, Khamis & Milner, 2013). Thirdly, similarity between communities in different stream types within altitudinal bands in alpine landscapes should decrease with a concomitant increase in species turnover (beta diversity). Finally, not all species seem to respond equally to glacial run-off-mediated changes in the environment (Jacobsen *et al.*, 2014), probably due to differences in biological traits such as resistance, resilience and dispersal capacity (Füreder, 2007). Range shifts of some species in a community can decouple biological interactions, and species may face changed interspecific interactions (Dangles *et al.*, 2011; Fugère *et al.*, 2012; Zarnetske, Skelly & Urban, 2012) at different distances along the stream. This community disassembly may lead to even further modified communities (Sheldon, Yang & Tewksbury, 2011) and potential extinction events (Urban, Tewksbury & Sheldon, 2012). During advanced glacial shrinkage with reduced meltwater run-off, we anticipate upwards range shifts. Upstream shifts could occur as in-stream lateral migration of aquatic stages or through dispersal of flying adults (e.g. Giller & Malmqvist, 1998), but, compared with downstream drift, both of these mechanisms would presumably be slower and with a time lag.

The idea of seasonal-scale shifts in longitudinal distribution patterns has been presented before (Finn *et al.*, 2010), and even the Milner *et al.* (2001) model for glacier-fed streams acknowledges that it refers only to high run-off conditions during temperate summers, while patterns are different during calm winter conditions when animals from lower altitudes may recolonise. However, our study is the first to demonstrate that even relatively short-term variations in run-off in glacier-fed streams are reflected in the spatiotemporal distribution patterns of the biota. As the variations found in our equatorial stream produced results very similar to the seasonal shifts found in the Alps (Finn *et al.*, 2010), there is good reason to believe that short-term longitudinal displacements can be used to predict altitudinal range shifts resulting from long-term changes in glacial status and meltwater run-off.

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