Glacial flood pulse effects on benthic fauna in equatorial high-Andean streams

Cauvy-Fraunié Sophie, Andino Patricio, Espinosa Rodrigo, Calvez Roger, Anthelme Fabien, Jacobsen Dean and Dangles Olivier

1 IRD, Institut de Recherche pour le Développement, UR 072, Laboratoire Evolution, Génomes et Spéciation, UPR 9034, Centre National de la Recherche Scientifique (CNRS), 91198 Gif sur Yvette Cedex, France
2 Pontificia Universidad Católica del Ecuador, Facultad de Ciencias Exactas y Naturales, Laboratorio de Entomología, Quito, Ecuador
3 IRD, Institut de Recherche pour le Développement, UMR G-EAU, Cemagref, 361 Rue Jean-François Breton, BP 5095 34196 Montpellier Cedex 5, France
4 IRD, Institut de Recherche pour le Développement, UMR AMAP, 911 avenue Agropolis, BP 64501, 34394, Montpellier Cedex 5, France
5 Freshwater Biological Section, Department of Biology, University of Copenhagen, Helsingørsøgade 51, 3400 Hillerød, Denmark

Abstract:

Equatorial glacier-fed streams present unique hydraulic patterns when compared to glacier-fed observed in temperate regions as the main variability in discharge occurs on a daily basis. To assess how benthic fauna respond to these specific hydraulic conditions, we investigated the relationships between flow regime, hydraulic conditions (boundary Reynolds number, Re*), and macroinvertebrate communities (taxon richness and abundance) in a tropical glacier-fed stream located in the high Ecuadorian Andes (> 4000 m). Both physical and biotic variables were measured under four discharge conditions (base-flow and glacial flood pulses of various intensities), at 30 random points, in two sites whose hydraulic conditions were representative to those found in other streams of the study catchment. While daily glacial flood pulses significantly increased hydraulic stress in the benthic habitats (appearance of Re* > 2000), low stress areas still persisted even during extreme flood events (Re* < 500). In contrast to previous research in temperate glacier-fed streams, taxon richness and abundance were not significantly affected by changes in hydraulic conditions induced by daily glacial flood pulses. However, we found that a few rare taxa, in particular rare ones, preferentially occurred in highly stressed hydraulic habitats. Monte-Carlo simulations of benthic communities under glacial flood reduction scenarios predicted that taxon richness would be significantly reduced by the loss of high hydraulic stress habitats following glacier shrinking. This pioneer study on the relationship between hydraulic conditions and benthic diversity in an equatorial glacial stream evidenced unknown effects of climate change on singular yet endangered aquatic systems.

KEY WORDS tropical; glacier; stream; flood; macroinvertebrate; Reynolds number

Received 9 January 2013; Accepted 22 April 2013

INTRODUCTION

Flow is a major determinant of physical habitat in streams (Poff and Zimmerman, 2010), which in turn has profound effects on the structure and function of living communities, as reported for benthic algae (Biggs and Smith, 2002), invertebrates (Milner et al., 2012), and fish (Xenopoulos et al., 2005). Consequently, the alteration of flow regimes as a result of increasing water abstraction and/or climate change is a critical factor for the decline in freshwater biodiversity (Dudgeon et al., 2006; Larned et al., 2010; Vorosmarty et al., 2010). The shrinking of mountain glaciers in response to ongoing climate change is an important process altering flow regime of rivers qualified as glacial meltwater (Bradley et al., 2006). While at the early stages of glacier retreat, the reduction in ice volume could yield a significant increase in annual runoff (Baraer et al., 2012), the annual average discharge would then decrease up to the end of the glacial influence on outflow (Huss et al., 2008). The effects of global warming on flow alteration and water availability in glacier fed catchments is an important and timely issue that has recently generated a strong interest by the scientific community in both temperate and tropical regions (Xu et al., 2009; Döll and Zhang, 2010; Immerzeel et al., 2010; Brown and Milner, 2012).

