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Laboratoire Évolution, Génomes et Spéciation

Équipe Diversité, Écologie et Évolution des Insectes Tropicaux

Hydro-écologie des communautés d'invertébrés aquatiques dans les rivières glaciaires équatoriennes

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Dirigée par Olivier Dangles

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Hydroecology of invertebrate communities in equatorial glacier-fed streams

By Sophie Cauvy-Fraunié

Doctoral thesis in Ecology

Headed by Olivier Dangles

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ABSTRACT

In the face of climate change, freshwater species in glacierized catchments are confronted to modifications in glacier runoff, linked to the acceleration of glacier retreat. This thesis aims to evaluate the effect of glacial meltwater contribution to alpine streams flow on the organization of aquatic communities in a glacierized catchment in the tropical Andes (Antisana, Ecuador). At different spatial and temporal scales, we quantified glacial influence, determined its effects on aquatic macroinvertebrate communities and anticipated the possible consequences of glacier retreat on aquatic biodiversity.

We first examined at the stream reach scale, the effect of the temporal variability in hydraulic stress generated by daily glacial floods on macroinvertebrates. Then at the catchment scale, we assessed the effect of spatial and temporal variability in glacial influence on macroinvertebrates community composition. For this, we developed new quantitative indices of glacial influence based on the diurnal flow variation identified by performing wavelet analyses on water level time series. Finally, we evaluated the effect of glacial meltwater contribution to alpine streams flow on the macroinvertebrate metacommunity structure and dynamics within the entire catchment.

At the stream reach scale, macroinvertebrate communities were poorly affected by the diurnal increase in hydraulic stress caused by daily glacial floods occurring all year round in the tropics. However, although those high flow events were frequent, temporal variability in flood intensity generated temporal β-diversity. At the catchment scale, local diversity peaked at intermediate level of glacial influence. In addition, metacommunity was structured by environmental filtering and dispersal processes among which glacial influence was not only the main environmental filter but also a significant factor limiting aquatic dispersion. Thus, glacial meltwater also engendered high spatial β-diversity.

We expect that reduction in glacier runoff would diminish hydraulic stress and harshness within glacier-fed streams and thereby spatial and temporal environmental heterogeneity within the catchment. Those changes would probably reduce both environmental filtering and aquatic dispersal limitation, allowing thus more generalist species not adapted to the harshness of glacial meltwater to colonize and establish throughout the entire catchment. Therefore, we assume that glacier retreat would provoke the extinction of specialized species adapted to glacier runoff (loss of α-diversity) and to a taxonomic homogenization of the aquatic fauna within the catchment (decrease in spatial and temporal β-diversity), both resulting in an irreversible reduction in regional diversity.

Keywords: climate change, glacier retreat, glacier-fed stream, hydroecology, aquatic macroinvertebrates, freshwater ecosystem structure, tropical Andes, Antisana, Ecuador.

RESUMEN

Hidroecología de las comunidades de invertebrados en los ríos glaciares del Ecuador

Frente al cambio climático, las especies de agua dulce en las cuencas glaciares se enfrentan a modificaciones del caudal glaciar relacionado con la aceleración del retroceso glaciar. El objetivo de esta tesis es evaluar la contribución de las aguas glaciares en la organización de las comunidades de organismos acuáticos en ríos alpinos de una cuenca glaciar en los Andes tropicales (Antisana, Ecuador). Para esto, a diferentes escalas espaciales y temporales, cuantificamos la influencia glaciar, determinamos sus efectos sobre las comunidades de macroinvertebrados acuáticos y anticipamos las posibles consecuencias del retroceso glaciar sobre la biodiversidad acuática.

En una primera instancia, a escala del río examinamos el efecto de la variabilidad temporal del estrés hídrico generado por las crecidas glaciares diarias sobre los macroinvertebrados. En una segunda instancia, a escala de la cuenca, evaluamos el efecto de la variabilidad espacial y temporal de la influencia glaciar sobre la composición de las comunidades de macroinvertebrados. Para ello, desarrollamos nuevos índices cuantitativos de influencia glacial basados en la variación diurna del flujo identificado mediante la realización de análisis de ondículas de series temporales de nivel de agua. Finalmente, evaluamos el efecto de la contribución de las aguas glaciares al flujo de ríos sobre la estructura y la dinámica de la metacomunidad de macroinvertebrados dentro de toda la cuenca.

A escala del río, la comunidad de macroinvertebrados fue levemente afectada por el aumento diurno del estrés hídrico causado por las crecidas glaciares diarias a lo largo de un año. Aunque los eventos de alto flujo fueron muy frecuentes, la variabilidad temporal de la intensidad del flujo generaba β-diversidad temporal. Por otra parte, a escala de la cuenca, la diversidad local alcanzó su máximo nivel en el rango de influencia glacial intermedia. Se encontró además, que la metacomunidad estaba estructurada por diversos filtros ambientales y procesos de dispersión entre los cuales la influencia glaciar era no solamente el principal filtro ambiental, sino también limitaba la dispersión acuática. Concluimos con esto, que las aguas glaciares contribuyen con una alta β-diversidad espacial.

En base a nuestros resultados, esperamos que en un escenario futuro de calentamiento global, la reducción del caudal glaciar disminuya el estrés hídrico y la dureza dentro de los ríos glaciares así como la heterogeneidad ambiental espacial y temporal dentro de la cuenca. Esos cambios probablemente reducirían tanto el filtro ambiental y la limitación de la dispersión acuática, permitiendo a las especies más generalistas no adaptadas a la dureza de las aguas glaciares colonizar y establecerse a través de toda la cuenca. Suponemos entonces que el retroceso glaciar generará la extinción de especies especializadas adaptadas a los ríos glaciares (pérdida de α-diversidad) y una homogeneización taxonómica de la fauna acuática dentro de la cuenca (disminución de β-diversidad espacial y temporal), resultando en una reducción irreversible de la diversidad regional.

Palabras claves: cambio climático, retroceso de los glaciares, ríos glaciares, macroinvertebrados acuáticos, estructura de ecosistema de agua dulce, Andes tropicales, Antisana, Ecuador

RÉSUMÉ

Hydro-écologie des communautés d’invertébrés aquatiques dans les rivières glaciaires équatoriennes

Les écosystèmes d’eaux douces sont fortement menacés par le réchauffement climatique ainsi que par les changements environnementaux qui en découlent. En particulier, un des effets du réchauffement climatique est l’accélération de la fonte des glaciers et par conséquent la diminution voire la disparition des rivières glaciaires. Cependant, ces rivières abritent une biodiversité locale exceptionnelle composée d’espèces rares, souvent endémiques, en raison de l’hostilité du milieu glaciaire et de l’isolement de ces rivières. La biodiversité régionale des rivières de montagnes englacées est également menacée par la réduction de l’apport en eaux glaciaires dans ces réseaux hydrographiques. En effet, dans les montagnes englacées, le réseau hydrographique est composé de différents types de rivières : les rivières d’eau de source ou d’eau de pluie et les rivières provenant de la fonte des neiges et des glaciers. Chacun de ces types de rivières présente des conditions environnementales spécifiques ainsi qu’un régime hydrologique qui lui est propre. En particulier, les rivières glaciaires sont froides, turbides, présentent une conductivité électrique très faible et le lit de ces rivières est instable. Le régime glaciaire est de plus caractérisé par une forte variabilité temporelle à différentes échelles de temps (journalier, saisonnier et interannuel). En aval, ces différents types de rivières se rejoignent pour former un réseau hydrographique complexe, dans lequel chaque segment de rivières présente des conditions hydrologiques et environnementales différentes résultant de la proportion de l’apport en eau de chacun des types de rivière. Les bassins versants de montagnes englacées présentent donc une très forte hétérogénéité d’habitats environnementaux, chacun étant relié à un certain assemblage d’espèces aquatiques. C’est pourquoi la biodiversité régionale des rivières de montagnes est menacée par la fonte des glaciers car une diminution de l’apport en eaux glaciaires diminuerait l’hétérogénéité environnementale. Dans le contexte du réchauffement climatique, il est donc indispensable de caractériser l’influence des eaux glaciaires sur les communautés aquatiques afin de pouvoir prévoir l’impact du retrait des glaciers sur la biodiversité aquatiques des rivières de montagnes.

L’objectif principal de cette thèse est d’estimer l’effet de l’apport en eaux glaciaires dans les rivières des bassins versants de montagnes englacées sur les communautés de macroinvertébrés aquatiques. À différentes échelles spatiales et temporelles, nous avons quantifié l’influence glaciaire, déterminé son effet sur ces communautés de macroinvertébrés et anticipé les potentielles conséquences du retrait glaciaire sur la biodiversité des rivières de montagnes englacées. Notre étude a été réalisée dans la réserve écologique du volcan Antisana dans les Andes tropicales en Équateur, dans un bassin versant incluant des rivières

glaciaires et de rivières d'eau de source (et/ou des rivières à régime pluvial). Au total, 51 sites ont été étudiés entre 3886 et 4835 m d'altitude. Cette thèse s'articule en trois parties.

Chapitre 1 - Réponse des communautés de macroinvertébrés à la variation journalière du débit des rivières glaciaires

Généralement, les augmentations brutales de débit ont un effet néfaste sur les communautés aquatiques. En effet, les crues augmentent le stress hydrique dans le fond des rivières et, en fonction de la force du courant, peuvent arracher le substrat, les ressources en nutriments ainsi que les organismes eux-mêmes. Pendant la saison d'ablation du glacier, le débit des rivières glaciaires augmente tous les jours en réponse à la fonte journalière du glacier pendant les heures chaudes de la journée. Cependant, contrairement aux zones tempérées, l'ablation des glaciers, et par conséquent les crues glaciaires, a lieu toute l'année dans les zones tropicales en raison du manque de saisonnalité de la température. Dans ce chapitre, nous étudions, à l'échelle du segment de la rivière, l'effet de la variabilité temporelle du stress hydrique générée par les crues glaciaires journalières sur les communautés de macroinvertébrés. Nos objectifs sont de (1) quantifier la variation du stress hydrique causée par les crues glaciaires journalières, (2) déterminer l'impact de cette variation temporelle du stress hydrique sur les communautés de macroinvertébrés et (3) envisager l'éventuelle réponse de ces communautés face à un changement des conditions hydriques dû à la diminution du débit glaciaire.