Glacier-fed streams present specific hydrological patterns resulting from a complex combination of factors including hydrological storage time, transfer processes (flow routing depending on channel topography), and spatio-temporal dependent changes in the relative influence of ice-melt,
goals were (1) to determine the impact of hydraulic stress variations caused by daily glacier melting on macroinvertebrate communities and (2) to predict the ecological response of these communities to potential hydrological shifts caused by accelerated shrinking glaciers under global warming. Two main hypotheses were tested: (1) macroinvertebrate communities will be affected by the hydraulic stress variations in the benthic habitats during the daily glacial flood pulses, and (2) some specific taxa (e.g. specialists, rare taxa) may be impacted by changes in hydraulic habitats resulting from glacier run-off alterations.

**METHODS**

**Study site**

The study was conducted at two sites in a glacier-fed stream located at 4100 m a.s.l. in the Ecological Reserve of Antisana, Ecuador (0° 29′ 06″ S, 78° 08′ 31″ W). Sites were located at 6.5 km from the glacier on a small plateau partially covered by páramo vegetation (grasslands of equatorial highlands) on the slopes of volcano Antisana (5758 m a.s.l.). The stream originates at 4730 m from the snout of the ‘Crespo’ glacier, which covers an area of about 1.7 km², with an ablation zone extending from 5150 m to 4730 m elevation, retreating 10–20 m per year (Vuille et al., 2008; Jacobsen et al., 2010). Physical characteristics (e.g. similar width, depth, and slope; see details in Table I) were similar at both sites but differed in terms of degree of glacial influence. One site (hereafter referred to as the ‘high glacial site’) recast no tributaries, high turbidity levels (mean = 284 NTU), low conductivity (≤ 15 µS cm⁻¹), and high flow variability on a daily basis due to glacier-melting (see Figure 1A). The

Table I. Physicochemical attributes of the study sites. Ranges are given in brackets

<table>
<thead>
<tr>
<th></th>
<th>High glacial site</th>
<th>Low glacial site</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coordinates</td>
<td>0°30′25″S,</td>
<td>0°30′28″S,</td>
</tr>
<tr>
<td></td>
<td>78°12′19″W</td>
<td>78°12′21″W</td>
</tr>
<tr>
<td>Wetted width (m)</td>
<td>&lt;1.50a</td>
<td>&lt;1.50a</td>
</tr>
<tr>
<td>Depth (cm)</td>
<td>&lt;12a</td>
<td>&lt;27.5a</td>
</tr>
<tr>
<td>Mean discharge (l s⁻¹)</td>
<td>59</td>
<td>103</td>
</tr>
<tr>
<td>Mean temperature (°C)</td>
<td>7.6 (0.0–19.8)</td>
<td>8.4 (2.0–19.9)</td>
</tr>
<tr>
<td>Conductivity (µS cm⁻¹)</td>
<td>9 (1–15)</td>
<td>125 (30–187)</td>
</tr>
<tr>
<td>pH</td>
<td>7.85 (6.92–8.42)</td>
<td>7.64 (6.52–7.99)</td>
</tr>
<tr>
<td>O₂ (mg l⁻¹)</td>
<td>7.19 (1.62–10)</td>
<td>8.23 (5.65–14.63)</td>
</tr>
<tr>
<td>PO₄³⁻ (mg l⁻¹)</td>
<td>&lt;0.01</td>
<td>0.8</td>
</tr>
<tr>
<td>NO₂⁻ (mg l⁻¹)</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>NO₃⁻ (mg l⁻¹)</td>
<td>0.8</td>
<td>0.2</td>
</tr>
<tr>
<td>SO₄²⁻ (mg l⁻¹)</td>
<td>1.3</td>
<td>34.2</td>
</tr>
</tbody>
</table>

a base-flow conditions
second site (hereafter referred to as the ‘low glacial site’) was located 175 m downstream of the high glacial site and 60 m downstream the confluence with a non-glacial, rain-, and groundwater fed stream (hereafter referred to as the ‘páramo stream’, the only tributary of the glacial stream). Lower turbidity (mean = 100 NTU), and daily flow variability, but higher conductivity (mean = 125 μS cm\(^{-1}\)) were found at the low glacial site, when compared to the high glacial site (Figure 1B).