Dans deux rivières glaciaires présentant des apports différents en eaux glaciaires, nous avons mesuré le débit et sur 30 sites pris au hasard la hauteur d'eau, la vitesse d'écoulement à proximité du fond de la rivière, caractérisé le substrat et échantillonné les macroinvertébrés avant et pendant deux crues glaciaires. Puis, nous avons calculé le nombre de Reynolds comme indice de turbulence. Afin d'identifier l'effet des crues sur le stress hydraulique (c.-à-d. la turbulence), nous avons analysé pour chaque événement de crue la distribution des fréquences des nombres de Reynolds ainsi que leur distribution spatiale à l'aide d'une interpolation de type Akima. Puis, en utilisant une analyse de variance, un test de Tukey, des corrélations de Spearman et une analyse de similarité, nous avons examiné l'effet des conditions hydrauliques (nombre de Reynolds et débit) sur la communauté de macroinvertébrés (c.-à-d. sur la richesse taxonomique, la densité et l'assemblage de taxons). Finalement, nous avons utilisé des simulations de Monte Carlo pour examiner l'effet qu'aurait une diminution du débit glaciaire sur les communautés de macroinvertébrés. Bien que le nombre de Reynolds augmente avec le débit, il restait faible à certains endroits de la rivière même pendant les plus fortes crues. Globalement, nous n'avons trouvé aucun effet significatif de l'augmentation du débit ni de l'augmentation associée de la turbulence sur les communautés de macroinvertébrés. Par contre, les simulations de Monte Carlo révèlent que les taxons ne sont pas distribués au hasard dans les habitats hydrauliques et que certains taxons, souvent les plus rares, sont apparus uniquement dans les habitats à plus haut niveau de turbulence.

Les macroinvertébrés aquatiques présents dans ces rivières glaciaires équatoriennes semblent peu affectés par la variation de débit journalière et par l'augmentation de la turbulence qui en découle. Ils ont probablement développé des mécanismes d'adaptation à ces crues glaciaires qui ont lieu presque tous les jours dans les rivières glaciaires équatoriennes. Par contre, les taxons rares, qui n'apparaissent que dans des zones à forte turbulence, pourraient être fortement affectés par la réduction du stress hydrique due à la diminution du débit glaciaire. En effet, ces taxons vont devoir tolérer des conditions abiotiques différentes et devront coexister avec d'autres taxons potentiellement plus compétitifs.

Chapitre 2 - Impact de la variabilité spatiotemporelle de l'influence glaciaire sur les assemblages de macroinvertébrés à l'échelle du bassin versant

Les bassins versants des montagnes englacées présentent un fort gradient environnemental allant des conditions rudes dans les rivières glaciaires proche du front glaciaire à des conditions plus clémentes dans les eaux de source. Ce gradient est fortement relié à l'influence glaciaire, maximale à proximité du glacier et qui diminue en s'éloignant du glacier, particulièrement après une confluence avec un autre type de rivière. Cette influence glaciaire varie aussi dans le temps en raison de la variabilité temporelle du débit glaciaire liée aux cycles de fonte du glacier. Dans ce chapitre, nous étudions l'effet de la variabilité spatiale et temporelle de l'influence glaciaire sur la composition des communautés de macroinvertébrés. Ce chapitre s'articule en 3 parties. Dans une première partie nous avons développé une nouvelle méthode afin de quantifier l'influence glaciaire. Dans la deuxième partie, nous étudions l'effet de la variabilité spatiale de l'influence glaciaire sur les communautés de macroinvertébrés à l'échelle du bassin versant. Dans la troisième partie, nous étudions l'effet de la variabilité temporelle de l'influence glaciaire sur les communautés de macroinvertébrés.

Plusieurs indices glaciaires existent déjà mais la plupart d'entre eux ne permettent pas d'identifier la variabilité temporelle de l'influence glaciaire. Dans cette première partie, nous avons développé une nouvelle méthode de quantification de l'influence glaciaire basée sur la variation journalière du débit induite par le cycle journalier dominant de la fonte du glacier pendant la saison d'ablation du glacier. Pour atteindre cet objectif, nous avons mesuré la hauteur d'eau à un intervalle de temps de 30 minutes pendant 10 mois sur 15 sites présentant une combinaison distincte d'apports en eau des différents types de rivières. Nous avons appliqué des analyses en ondelettes aux séries temporelles de hauteur d'eau. Le spectre d'ondelettes donne la magnitude de la variance de la hauteur d'eau pour chaque période et à chaque date et permet ainsi de déterminer à quelles périodes ont lieu les variations de hauteurs d'eau. À partir du spectre d'ondelettes, nous avons isolé la variation de hauteur d'eau à 24h qui correspond à la crue glaciaire journalière (spectre d'ondelette à 24h). Puis, nous avons testé sa significativité en comparant ce spectre d'ondelette à 24h avec un spectre de bruit rouge. Ce spectre d'ondelettes à 24h permet de visualiser la fluctuation dans le temps de la variation journalière de hauteur d'eau. À partir de ce spectre d'ondelettes à 24h, nous avons déterminé trois indices glaciaires: l'intensité (l'aire entre la courbe du spectre d'ondelette à 24h et la courbe de significativité à 24h), la fréquence (nombre de jours avec une variation journalière significative divisé par le nombre de jour total) et le regroupement temporel (indice de regroupement des jours avec une crue significative) de la variation journalière de la hauteur d'eau. En parallèle, nous avons calculé pour chaque site le pourcentage de la superficie du glacier par rapport à la superficie du bassin versant (un des indices glaciaires le plus utilisé) et nous avons comparé les trois nouveaux indices glaciaires avec ce pourcentage. La variation journalière de hauteur d'eau à 24h était significative tout au long de l'année. Ceci est dû au fait que la fonte du glacier a lieu toute l'année en Équateur à cause du manque de saisonnalité. L'intensité de la variation journalière était significativement corrélée avec le pourcentage de la superficie du glacier par rapport à la superficie du bassin versant, c.-à-d. l'intensité diminuait vers l'aval, et cette diminution était plus prononcée après une confluence avec une rivière non glaciaire. Ceci confirme que cet indice peut être utilisé comme indice glaciaire. Par ailleurs, un site supposément d'eau de source présentait une forte intensité et fréquence de variation journalière de hauteur d'eau. Par conséquent, cette nouvelle méthode permet également de détecter des résurgences d'eau glaciaire. Ainsi ces nouveaux indices glaciaires permettent non seulement de quantifier l'influence glaciaire mais aussi de caractériser sa fluctuation dans le temps (fréquence, agrégation temporelle).

Pour l'étude spatiale, nous avons utilisé les mêmes 15 sites que dans la section précédente. Sur ces 15 sites, nous avons mesuré les hauteurs d'eau à un intervalle de temps de 30 minutes pendant 10 mois et échantillonné les macroinvertébrés (une date) pour 15 sites. Nous avons ensuite calculé les 3 indices glaciaires: intensité, fréquence et regroupement temporel de la variation de hauteur d'eau pour cette période de 10 mois pour les 15 sites. Ensuite, en utilisant des modèles de régression d'ordre 2 et des modèles additifs généralisés (GAM), nous avons déterminé l'effet de l'intensité, de la fréquence et du regroupement temporel des variations journalières du flux de l'eau sur la densité, la richesse taxonomique, et la dominance des macroinvertébrés. En règle générale, nous n'avons pas trouvé d'effet significatif de la fréquence et du regroupement temporel sur la structure des communautés de macroinvertébrés. Par contre, la richesse taxonomique culminait pour des valeurs intermédiaires d'intensité. De plus, certains taxons n'apparaissent qu'à des niveaux intermédiaires d'intensité. Nos résultats montrent donc qu'à l'échelle du bassin versant les eaux glaciaires non seulement génèrent de la diversité locale (α) mais aussi de la diversité béta spatiale, et par conséquent augmentent la diversité régionale (γ).

Pour l’étude temporelle, nous avons sélectionné 3 sites, présentant une combinaison distincte d’apports en eau des différents types de rivières. Dans ces 3 sites, nous avons mesuré les hauteurs d’eau à un intervalle de temps de 30 minutes pendant 29 mois et nous avons échantillonné les macroinvertébrés à 14 dates différentes. Nous avons calculé les trois mêmes indices glaciaires: intensité, fréquence et regroupement temporel de la variation journalière du flux d’eau pour des séries temporelles de 2 à 50 jours avant chaque échantillonnage. Nous avons calculé la dissimilitude entre les communautés échantillonnées aux différentes dates en utilisant les indices de Sørensen et Bray-Curtis. Puis, en utilisant des modèles de régression linéaire, nous avons examiné la relation entre la différence des indices glaciaire et la dissimilitude entre les communautés entre les différentes dates. La fréquence ainsi que le regroupement temporel de la variation journalière du flux d’eau n’avaient en général pas d’effet significatif sur l’assemblage des macroinvertébrés. Par contre, la dissimilitude entre les communautés augmente significativement avec la différence en intensité. Cette dissimilitude était liée à une baisse de la densité des taxons dominants ainsi qu’au remplacement de certains taxons. Bien que ces crues glaciaires journalières soient très fréquentes et prédictibles, la variabilité temporelle de l’intensité de la crue glaciaire générait une variabilité temporelle de la composition des communautés de macroinvertébrés. Nous expliquons le turnover des taxons (le remplacement de certains taxons) par un déplacement des taxons le long du gradient d’influence glaciaire : en aval lors de fortes crues glaciaires, et en amont pendant des périodes avec peu ou de faibles de crues glaciaires.

Les résultats de cette étude spatiale et cette étude temporelle indiquent que l’influence glaciaire engendre non seulement une diversité locale spécifique mais aussi que la variabilité de l’influence glaciaire, aussi bien spatiale que temporelle, engendre à l’échelle du bassin versant de la diversité béta (spatiale et temporelle). C’est pourquoi, dans le contexte actuel du réchauffement climatique, nous nous attendons à ce que la diminution de l’apport en eaux glaciaires dans les bassins versants de montagnes englacées due au retrait glaciaire réduise la diversité béta spatiale et temporelle.

Chapitre 3 – Influence des eaux glaciaires sur la structure et la dynamique de la métacommunauté de macroinvertébrés dans un réseau hydrographique andin

Dans les réseaux hydrographiques, la distribution spatiale des organismes aquatiques est en partie structurée par des processus locaux comme les conditions environnementales et par des processus régionaux comme la dispersion des organismes entre les communautés locales. Dans ce chapitre, nous étudions la structure de la métacommunauté de macroinvertébrés dans un bassin versant de montagne englacée. Nos objectifs étaient d’identifier les mécanismes expliquant la distribution spatiale des macroinvertébrés ainsi que de déterminer la contribution des eaux glaciaires à la variabilité des communautés locales.