**Coupled physical measurements - macroinvertebrates sampling**

At each site, water depth and near-bed velocity (2 cm above substratum) were measured at 30 randomly selected points (whose coordinates were generated using the runifpoint function in the software R, version 2.14) along a single longitudinal 10 m-transect, using a current meter (OTT C2, Kempten, Germany) with a 3 cm diameter propeller. This section was representative of the geomorphic variability found in the stream. A parallel study using 60 measurement points revealed that 30 points were sufficient to properly characterize the distribution of flow velocities and water depths at the low glacial site (the frequency distribution of both variables did not differ significantly between 30 and 60 measurements; \(\chi^2\) test, \(p=0.831\) and 0.977 and \(\chi^2=2.82143\) and 1.63571 for water depths and flow velocities, respectively). The coordinates (\(x, y\)) of each point were recorded precisely using two retractable tape measures, one parallel and the other perpendicular to the studied stream segment. Macroinvertebrate communities were then sampled at each point using a Surber net with small sampling area (125 cm\(^2\); mesh size 200 μm). Following Statzner et al. (1988), we defined the dominance of the substratum size classes and calculated the substratum roughness. All macroinvertebrate samples were preserved in 70% ethanol and brought to the laboratory where they were rinsed through a 200 μm sieve and sorted. Invertebrates were identified under a microscope at 0.67–4.5\(\times\) magnification range (Olympus SZ2-IL ST, Tokyo, Japan) to morphospecies, genus, or (sub) family, according to Fernández and Domínguez (2001).

These coupled measurements of abiotic and biotic variables were performed at four different times to obtain a wide range of discharge conditions (25 March and 15 April 2010, morning and afternoon for base-flow and glacial flood pulses, respectively). Two sampling times corresponded to base-flow conditions in both stream sites \(Q_1 = 0.024\) and 0.033 m\(^3\) s\(^{-1}\), \(Q_2 = 0.043\) and 0.073 m\(^3\) s\(^{-1}\) for the high glacial and low glacial site, respectively). The two others corresponded to (1) a moderate glacial flood pulse \(Q_3 = 0.2420\) and 0.384 m\(^3\) s\(^{-1}\) for the high glacial and low glacial site, respectively) and (2) a high glacial flood pulse \(Q_4 = 0.515\) and 0.526 m\(^3\) s\(^{-1}\) for the high glacial and low glacial site, respectively). All Q values correspond to the maximum value of stream discharge calculated from five measurements over the sampling period at a fixed transect (12 depth and velocity measurements performed using a current meter OTT C2, Kempten, Germany). Based on continuous two-year measurements of water depth in both
we calculated that the two flood events Q3 and Q4 had a yearly frequency of 0.33 and 0.02, respectively.

**Data analysis**

**Impact of discharge conditions on boundary Reynolds numbers.** To describe the hydraulic conditions experienced by benthic organisms at the substrate surface during different flood events, we used the Boundary Reynolds number Re*, an index of near-bed turbulence (see Statzner, 1988, for a detailed description of Re* calculation). While a wide array of hydraulic variables can be found in the literature (e.g. water velocity, Re, turbulence, Shear stress, and Froude number), we selected Re* as it represents an integrated indicator of the impact of hydraulic stress on macroinvertebrate distribution and behavior (Snook and Milner, 2002; Lancaster et al., 2006). Re* distributions from the 30 measurements at each site were plotted for the four discharge conditions and fitted to log-normal models, the best peak-function models based on AIC values, using Table Curve 5.01 (Systat Software, Chicago, Illinois) and R (version 2.14).