Pour cela, sur 51 sites présentant une combinaison distincte d’apports en eau des différents types de rivières, nous avons mesuré les conditions environnementales (température, conductivité, turbidité, stabilité du lit de la rivière, largeur, profondeur moyenne, pente, pH) et échantillonnés les macroinvertébrés, les détritus benthique, et les algues. Nous avons calculé l’influence glaciaire en utilisant un indice d’influence glaciaire, nommé «glacialité» basé sur la température, la conductivité, la turbidité et la stabilité du lit de la rivière. Puis nous avons calculé la distance géographique, le dénivelé ainsi que la différence de « glacialité » entre chaque site, soit en passant par la plus courte distance (euclidienne) soit en passant par les cours d’eau. Nous avons ensuite construit des variables explicatives environnementales dont la variable « glacialité », la variable ressource alimentaire et la variable forme de la rivière. Nous avons aussi construit des variables explicatives spatiales (à partir de vecteurs propres) à partir des différents types de distances entre les sites. Puis, en utilisant une analyse partielle de redondance, nous avons calculé quelle était la part de la variation des communautés entre les sites expliquée par chacune des variables explicatives: environnementales et spatiales. Nos résultats montrent que les variables spatiales et environnementales expliquaient une part significative de la variation des communautés entre les sites. Parmi les variables environnementales, l’influence glaciaire apparaît comme la variable qui explique le mieux la variation des communautés entre les sites. La distance géographique, le dénivelé et la différence de « glacialité » entre les sites ont aussi un effet significatif sur la variation de communauté entre les sites.

Ces résultats indiquent que la distribution spatiale des macroinvertébrés est en partie dictée par des filtres environnementaux mais aussi par la dispersion des macroinvertébrés. L’influence glaciaire joue un rôle majeur dans la structure de la métacommunauté aquatique des bassins versants montagneux dans les Andes équatoriennes. En effet, elle est le filtre environnemental le plus important. De plus, la différence de « glacialité » entre deux sites limite la dispersion aquatique des macroinvertébrés non adaptés aux eaux glaciaires. Ainsi en créant une forte hétérogénéité environnementale les eaux glaciaires induisent une forte diversité béta spatiale limitant ainsi la colonisation des espèces généralistes dans toutes les rivières du bassin versant. Nous supposons donc que la diminution des apports en eaux glaciaires entraînera une diminution du filtre environnemental ainsi que de la limitation de la dispersion. Ceci entraînera une homogénéisation taxonomique à l’échelle du bassin versant (diminution de la diversité spatial béta) et par conséquent une réduction de la diversité régionale.

Les résultats de cette thèse montrent qu'à l'échelle de la rivière les communautés de macroinvertébrés aquatiques ne sont pas fortement affectées par les crues glaciaires journalières. Les macroinvertébrés semblent avoir développé une certaine adaptation à l'augmentation journalière du stress hydrique causée par les crues glaciaires qui ont lieu presque tous les jours dans les rivières glaciaires équatoriennes. Néanmoins, bien que ces crues soient très fréquentes et fortement prédictibles, la variabilité de l'intensité de ces crues génère une variabilité temporelle de la composition des communautés de macroinvertébrés (c.-à-d. induit une diversité temporelle béta). Nos résultats montrent également que l'apport en eau glaciaire dans le réseau hydrographique induit de la diversité locale (α) à un niveau intermédiaire d'influence glaciaire. De plus, les rivières glaciaires génèrent non seulement une forte hétérogénéité environnementale spatiotemporelle à l'échelle du bassin versant mais limitent également la dispersion aquatique des macroinvertébrés non adaptés aux conditions rudes des eaux glaciaires. Elles empêchent ainsi des espèces généralistes de coloniser toutes les rivières du bassin versant. Par conséquent, les eaux glaciaires engendrent également une forte diversité spatiale béta.

La réduction du débit glaciaire va théoriquement engendrer une diminution du stress hydrique et environnemental des rivières glaciaires ainsi que de l'hétérogénéité environnementale spatiotemporelle à l'échelle du bassin versant. Ces changements vont probablement diminuer le filtre environnemental ainsi que la limitation de la dispersion, permettant ainsi aux espèces généralistes de coloniser et de s'établir dans tout le réseau hydrographique. Nous prévoyons donc que le retrait glaciaire va mener à l'extinction d'espèces spécialistes qui devront survivre à des changements de conditions environnementales et à la migration de nouvelles espèces potentiellement plus compétitives. De plus, nous anticipons une homogénéisation taxonomique de la faune aquatique dans le réseau hydrographique (diminution de la diversité béta spatiale et temporelle). Ceci mènera certainement à une réduction irréversible de la diversité régionale.

Mots clés : réchauffement climatique, retrait glaciaire, rivière glaciaire, hydro-écologie, macroinvertébrés aquatiques, structure d'écosystème d'eau douce, Andes tropicales, Antisana, Équateur.

FOREWORD

LIST OF PAPERS

1. Cauvy-Fraunié, S., P. Andino, R. Espinosa, R. Calvez, F. Anthelme, D. Jacobsen, and O. Dangles. 2014. Glacial flood pulse effects on benthic fauna in equatorial high-Andean streams. *Hydrological Processes* **28**:3008-3017.

2. Cauvy-Fraunié, S., T. Condom, A. Rabatel, M. Villacis, D. Jacobsen, and O. Dangles. 2013. Technical Note: Glacial influence in tropical mountain hydrosystems evidenced by the diurnal cycle in water levels. *Hydrology and Earth System Sciences* **17**:4803-4816.

3. Cauvy-Fraunié, S., R. Espinosa, P. Andino, O. Dangles, and D. Jacobsen. 2014. Relationships between stream macroinvertebrate communities and new flood-based indices of glacial influence. *Freshwater Biology* **59**:1916-1925.

4. Cauvy-Fraunié, S., R. Espinosa, P. Andino, D. Jacobsen, and O. Dangles. Temporal scaling of flow disturbance effects on benthic fauna: insights from equatorial glacier-fed streams. *To submit to Limnology and Oceanography.*

5. Cauvy-Fraunié, S., R. Espinosa, P. Andino, D. Jacobsen, and O. Dangles. Glacier influence on invertebrate metacommunity structure and dynamics in an Andean stream network. *To submit to Global Change Biology.*

6. Jacobsen, D., P. Andino, R. Calvez, S. Cauvy-Fraunié, R. Espinosa, and O. Dangles. 2014. Temporal variability in discharge and benthic macroinvertebrate assemblages in a tropical glacier-fed stream. *Freshwater Science* **33**:32-45.

7. Jacobsen, D., S. Cauvy-Fraunie, P. Andino, R. Espinosa, D. Cueva, and O. Dangles. 2014. Runoff and the longitudinal distribution of macroinvertebrates in a glacier-fed stream: implications for the effects of global warming. *Freshwater Biology* **59**:2038-2050.

8. Anthelme F., S. Cauvy-Fraunié, B. Francou, B. Cáceres, and O. Dangles. Plant community traits and spatial organization along a 2-13 year chronosequence of a rapidly retreating glacier in the tropical Andes. *To submit to Global Change Biology.*

CONFERENCES:

1. European Science Foundation Exploratory Workshop GLAC-HYDRECO-NET: Glacier-Fed Rivers, Hydroecology and Climate Change; Current Knowledge and Future Network of Monitoring Sites, convened by Alexander Milner (University of Birmingham, UK), Dean Jacobsen (University of Copenhagen, Denmark) and David Hannah (University of Birmingham, UK), Birmingham, UK 2013.
Oral presentation: Diurnal cycle amplitude as a quantitative measure of glacial influence in tropical mountain hydrosystems

2. INTECOL, International Congresses of Ecology London, UK 2013.
Oral presentation: Glacial flood effects on macroinvertebrate communities in tropical mountain streams

3. SEFS, Symposium of European Freshwater Sciences, Münster, Germany 2013.
Poster: Using wavelet analyses on water level time series to detect glacial influence in mountain hydrosystems

ADDITIONAL INFORMATION

This thesis was mainly conducted in South America at the *Pontificia Universidad Católica del Ecuador* and the *French Institute for Development* in Quito (Ecuador) and at the *Universidad Mayor San Andrés* and the *French Institute for Development* in La Paz (Bolivia) but also at the *Laboratoire Évolution, Génomes et Spéciation, Université Paris-Sud 11* in Gif sur Yvette (France).

All field work was performed at the Antisana in Ecuador

During this thesis, I co-supervised an Ecuadorian student, Daniela Cueva, from the *Pontificia Universidad Católica del Ecuador* for her *Tesis de Licenciatura* (Ecuador) and a Bolivian student, Antonio Daza Kucharsky, from the *Universidad Mayor San Andrés* for his *Tesis de Licenciatura* (Bolivie).

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INTRODUCTION

1. Effect of climate change on mountain glaciers

1.1. General background on glaciers

Glaciers and ice sheets cover about 10% of the land surface area of the Earth (0.5% of glaciers, 9.5% of ice sheets; Intergovernmental Panel on Climate Change, IPCC, 2013), corresponding to 15 million km^2 (Anesio and Laybourn-Parry 2012). Glaciers are distributed worldwide, mostly at high latitudes but also in mountainous areas of lower latitudes (Fig. 1; Milner et al. 2009). Among mountain glaciers, some are located in temperate zones (e.g., European Alpes, Himalayas, American Rockies) and around 5% in the tropical zone (South America, Africa, and New Guinea; Francou et al. 2000). Tropical glaciers are exclusively present at high altitude, i.e. above 4500 m a.s.l. (Francou et al. 2000), and represent around 0.15% of the global ice cover (Vuille et al. 2008). More than 99% of tropical glaciers are located in the tropical Andes (Kaser 1999), in Peru (71%), Bolivia (20%), Ecuador (4%) and Colombia-Venezuela (4%), corresponding to around 1920 km^2 in the early 2000s (Rabatel et al. 2013).