Due to logistical limitations, we were unable to expand our fine-scale study to other stream sites in the study catchment. However, to verify that the hydraulic conditions at our sites were representative to those occurring in other streams, we calculated the Reynolds number Re, see Statzner, 1988 for a detailed description of Re calculation) at 29 additional stream sites (including sites on the same stream and others in different streams) located in the same catchment (see APPENDIX 1 for details). Mean Re values calculated at our two studied sites encompassed most of the range of Re values found in other stream sites. Thus, we assumed that the variability of the hydraulic conditions across our two study sites was representative of the entire stream and of other sites located in studied glacial-fed catchment.

To visualize how the four discharge conditions influenced the spatial distribution of Re* in the streambeds, we plotted the coordinates (x, y) of the 30 measurement points within the digitalized shapes of the two sites. Then, we fitted their corresponding Re* to a surface of the form Re*(x, y) using the INTERP function written in R (version 2.14). Re* values were smoothed by Akima interpolations. We then used these modeling surfaces to estimate how Re* would change at a given sampling point of the streambed among the four discharge conditions. To achieve this, we randomly selected 30 points from the modeling surface at Q1, Q2, Q3, and Q4 and compared their Re* values in both sites. These simulations were repeated 40 times.

**Impact of hydraulic conditions on macroinvertebrate communities.** At both sites, we tested the effect of Q and Re* on taxa richness (number of taxa) and total abundance (N/m²) of macroinvertebrate communities using one-way ANOVA followed by Tukey tests and Spearman correlation coefficients, respectively. We further carried out a non-metric multidimensional scaling (NMDS) analysis to examine patterns of similarity in macroinvertebrate assemblages among hydraulic conditions defined as Re* classes determined by natural breaks using the Fisher–Jenks algorithm (see Re* classes distribution in appendix 1). The Bray–Curtis index was used as a measure of similarity with samples from the same Re* classes being grouped with convex hulls. The NMDS goodness of fit was estimated with a stress function R (which ranges from 0 to 1) with values close to zero indicating a good fit. The difference in composition of benthic communities among hydraulic conditions was tested using an analysis of similarities (ANOSIM). ANOSIM tested the null hypothesis that the within-sites similarity was equal to the between-sites similarity. Monte-Carlo randomizations of the group labels were used to generate null distributions in order to test the hypothesis that within-group similarities were higher than would be expected by chance alone. All analyses were performed using PAST (Paleontological statistics, version 1.79) on log (X + 1) transformed data.

**Simulating the effect of glacier run-off decrease on macroinvertebrate communities.** Over the long term, glacier volume reduction induced by global warming will inevitably translate into a decrease in the volume of glacier run-off and subsequently in the mean discharge of glacier-fed streams (Milner et al., 2009; Baraer et al., 2012). Because Re* distribution in a streambed is greatly dependent on discharge characteristics (Lancaster and Hildrew, 1993; Rempel et al., 2000, see also our Figure 2A and B), one can hypothesize that glacier volume reduction would affect macroinvertebrate communities through a modification in Re* distribution. We used Monte Carlo simulations to examine how the predicted decrease in glacier run-off in the Antisana glacier (Vuille et al., 2008) may affect macroinvertebrates distribution and lead to potential extinctions at both fully high glacial and low glacial sites. From these simulations, we created null model, randomized communities of macroinvertebrates in the different flow habitats, which were then compared with real data matrices. To achieve this goal, we first created for the two sites a presence–absence matrix of all macroinvertebrate taxa in each Re* class (identified in the NMDS) based on observed data. Then, for each site, the simulation created 100 replicate null communities by selecting a set of taxa from the total taxon pool and randomly distributing the taxa in the different Re* classes. The probability of selection of each taxon was assigned based on the abundance of those taxa in the observed communities.