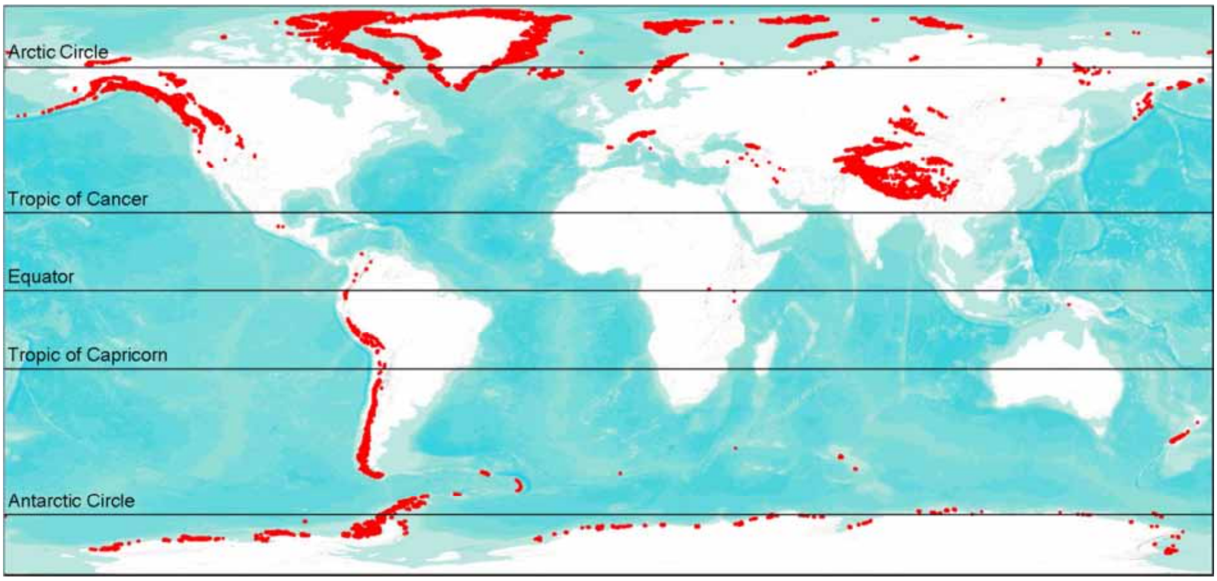


Figure 1: Worldwide distribution of glaciers. Glacier outlines were taken from the Randolph Glacier Inventory (http://glims.org/RGI/). The map was made using ArcGis (10.0)

Glaciers occur where climate conditions (i.e. precipitation and temperature) and topographic characteristics allow snow to accumulate over several years and to gradually transform into ice (Benn and Evans 2014). Non-polar glaciers are characterized by two zones: the accumulation zone, above the Equilibrium Line Altitude (ELA), where annual gain of ice exceeds loss; and the ablation zone, below the ELA, where annual loss of ice is higher than gain (Fig. 2; Cuffey and Paterson 2010, Anesio and Laybourn-Parry 2012). Solid precipitations accumulate in the accumulation zone and convert into ice more or less rapidly depending on the climatic region and especially on the air temperature. Transformation process of snow to ice begins when the last snow layer is overlaid and compressed by a new snowfall; it passes by an intermediate stage called *firn*. The weight of ice and snow accumulation leads to a downwards flows of the glacier, especially on sloping bedrock. This ice flow generates deformation of the bedrock at the base of the glacier, formation of crevasses at the surface, and displacement of the substrate on the side and at the extremity of the glacier tongue (moraine, Fig. 2). In the ablation zone, ice is removed by sublimation and melting. The sum of all accumulation and ablation processes determines the mass balance of a glacier, which permits to identify whether a glacier grows (positive mass balance) or shrinks (negative mass balance; Cuffey and Paterson 2010).

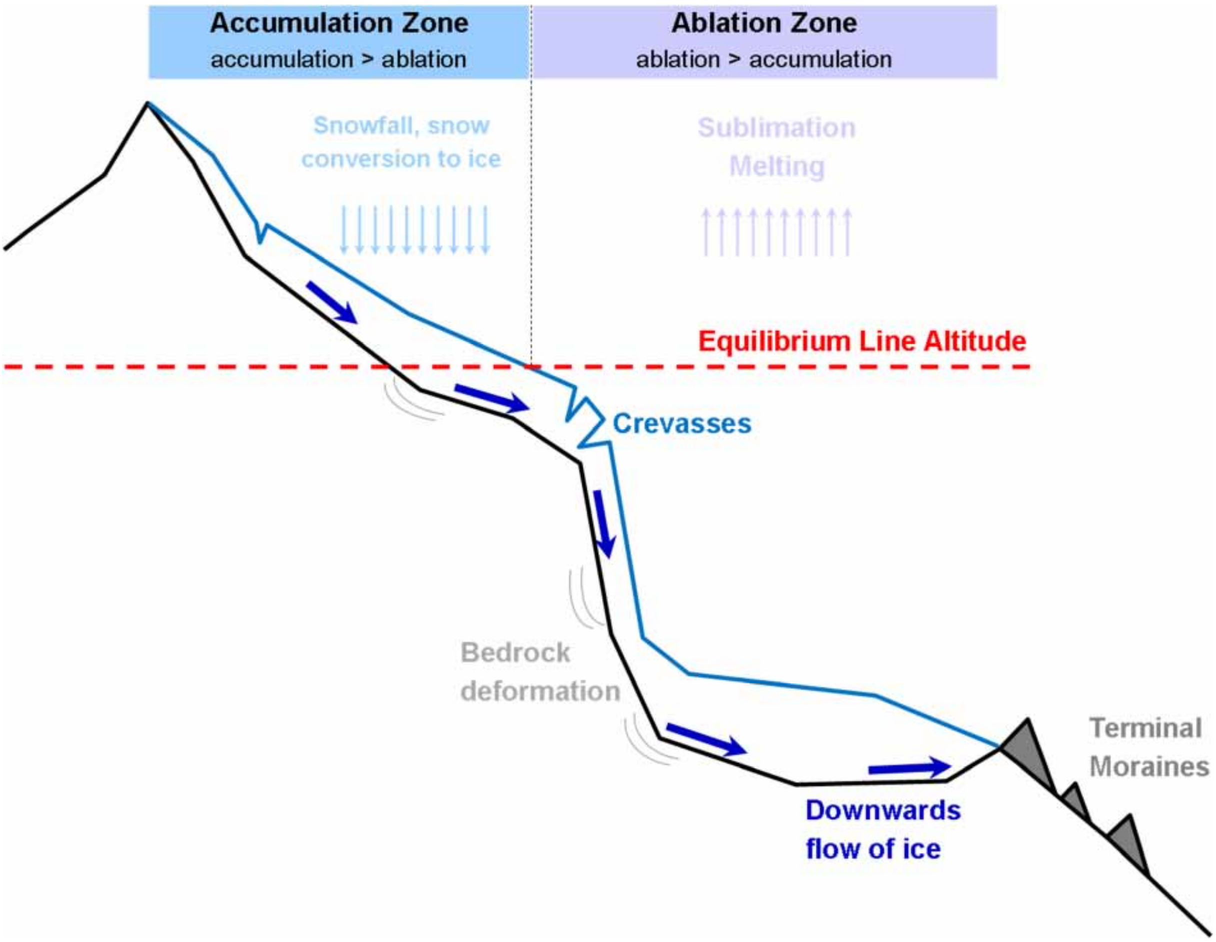


Figure 2: Schematic illustration of the different zones in a glacier. In the accumulation zone, above the Equilibrium Line Altitude, annual accumulation exceeds ablation. Solid precipitations accumulate in this zone and convert into ice. In the ablation zone, below the Equilibrium Line Altitude, annual ablation exceeds accumulation. Most ice ablation (either sublimation or melting) occurs in this zone. Glacier flows downward (blue arrows), engendering deformation and erosion of the bedrock at the base of the glacier (grey arcs), and the formation of crevasses at the surface and moraines at the extremity of the glacier tongue.

Water sources in glaciers are rain and melt from the surface, along the bed and within the ice. Surface melt provides by far the largest water source for many glaciers, but mostly occurs in the ablation zone. In the upper parts of the accumulation zone, surface meltwater mainly originate from snow and *firn*. Melt along the bedrock is caused by frictional heat of the ice flow and eventually by geothermal activity (e.g. warm-based and polythermal glaciers; Anesio and Laybourn-Parry 2012). During the ablation season, meltwater is either trapped in depression at the surface of the glacier (e.g., ponds, supraglacial lake) and inside the glacier (e.g., in cavities, fractures, crevasses), or flows down through supraglacial (e.g., surface streams), englacial (e.g., crevasses, moulins, veins) and subglacial passages (e.g. tunnels) until the glacier terminus where larger streams are formed (Fig. 3; Fountain and Walder 1998, Cuffey and Paterson 2010). Most drainage occurs along the interface between the ice and its substrate. Note that some subglacial water might also escape at the base of the glacier through fractured or porous layers and emerges in seeps and springs in the forelands of the glacier. Water discharge emerging from the glacier has a marked diurnal variation superimposed on a base flow. Base flow generally consists of meltwater from snow and *firn*, water that travels slowly through the glacier, and water released from temporary storage. Contrastingly, daily flow fluctuation is caused by the daily ice melting in the ablation zone. In temperate zones in winter, channels and cavities are mostly closed by frost, isolating water.

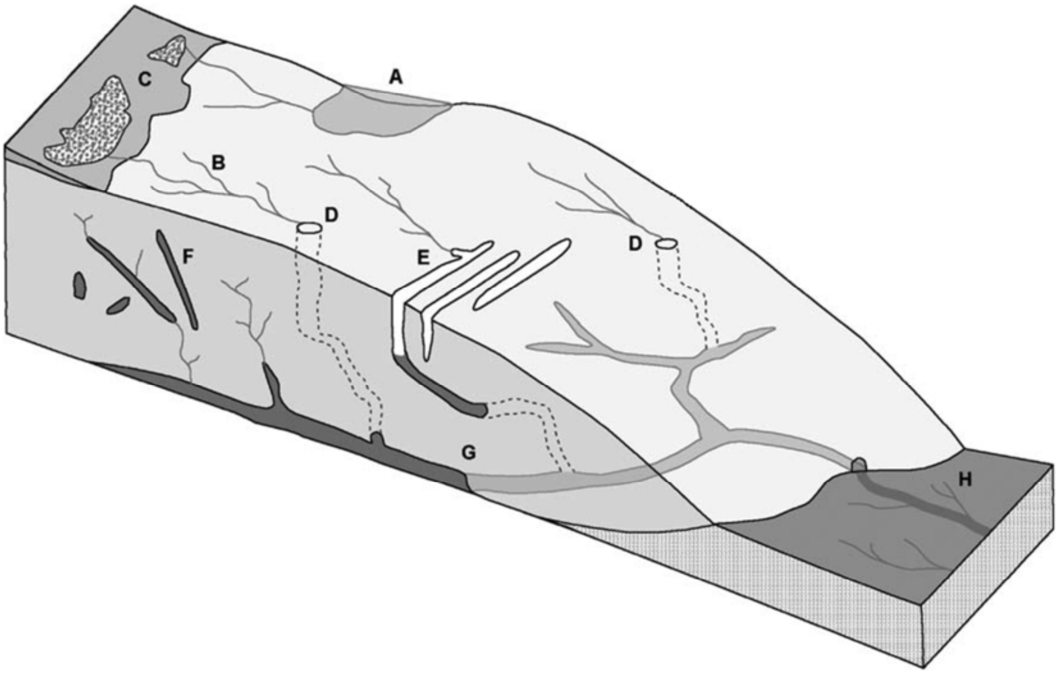


Figure 3: Some elements of the glacier water system. A: Supraglacial lake. B: Surface streams. C: Swamp zones near the edge of the firn. D: Moulins, draining into subglacial tunnels. E: Crevasses receiving water. F: Water-filled fractures. G: Subglacial tunnels, which coalesce and emerge at the front. H: Runoff in the glacier foreland, originating from tunnels and also from upwelling groundwater. Figure taken from Cuffey and Paterson (2010).