All simulations were performed using the co-occurrence...
module in ECOSIM (http://www.garyentsminger.com/ecosim/index.htm). As we were interested in examining the potential consequences of stream discharge reduction on macroinvertebrate taxon extinction, these simulations were performed for both total number of taxa and rare taxa. We used a data set of macroinvertebrate taxa collected in 50 stream sites of the Antisana area around our study sites (Jacobsen and Dangles, 2012) to identify rare taxa as defined by their occurrence frequency. Based on Cao et al. (1998), taxa occurring no more than five times in all 50 sites were considered as rare.

RESULTS

Impact of discharge on boundary Reynolds numbers. Water depth in both the high glacial and the low glacial sites increased around 12:00 h on a daily basis (Figure 1A and B). This pattern strongly differed from that classically observed in páramo streams with no glacial influence (Figure 1A). Re* distribution on the streambed was strongly influenced by the discharge. As discharge increased, new higher Re* values appeared on the streambed (Re* > 2000 in both sites) and the inflection point of the Re* frequency curves shifted toward higher values (Figure 2A and B). Both high glacial and low glacial sites presented a high spatial heterogeneity in hydraulic habitats during base-flow conditions (Figure 3A and B). While there was a general tendency for Re* values to increase in most streambed zones as discharge increased, a few zones with low Re* values were still observed even during high floods (Figure 3A and B and Figure 4A and B). Also, while Re* values estimated at a given point in the stream generally increased with glacial flood (dots above the 1:1 line in Figure 4A and B), a few locations showed either unchanged or decreased Re* values during the flood (dots in the CI or below the 1:1 line in Figure 4A and B). Thus, even during glacial flood pulse, both sites still presented a very high spatial heterogeneity in hydraulic habitats.

Impact of hydraulic conditions on macroinvertebrate assemblages. Macroinvertebrate abundance was lower at the high glacial site (633 individuals) than at the low glacial site (2967 individuals) whereas macroinvertebrate richness was similar in both sites (35 and 38 for high...
glacial and low glacial site, respectively). At the high glacial site, communities were dominated by Orthocladiinae (indeterminate genus) (> 40%) and Alluaudomyia sp. (Ceratopogonidae) (> 15%), while at the low glacial site Hyallela sp. (Hyallellidae) (> 45%) and Alluaudomyia sp. (> 13%) were the most abundant taxa. At the high glacial site, mean abundance and number of taxa differed significantly among the four studied discharges (ANOVA, \( p < 0.001 \), \( F_{3,107} = 6.53 \) and 13.53, respectively, Figure 5A and C). The mean values of both variables for Q2 were significantly smaller than for Q1 and Q4 and the mean values for Q4 significantly higher than for Q3. At the low glacial site, mean abundance and number of taxa differed significantly among the four studied discharges (ANOVA, \( p < 0.001 \), \( F_{3,107} = 6.53 \) and 13.53, respectively, Figure 5A and C). The mean values of both variables for Q2 were significantly smaller than for Q1 and Q4 and the mean values for Q4 significantly higher than for Q3.
site, on the other hand, both abundance and richness did not vary among the four discharges (ANOVA, \( p > 0.05 \), Figure 5B and D). While abundance and richness were not correlated to \( \text{Re}^* \) values at the high glacial site (Spearman rank test, \( p > 0.05 \), Figure 6A and C), they significantly increased with increasing \( \text{Re}^* \) values at the low glacial site (Spearman rank test, \( p < 0.01 \), \( F_{1,117} = 7.82 \) and 11.41 for abundance and richness, respectively, Figure 6B).

At the high glacial site, the NMDS did not reveal significant differences in macroinvertebrate assemblage composition between the different classes of \( \text{Re}^* \) (ANOSIM, \( p > 0.05 \), Figure 7A). However, at the low glacial site, we found that macroinvertebrate assemblages occurring in habitats with \( \text{Re}^* > 1000 \) differed significantly from those found in other \( \text{Re}^* \) habitats (ANOSIM, \( p < 0.05 \), \( R = 0.019 \), Figure 7B).