1.2. Glacier retreat

Human activities affect Earth’s energy budget by changing the emissions and resulting atmospheric concentrations of radiatively important gases and aerosols and by changing land surface properties. These modifications have been shown to be a primary driver of the ongoing climate change (Matthews and Weaver 2010, Seinfeld and Pandis 2012). Main evidence of climate change is the increase in global mean surface air temperature by 1° C over the last 100 years (trend was estimated to be 0.101 ± 0.017° C per decade between 1901 and 2012 in Rohde et al. 2013, IPCC, 2013), with an acceleration since 1979 (trend estimated to be 0.254 ± 0.049° C per decade between 1979 and 2012). However, climate change also leads to change in atmospheric water vapor, precipitation pattern, extreme events, cryosphere extent, and sea level among others (Trenberth 2011, Doney et al. 2012). Climate is expected to continue to change in the future (IPCC, 2013).

In all mountain regions, glacier volume has decreased considerably over the past 150 years (Lemke et al. 2007, Leclercq et al. 2014); i.e. since the maximum extent of the Little Ice Age (LIA, an interval during the last millennium characterized by a number of extensive expansions of mountain glaciers, dated 15th - 19th century in the Northern Hemisphere; IPCC, 2013). Over that time, it is estimated that more than 600 small glaciers have disappeared worldwide (IPCC, 2013). With some local exceptions, glacier shrinkage (area and volume reduction) was globally widespread since the 1940s and has turned particularly strong since the 1980s (IPCC, 2013). Glaciers change in size in response to changes in climate (e.g., temperature, precipitation) can be delayed by decades in relation to climate change pattern modifications (Cuffey and Paterson 2010, Adhikari and Marshall 2012). Thus, most glaciers are currently larger than they would be if they were in balance with current climate (Paul and Haeberli 2008). As the time required for adjustment increases with glacier size, small mountain glaciers usually respond faster than larger ones (Bahr et al. 1998). Air temperature increase engenders an upwards shifts of the ELA and thus a reduction of the accumulation zone, while change in precipitation regime (quantity and seasonality) affect accumulation rate but also the ELA shifts. Glaciers disappear when the ELA raise permanently the glacier's highest point (Rabatel et al. 2013). However, the rate of retreat varies strongly according to the climatic region, local climatic conditions (Jomelli et al. 2009, Loibl et al. 2014), glacier topography and geomorphology (i.e. size, slope, orientation, elevation range, area, altitude distribution), and the presence of debris cover, or dust (Paul and Haeberli 2008, Oerlemans et al. 2009, Scherler et al. 2011, Kulkarni 2013). While most glaciers have been in retreat over the last decades, some individual glaciers have advanced in a few regions (e.g., on the coasts of New Zealand, Norway and Southern Patagonia, Chile, or in the Karakoram Range in Asia; IPCC, 2013). In general, these advances are the result of special topographic and/or local climate (e.g. increased precipitation; Scherler et al. 2011).

Glacier retreat is calculated by measuring the length and area change or the volume and mass change (see Hubbard and Glasser 2005 for details on the methods). According to the IPPC, 2013, glacier terminus of mid-latitude mountain glaciers decreased from 5 to 20 m yr^{-1} for the last 120 years and mass change rates ranged from - 200 ± 100 kg m^{-2} yr^{-1} (in high mountain Asia) to -1060 ± 170 kg m^{-2} yr^{-1} (Central Europe) for the period 2003-2009 (Fig. 4). As most mountain glaciers worldwide, tropical glaciers are shrinking since the LIA maximum extent (Thomson et al. 2012, Rabatel et al. 2013). Note, however, that the date of the LIA differs among regions. In the tropical Andes, glaciers reached their maximal extent during the second half of the 17th century and started to retreat in the early 18th century (i.e. before mountain glaciers in temperate zones; Rabatel et al. 2008). In addition, tropical glaciers seem particularly sensitive to climate change (Kaser and Osmaston 2002, Vuille et al. 2008) as they present a more negative mass balances than glaciers monitored worldwide (Rabatel et al. 2013). According to the IPPC, 2013, tropical glacier mass change rate was about - 1080 ± 360 kg m^{-2} yr^{-1} for the period 2003-2009 (Fig. 4). In fact, climate in the tropical zone is characterized by relatively homogeneous temperature conditions throughout the year, leading to glacier ablation all year round and resulting in a short-time response of the position of the glacier terminus to changes in climate. In other words, as ice melt occurs all year round, changes in temperature and precipitation have immediate impacts on the glacier mass balance (Favier et al. 2004, Francou et al. 2004). In the tropical Andes, the rate of glacier retreat increased since the late 1970s ranged from - 200 kg m^{-2} yr^{-1} over the 1964-1975 period to -760 kg m^{-2} yr^{-1} over the 1976-2010 period. Over the last 40 years, magnitude of glacier mass loss is about - 600 kg m^{-2} yr^{-1} for glacier with a maximum altitude above 5400 m a.s.l, and about - 1200 kg m^{-2} yr^{-1} for glacier with a maximum altitude above 5400m a.s.l. (i.e. with smaller accumulation zone; Vuille et al. 2008, Rabatel et al. 2013).

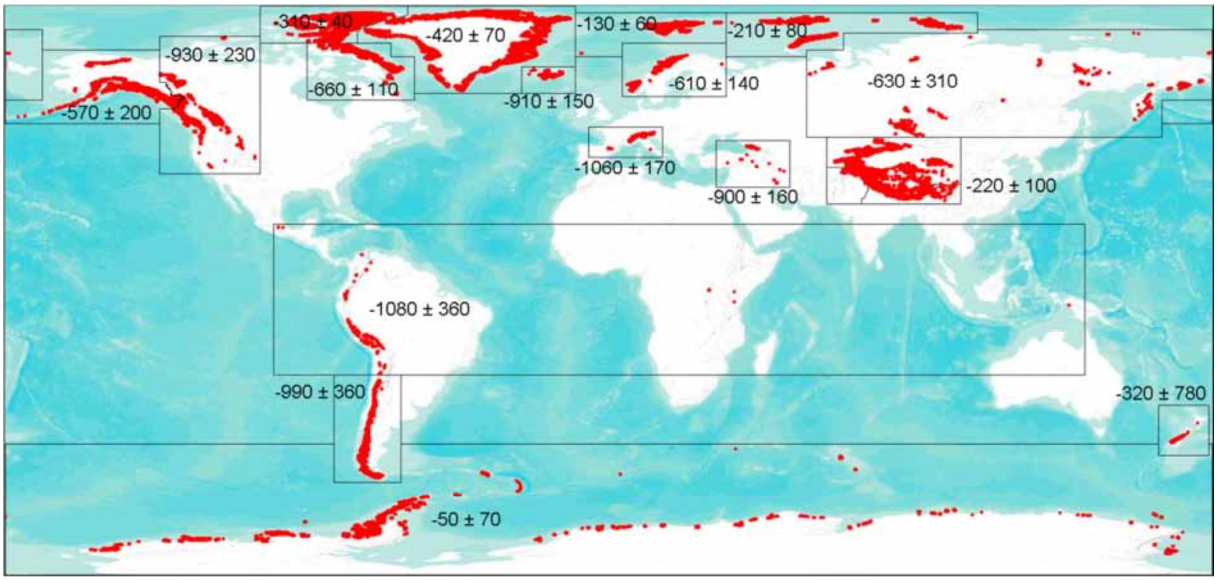


Figure 4: Regional glacier mass change rates in kg m^{-2} yr^{-1} for the period 2003-2009. Mean mass changes with the 95% confidence intervals are available for each Randolph Glacier Inventory region (see Gardner et al. 2013). Glacier outlines were taken from the Randolph Glacier Inventory (http://glims.org/RGI/). The map was made using ArcGis (10.0).

1.3. Glacier runoff alteration

Although mountain glaciers represent less than 0.5% of the total volume of ice, they are critical in supplying freshwater to alpine ecosystems and populations inhabiting the valleys downstream (Casassa et al. 2009). Mountain glaciers act as natural reservoirs storing water in solid form and releasing it as meltwater during the ablation season (Cuffey and Paterson 2010). They contribute significantly to alpine stream flow and water resources across the globe (Fleming and Clarke 2005, Huss 2011), especially during summer dry seasons when water from other sources is in short supply (Barnett et al. 2005, Kaser et al. 2010). Thus, in some regions, such as in the Himalayas and in the Andes, glacial runoff is an essential element of water budget, assuring year-round flows for agriculture, drinking water, power generation, and ecosystem integrity (Bradley et al. 2006, Casassa et al. 2009, Immerzeel et al. 2010).

However, the ongoing climate change is accelerating the shrinking of mountain glaciers, resulting in an alteration of glacier runoff (Stahl et al. 2008, Huss 2011). At the early stages of glacier retreat, the reduction in ice volume would yield a significant increase in annual and dry-season glacial runoff (Baraer et al. 2012). However, this increase is limited in time as the amount of frozen water stored in the glaciers decreases (Mark et al. 2005). Thus, after a critical threshold (Baisheng et al. 2003), annual glacial runoff should decrease until the complete disappearance of the glacier (Fig. 5; Braun et al. 2000, Huss et al. 2008). Glacier runoff stage as well as the rate of glacier runoff increase and decrease depends on glacier size and elevation, and on the rate of glacier retreat (Casassa et al. 2009, Baraer et al. 2012). In a recent study, Casassa et al. (2009) found that the critical stage associated with decrease in glacier runoff has already been attained in southern and central British Columbia in Canada, and in low elevation/low glacierization basins in the Swiss Alps and in the central Andes of Chile. In contrast, significant runoff increases were reported in north-western British

Columbia and Yukon in Canada, in highly glacierized basins in the Swiss and Austrian Alps, the Tianshan Mountains and Tibet in central Asia and in the tropical Andes of Peru (Casassa et al. 2009).