---

**Figure 6.** Scatter plot of abundance: total of individuals in one square meter (A, B) and taxa richness: number of taxa (C, D) versus boundary Reynolds number values at each sampling points, fitted by a non-parametric curve LOWESS. In high glacial (A, C) and low glacial (B, D) sites, all discharges were represented.

**Figure 7.** Non-metric multidimensional scaling ordination of log-transformed macroinvertebrate community data in the both high glacial (A) and low glacial (B) sites. The five different classes of boundary Reynolds number are shown (stress = 0.3622 and 0.3058 for high glacial and low glacial site, respectively).
Simulating the effect of glacier run-off decrease on macroinvertebrate assemblages. Our hydraulic data showed that a reduction in glacier run-off would shift the Re* distribution toward lower values in both sites (Figure 3A and B and Figure 4A and B). Consequently, habitats with high Re* values (Re* > 1000) might completely disappear under low flow conditions (Figure 2A and B). Our Monte-Carlo simulations further revealed that, under reduced glacial flow conditions, taxon extinction levels based on real assemblages would be much higher than those predicted for null assemblages (Figure 8A and B). This confirms that, despite overall non-significant effects of flow conditions on benthic communities, taxa were not randomly distributed among the different Re* classes and that some taxa only occurred in some type of habitat. In total, 11 taxa were only found in the high glacial site, and half of them were restricted to habitats with Re* > 900. Our simulations showed that rare taxa living in high flow habitats would be particularly sensitive to a decrease in high flows, suggesting that extinction events might occur in the early phase of glacier run-off reduction. In both sites, 13% of all taxa would disappear with a complete loss of habitats with Re* > 1000 (vs 6% predicted by the null model, Figure 8A and B). This represents 25% of all rare taxa in the high glacial site and 40% in the low glacial site (vs 11% for both sites in the null model, Figure 8C and D).

DISCUSSION

Impact of glacial flow regime on hydraulic stress. Discharge increase caused by glacial flood pulses generated high hydraulic stress (increased Re*, shear stress, and shear velocity values), a pattern commonly found in other types of streams (Lancaster and Hildrew, 1993; Rempel et al., 2000; Lancaster et al., 2006). However, high flow events in temperate streams are generally stochastic and unpredictable, while in equatorial glacial streams, they occur mostly on a daily basis making hydraulic stress variations in equatorial glacial streams quite common and predictable (see Figure 1). While our study revealed that high stream discharge translated into a general increase in the occurrence of benthic habitats with high Re*, it also showed that a few habitats with low Re* persisted during high floods. Indeed, we found a high heterogeneity in hydraulic habitats on the bottom of both studied sites (see Figure 3), in agreement with studies performed in streams of similar stream-order, either glacier-fed (Snook and Milner, 2002) or not (Lancaster and Hildrew, 1993). In particular, the presence of ‘low flow patches’ with low shear stress and velocity, regardless of discharge values, may create flow refugia of particular importance for living benthic organisms (Lancaster et al., 2006), especially during high flood events.