Hence, glacier retreat in mountainous catchment will affect both annual glacier runoff and annual alpine streams flow (Rees and Collins 2006, Huss et al. 2008).Therefore, under the ongoing warming, decrease in water storage capacity of glaciers caused by accelerated shrinkage may have major consequences on downstream freshwater supply and thus on water quality and security for both human populations, and freshwater biodiversity (Sorg et al. 2012).

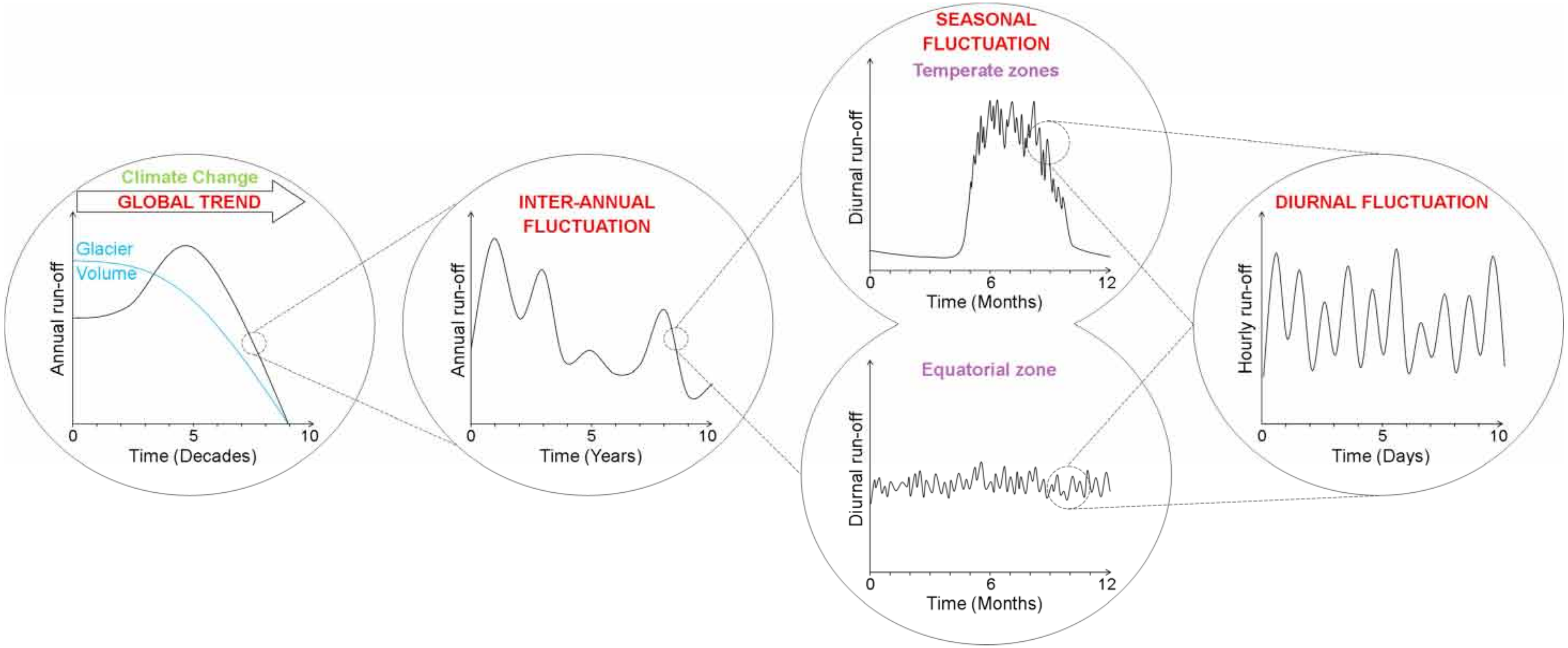


Figure 5: Illustration of the temporal variability in glacier runoff at different temporal scale. At a decadal time scale, reduction in glacier volume (caused by global climate change) induces first an increase in annual glacial runoff followed by a decrease until the complete disappearance of the glacier. At the inter-annual time scale annual glacier runoff exhibits fluctuation due to the variability in regional or local climatic conditions (e.g. ENSO phenomenon). At the seasonal time scale, glacier runoff strongly varies in temperate zones due to the alternation of precipitation storage in winter and meltwater release in summer, while glacier runoff does not display seasonal pattern in the equatorial zone. During the ablation season of the glacier, glacier runoff exhibits high flow variation at the diurnal time scale.

2. Hydrosystems in glacierized catchment

2.1. Glacier-fed streams

2.1.1. Harshness and temporal variability in environmental conditions

Glacier-fed streams (kryal streams) emerging from the glacier snout are characterized by low water temperature (< 4℃), low channel stability, high turbidity (i.e. high amount of suspended sediments, > 30 NTU), and low electrical conductivity (< 10 μS cm^{-1}; Milner and Petts 1994, Ward 1994). At the glacier snout, channel instability is caused by the downwards ice flow deforming the substrate on the glacier foreland and potentially moving stream channels (Fig. 2). Further downstream, high glacial flow events (see below) scour and transport the bed load, reducing thus channel stability (Slemmons et al. 2013). The high amount of suspended sediments, called rock flour or glacial flour, results from the bedrock erosion by the downwards ice flow evacuated by subglacial water flow (Fig. 2 and 6; Hallet et al. 1996, Clarke 2005). Generally, electrical conductivity of alpine glacier-fed streams is low as the ionic concentration of rainwater is generally very dilute (Berner and Berner 1987). However, chemical weathering of the bedrock is likely to occur when meltwater flows at the ice-rock interface (i.e. in the subglacial tunnels), increasing electrical conductivity according to the duration of water-rock interaction (Brown 2002, Dzikowski and Jobard 2012, Singh et al. 2012). Moreover, meltwater also acquires solute from the comminuted sediment, (i.e. rock flour, Tranter et al. 2002). Thus, meltwater chemical composition strongly depends on the underlying bedrock (Fig. 6; Nelson et al. 2011). Atmosphere also provides aerosol particles (e.g., ammonium, calcium, hydrogen ion, nitrate, sulfate, soot, organic components, insoluble minerals, trace metals, sea salts) and gases (e.g., hydrochloric acid, nitric acid, hydrogen peroxide) through precipitation and dry deposition that are accumulated in the ice and released in meltwater (Schwikowski and Eichler 2010). These chemicals may therefore also influence meltwater chemical composition (Steingruber and Colombo 2010, Zobrist 2010).

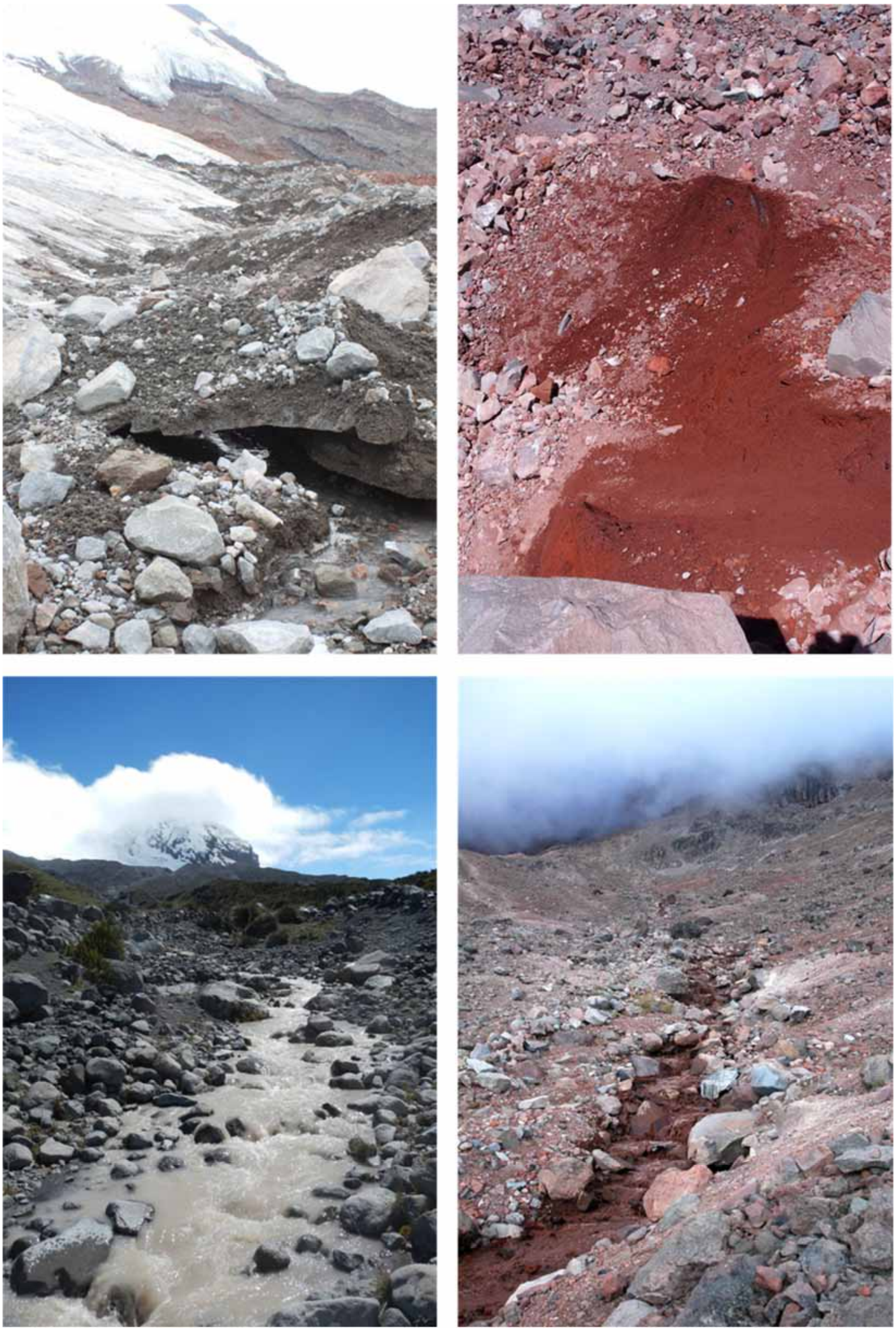


Figure 6: Picture of glacial flour (top) and glacier-fed streams (bottom) with high turbidity. Nature of sediments in the streams and on the glacier margin depends on bedrock composition. Pictures on the left side were taken in the Antisana reserve, while pictures on the right side in the Chimborazo, two volcanoes in the tropical Andes in Ecuador.

Glacier-fed streams display a particular flow regime with strong temporal variability due to the complexity of the water storages and releases by glaciers (see above 1.1; Cuffey and Paterson 2010). Indeed, glacial runoff exhibits temporal variability at the inter-annual, seasonal and diurnal time scale (Fig. 5 and 7; Jansson et al. 2003, Milner et al. 2009). At the inter-annual time scale (from few years to centuries), variability of total meltwater emerging from the glacier depends on the variation in snow accumulation, melt, and water release, which is mostly driven by change in climatic conditions (i.e. air temperature and precipitation regime; Stahl et al. 2008). Thus, inter-annual variability in glacier-fed stream discharge depends on long-term climate trend such as the ongoing global warming as well as regional (or local) climatic fluctuation such as the El Niño-Southern Oscillation (ENSO) phenomenon (see part 4.1.2; Rabatel et al. 2013). At the seasonal time scale, variability in glacier-fed stream discharge is caused in temperate zones by the alternation of precipitation storage in winter and meltwater release in summer (Hannah et al. 1999). There, meltwater flow is very low in winter, and stream channels can be covered by snow, can freeze or fall dry (Malard et al. 2006). Contrastingly, stream flow is at its maximum in summer, punctuated by diurnal flow pulses (Milner et al. 2009). In tropical zones, in the outer tropics, seasonal variability in glacier-fed stream discharge is caused by the alternation of the dry and wet seasons. While in the inner tropics, there is no seasonal discharge pattern because ablation occurs all year round due to the lack of temperature and precipitation seasonality (see part 4.1.2 for details; Vuille et al. 2008, Jomelli et al. 2009). During glacier ablation season (i.e. in summer for temperate glaciers and all year round in the inner tropics), glacier-fed stream discharge exhibits high flow events at the diurnal time-scale linked to the diurnal cycles of temperature (Hannah et al. 2000). Occasionally, high magnitude discharge might occur due to intern storage outburst (e.g., glacier surges, drainage of dammed water) or rainfall (Milner et al. 2009, Cuffey and Paterson 2010, Slemmons et al. 2013).

In addition, the high temporal variability in glacial meltwater runoff engenders a temporal fluctuation of sediment transport, water temperature, hydrochemistry, and channel stability at the multiple time scales. Therefore glacier-fed streams are characterized by harsh environmental conditions (i.e. low water temperature, low channel stability, low electrical conductivity, and high turbidity), and high temporal variability in flow and environmental conditions, with major implications for aquatic life (Milner et al. 2001a).

Figure 7: Illustration of the temporal variability in glacial meltwater contribution to stream flow. Confluence of one glacier-fed stream (on the left) and one groundwater stream (on the right). Pictures were taken in the Antisana reserve.

2.1.2. *Specialization and temporal variability in aquatic community*

Aquatic communities close to the glacier snout are composed by microorganisms (e.g., bacteria, fungi; either in the water column or aggregate in benthic biofilms; Battin et al. 2004, Eisendle-Flöckner et al. 2013, Wilhelm et al. 2013), algae (e.g., diatoms, cyanobacteria, chrysophytes; Rott et al. 2006, Gesierich and Rott 2012), and invertebrates (e.g., rotifers, nematodes, Diamesinae, Orthocladiinae, Podonominae, Simulidae; Jacobsen et al. 2010, Milner et al. 2010, Eisendle-Flöckner et al. 2013). However, local richness and density are typically very low for all taxonomical groups due to the harshness of environmental conditions in glacier-fed streams (see above; Milner et al. 2001a, Milner et al. 2001b, Rott et al. 2006, Wilhelm et al. 2014). Note that bacteria and fungi are already present at the surface of the glacier (e.g. in cryoconite holes), within the glacier, and in subglacial waters constituting thus a source of nutrient and organic matter for freshwater ecosystem in glacier-fed streams (Anesio and Laybourn-Parry 2012).

Several abiotic factors limit aquatic life in glacier streams (Fig. 8). First, high amount of suspended sediment decreases light resources, inhibiting the photosynthesis and thus the algae growth (Rott et al. 2006). Indeed, turbidity of 250 NTU attenuate about 95% of the incident light in a water column of 0.5 m depth (Uehlinger et al. 2010). Moreover, allochthonous organic inputs are typically scarce in glacier-fed streams due to the lack of riparian and upland vegetation. Zah and Uehlinger (2001) found allochthonous organic inputs were lower than 1.1 g ash free dry matter m^{-2} y^{-1} in the proglacial area above 2080 m in the Switzerland Alps. Thus, instream primary production (e.g. algae) is an important energy source supporting the heterotrophic community in glacier-fed ecosystems (Zah et al. 2001, Füreder et al. 2003, Clitherow et al. 2013). In addition, high amount of suspended sediment increases abrasion of small organisms (Milner et al. 2009), affects algal and invertebrate attachment to substrate and restricts benthic invertebrate filter feeders (Milner and Petts 1994). Second, low water temperature and conductivity inhibit primary production and restrict aquatic flora and fauna in both abundance and species richness (Brown 2003, Uehlinger et al. 2010). Indeed, low temperature (i.e. maximum temperature < 2℃) reduces algae growth rate, decomposition rate and microbial activity, and consequently invertebrate feeding habits (Rott et al. 2006, Friberg et al. 2009). Moreover, temperature affects invertebrate size, growth rate and life cycle (i.e. length and number of generations per year; Brown et al. 2004) and subzero temperature induces organism freezing and desiccation (Lencioni 2004). Besides, stream-dwelling organisms require water of some minimal ionic concentration (Allan and Castillo 1995). Low conductivity indicates a low level of nutrient enrichment and consequently inhibits algae growth (Rott et al. 2006) and invertebrate occurrence (Robinson et al. 2001). However, the effect of conductivity on aquatic organisms strongly depends on the nature of the ions dissolved (e.g., Silica is used by diatoms in the formation of their external cell wall, Calcium is used by mollusks in the formation of their shell, inorganic Phosphorus and Nitrogen are primary nutrients that limit plant and microbial production – Allan and Castillo 1995). Finally, high flow events have many effects on aquatic organisms both directly and indirectly through changes to habitat (Lamouroux et al. 2004). First, high flow events reduce channel stability. High volume and speed of the water creates high shear stress on the stream bed and surrounding channel that scours, abrades or moves substrates, suspends sediment in the water column, and potentially alters channel shape (Lake 2000). Substrate movement scours algae and invertebrates. Second, during high flow events organisms shift out of the rising channel, and are washed away or are crushed by moving substrate and debris (Death 2008). Thus, depending on the magnitude of the forces, organisms may be killed or displaced, consumable resources may be depleted, and habitat structure may be degraded or destroyed (Death 2008, Milner et al. 2012). Besides, in temperate zones, prolonged snow cover and drought in winter have strong negative impact on the aquatic community. While, drought enhances organism desiccation, snow cover prevents gas exchanges and light penetration (e.g. a snowpack of 60 cm may reduce incident photosynthetically active radiation light by 99%; Uehlinger et al. 2010), therefore hindering photosynthesis and favoring accumulation of carbon dioxide and depletion of oxygen (Schütz et al. 2001, Lencioni 2004).

In addition to such harsh conditions, aquatic organisms in glacier-fed streams have to cope with the high temporal variability in those environmental conditions. Therefore, previous studies have evidenced a temporal variability in aquatic community composition linked to temporal variability in environmental conditions (e.g., Uehlinger et al. 1998, Robinson et al. 2001). Uehlinger et al. (2010) observed a seasonal pattern of periphyton in the Alpes, characterized by low biomass during late spring and summer due to high flow (bed load transport), high turbidity (limiting light availability) and low temperature. In their study, periphyton biomass was relatively high in autumn where benign conditions prevail, while it strongly depended on the snow cover (limiting light availability) in winter. This seasonal change in quantity and quality of food sources is also expected to affect population dynamics of invertebrates. Burgherr and Ward (2001) and Burgherr et al. (2002) found that macroinvertebrate density and taxon richness peaked during periods of favorable environmental conditions, i.e. spring and late autumn/early winter. Similarly, Robinson et al. (2001) found that macroinvertebrate taxon richness and density were two to three times higher in winter than in summer and Schütz et al. (2001) found significant differences in species composition between summer and winter.

Therefore, most species inhabiting at the upper reaches of glacier-fed streams have developed physiological, behavioral and/or life cycle adaptations to survive harsh and variable environmental conditions caused by the glacier melt (Schütz et al. 2001, Snook and Milner 2001, Ilg and Castella 2006, Füreder 2007). Furthermore, high mountain habitats often represent isolated islands that restrict immigration, increasing the likelihood of speciation, and leading to a high degree of endemism (Brown et al. 2009a). Consequently, glacier-fed streams often shelter a number of rare and endemic species (e.g., *Rhyacophila anglieri*, *Diamesa latitarsis*, *Zapada glacier*; Snook and Milner 2001, Brown et al. 2007a, Stagliano et al. 2007, Winterbourn et al. 2008).