Impact of hydraulic conditions on macroinvertebrate assemblages. The influence of hydraulic conditions on the distribution of benthic macro-invertebrates has long
been an area of interest among stream ecologists (e.g. Robertson et al., 1995; Hart et al., 1996). Most studies have shown that both total abundance and richness of macroinvertebrate are generally negatively impacted by increasing hydraulic stress (Rempel et al., 2000; Brooks et al., 2005). However, the response of benthic organisms to hydraulic stress is often highly species/strain-specific (Lancaster and Hildrew, 1993; Snook and Milner, 2002). The lack of a significant relationship between hydraulic stress and most measured biological variables (macroinvertebrate abundance, taxa richness, and community composition) compared to other studies may be due to several reasons. First and most importantly, discharge and hydraulics stress values measured in our study were much lower than those measured in most previous works (e.g. discharge > 5 m³ s⁻¹, Quinn and Hickey, 1994; Rempel et al., 2000). Second, the high heterogeneity in hydraulic conditions in our stream may allow benthic macroinvertebrates to find refugia even at high discharges (Lancaster et al., 2006). However, we did not detect any macroinvertebrate displacement towards flow refugia as their abundance and taxa richness were similar in the different hydraulic habitats before and during flood events. Third, benthic macroinvertebrates in tropical glacier-fed streams are submitted to increased hydraulic stress on a daily basis. While we have no evidence of potential adaptations developed by benthic species in tropical glacier streams, studies from other systems experiencing daily disturbance (e.g. intertidal zones) revealed morphological and/or behavioral adaptation of organisms to minimize physical stress (Friedland and Denny, 1995).

Risk of taxa loss with glacier retreat. Benthic macroinvertebrate communities were overall slightly affected by daily glacial flood pulses in the studied sites mainly due to the fact that most abundant taxa did not show any hydraulic preference and were found in similar abundance across all Re* classes (data not shown). However, we found that several rare taxa such as Blepharicera sp. (Blephariceridae) and Tipula sp. (Tipulidae) preferentially occurred in highly stressed hydraulic habitats, perhaps because they require the special environment found there, or because these habitats act as refuges from competitive exclusion (Jacobsen et al., 2010). Under a scenario of decreasing glacier run-off due to glacial shrinkage (Baraer et al., 2012), the proportion of benthic habitats with frequently high hydraulic stress would decrease and eventually disappear as a result of lower glacier stream discharge. Based on this assumption, our Monte-Carlo simulations predicted that a significant diversity of taxa, in particular rare taxa (which explain the discrepancy between data and model), would become extinct from both glacial and semi-glacial sites. Indeed, taxa only occurring in those high Re* habitats would have to remain in lower Re* habitats. And even if they tolerate the new abiotic conditions, they might not be able to co-exist with others species, potentially more competitive (Brown et al., 2007). The common lower Re* species might replace the rarer ones that are more specialized to harsh hydraulic conditions meaning that highly adapted species would disappear (Füreder, 2012).

Our results add a new dimension to the topical and timely issue surrounding the effects of glacial retreat on benthic biodiversity (Füreder, 2012). Previous studies indicated that both local (α) and regional (γ) diversity, as well as taxon turnover among reaches (β diversity) would be modified along with the shrinkage of glaciers (Jacobsen et al., 2012). In particular, diversity reductions are predicted to occur at severe degrees of glacial recession, for example when melt water contribution ceases (Brown et al., 2007). Our findings indicate that reduction in taxon richness may also occur through more subtle changes in the frequency of high velocity flow habitats, which could materialize even at relatively moderate glacier loss levels (Baraer et al., 2012), especially during the low flow season (Malard et al., 2006). Determining whether these predictions are specific to equatorial glacial streams or could be extended to their temperate counterparts is an important and timely task for limnologists working on these rapidly vanishing systems.

ACKNOWLEDGMENTS
We thank Vincent Fugère, Gabriel Mosquera, and Ricardo Mogollón for technical support during invertebrate sampling. The funding by an Ecofondo grant no. 034-ECO8-inv1 to O.D. is greatly appreciated.

REFERENCES


Immerzeel WW, van Beek LPH, Bierkens MFP. 2010. Climate change will affect the Asian water towers. *Science* 328: 1382–1385.


**APPENDIX 1**

Box plot of Reynolds number values, Re (see Statzner, 1988 for formula details) calculated in 31 stream sites located in our studied catchment. Re was calculated using data from Jacobsen and Dangles (2012), in which details) calculated in 31 stream sites located in our studied catchment. Re was calculated using data from Jacobsen and Dangles (2012), in which