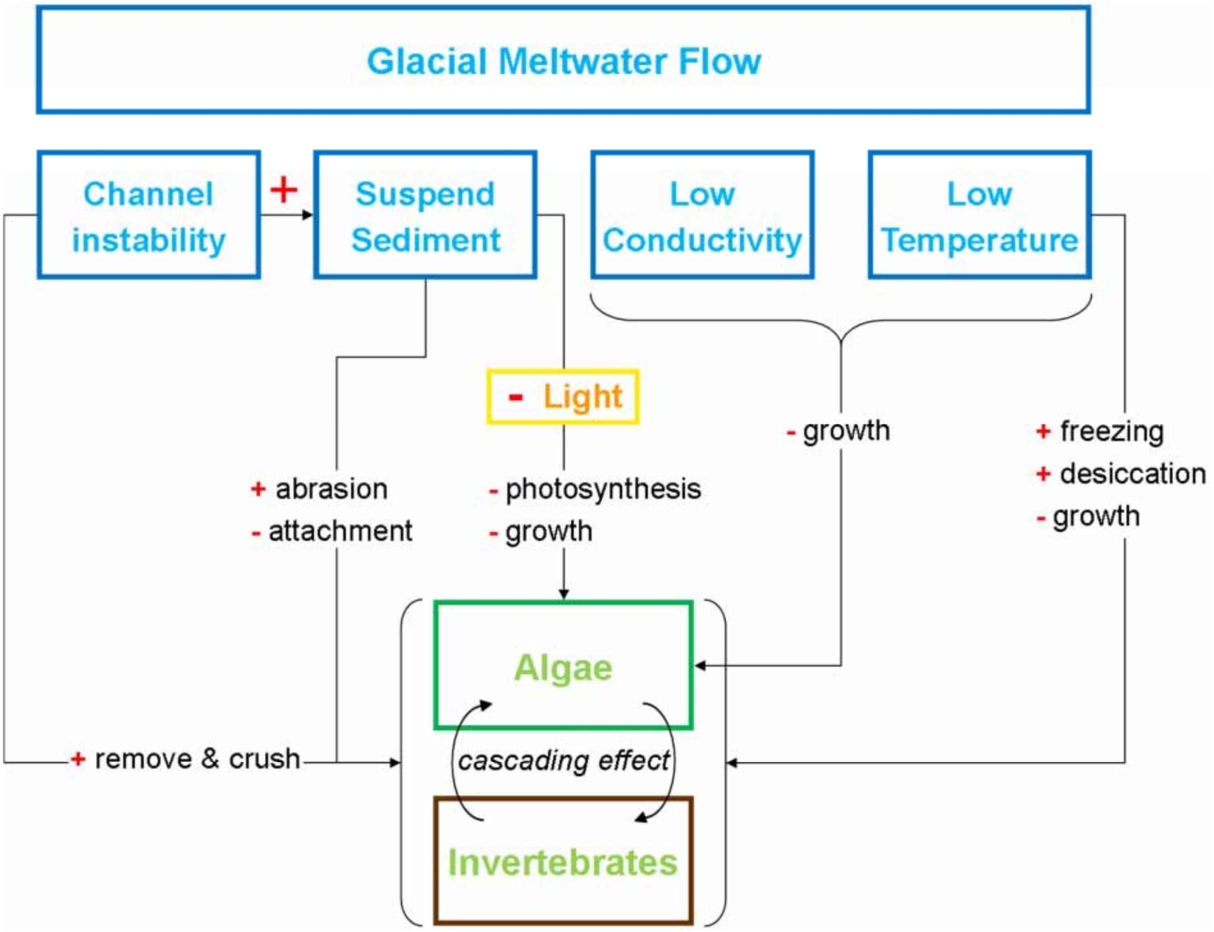


Figure 8: Simplified conceptual model of glacial meltwater effects on aquatic organisms. Red plus signs signify “induce” or “increase” (e.g. channel instability induces algae removal). Red minus signs signify “reduce” or “decrease” (e.g. suspended sediments reduce invertebrate attachment).

2.2. Glacierized catchments

2.2.1. Spatio-temporal environmental heterogeneity at the basin scale

In addition to purely glacier-fed streams, glacierized catchments encompass first-order rhithral (i.e. seasonal snow-fed) and krenal streams (i.e. groundwater-fed or spring-fed) and second-order streams showing a combination of these characteristics. These catchments therefore exhibit a complex mosaic of streams with contributions from different water sources, from meltwater (ice and snow) to groundwater-dominated streams (Füreder et al. 2001, Brown et al. 2003). Close to the glacier, glacial influence is at its maximum. It decreases progressively with increasing distance from the glacier snout and abruptly after a confluence with non-glacial tributaries depending on their discharge (Brown et al. 2007b). Besides, as rhithral and krenal streams present distinct hydrological and physico-chemical conditions compare to glacier-fed streams (Ward 1994), all stream segments display specific environmental conditions linked to the relative contribution of each water source, and thus also related to glacial influence. Along the streams, any decrease in glacial influence enhances a downstream shift in physicochemical conditions (e.g. increase in water temperature and channel stability; Milner et al. 2001a).

Contrary to glacier-fed streams (see above), groundwater streams are characterized by relatively constant flow regime (but with peaks following precipitation events; Ward 1994); low turbidity (Füreder 1999), physico-chemical constancy (Füreder et al. 2001) with generally high conductivity (but depending on the bedrock substrates and duration of water-rock interaction; Nelson et al. 2011). Water temperature mostly depends on air temperature and the depth of the water table (Menberg et al. 2014). Rhithral streams are characterized by high flow variability with peak discharge in spring (or early summer) and very low or nil discharge in winter. Usually snowmelt streams are very clear and transport little sediment, but during high flows they may have elevated turbidity due to resuspension of fine sediments from the streambed (Brown et al. 2004). Kryal, rhithral, and krenal streams exhibit a distinct temporal variability in flow regime but also in environmental conditions. Hence, at a given stream segment, glacial influence also temporally varies from diurnal to inter-annual temporal scales. Therefore, glacierized catchments exhibit high spatial and temporal environmental heterogeneity of habitats (Brown et al. 2009b, Finn et al. 2010) linked to the spatio-temporal dynamics of water source contributions.

2.2.2. Spatio-temporal taxonomic heterogeneity at the basin scale

Most ecological studies in glacier-fed catchments found an increase in local richness (α-diversity) and total biomass with decreasing glacial influence either for microorganisms (Battin et al. 2001, Eisendle-Flöckner et al. 2013, Wilhelm et al. 2013), algae (Lods-Crozet et al. 2001, Bürgi et al. 2003, Rott et al. 2006), or macroinvertebrates (Castella et al. 2001, Milner et al. 2001a, Milner et al. 2001b, Ilg and Castella 2006, Jacobsen et al. 2010). Milner and Petts (1994) proposed a conceptual model to explain invertebrate longitudinal succession along environmental downstream gradients, assuming that water temperature and channel stability were the primary variables affecting stream invertebrate distribution. However, Snook and Milner (2001) and Malard et al. (2003) show that hydraulic stress and organic matter were also important factor structuring invertebrates distribution. In addition, longitudinal succession of invertebrates is also modified by lakes and tributaries confluences (Milner et al. 2001a). Indeed non-glacial tributaries (or lakes) inputs of water, matter and energy can cause abrupt changes in environmental conditions, and thus provoking changes in the species assemblage of invertebrates (Brown et al. 2007a, Finn et al. 2010) and algae (Roy et al. 2011). Moreover, by compiling data sets from three continents, Jacobsen et al. (2012) recently demonstrated that local macroinvertebrate richness peaked at intermediate levels of glacial influence. The seasonal changes in glacial influence in the catchment (i.e. shifts in sources and flow paths of water) also affect the aquatic community composition. Uehlinger et al. (1998) and Burgherr and Ward (2001) found that the longitudinal response patterns of benthic macroinvertebrates and algae varied across seasons.

Although, these apparently conflicting findings suggest that mechanisms driving aquatic biodiversity in glacierized catchments are still far from completely understood, there is a general agreement that aquatic species assemblage varies downstream following the glacial influence gradient (Milner et al. 2010, Slemmons et al. 2013), and that this variation in community composition (i.e. β-diversity) increases with increasing difference in glacial influence (Brown et al. 2007a). Therefore, although glacial runoff creates a harsh aquatic environment that drives low α-diversity, this unique environment contributes to environmental heterogeneity at the basin scale (Hannah et al. 2007), generating high β-diversity among stream segments (Jacobsen and Dangles 2012, Finn et al. 2013). In addition, non-glacial streams present different aquatic species assemblage, due to their very dissimilar environmental conditions (see above; Füreder et al. 2001, Hieber et al. 2001, Battin et al. 2004, Hieber et al. 2005, Rott et al. 2006), which also generates high regional aquatic diversity at the catchment scale (Finn et al. 2013).

2.3. Risk of loss of freshwater biodiversity following glacier retreat

Under ongoing climate change, glacier retreat would yield to an alteration of glacial meltwater contribution to stream flow in glacierized catchment (Huss 2011). Within the glacierized catchment systems, this change will engender strong changes in environmental conditions at both temporal and spatial scales. Reduction (or loss) in glacial meltwater would induce a decrease in physicochemical habitat heterogeneity across alpine streams (Brown et al. 2007a). In addition, meltwater reduction will cause temporary (particularly in summer) but also permanent desiccation within riverine sectors due to the resulting absence of direct (melt water effluent) and indirect (replenishing groundwater storage) glacier influences (Tockner and Malard 2003). Although there are very few studies about the effect of glacier retreat on aquatic biodiversity over long time-scales (but see Milner et al. 2008, Finn et al. 2010), previous works about the effect of glacial meltwater contribution to alpine streams on aquatic communities suggest that the decrease in meltwater contribution within glacierized catchments would yield to the loss of species and changes in aquatic community composition at the basin scale (Jacobsen et al. 2012).

3. Thesis justification

One impact of climate change is the acceleration of glacier retreat, resulting in an alteration of glacial meltwater contribution to alpine stream flow, with major impact on the aquatic biodiversity in glacierized catchment (Füreder 2012, Jacobsen et al. 2012). Therefore, in the context of global warming, it is of critical importance to understand the relationship between glacial influence and aquatic communities in order to be able to predict the effect of the alteration of glacial meltwater contribution to alpine streams on aquatic biodiversity (Brown et al. 2007a). While many studies have been performed on this thematic, we list below three key remaining challenges.

- As a first and crucial step, it is necessary to develop more effective tools to quantify glacial influence on aquatic systems (Brown et al. 2010). Several indices have been proposed and used as a proxy for glacial influence (e.g., Brown et al. 2006, Ilg and Castella 2006, Milner et al. 2009); however most failed to describe the high spatio-temporal variability of the different water source contributions to the alpine streams and to incorporate all the hydrological and physicochemical changes caused by the variation in meltwater contribution to stream flow.
- Second, it is essential to deepen our knowledge about both the effect of hydrological and physicochemical stress caused by glacier runoff on aquatic organisms and the effect of glacial influence on aquatic communities at both spatial and temporal scales (Brown et al. 2007a). Although many studies investigated the relationship between glacial influence and aquatic communities, we are still far from being able to predict accurately the response of alpine stream species to reduced glacial runoff and consequently to anticipate the future species distribution at the basin scale under ongoing climate change.

- Finally, it is urgently necessary to study glacial hydrosystems in tropical regions as glacier runoff dynamics differ from those observed in temperate zones because ablation occurs all year round (Vuille et al. 2008, Rabatel et al. 2013). Tropical glacierized catchments exhibit different seasonal variability in meltwater contribution to alpine streams, and thus probably distinct temporal variability in aquatic community composition than their temperate counterparts. Besides, tropical mountain glaciers are particularly sensitive to climate change (see above 1.2; Bradley et al. 2006, Rabatel et al. 2013), and their aquatic communities have been poorly studied so far (Jacobsen et al. 2010).

This thesis aims to improve the general knowledge about the relationship between glacial influence and aquatic biodiversity in tropical regions and more specifically to better understand the effect of glacial meltwater on aquatic invertebrate communities. In the following, we present the study region and study sites, and then exposed the main objectives of our work.

4. Study site

4.1. *The Tropical Andes*

4.1.1. Geographical and geological settings

The tropical Andes are located in South America; they extend over 1.5 million km^2 from 11º N to 23º S, i.e. from west Venezuela to north Chile, and Argentina, encompassing Colombia, Ecuador, Peru and Bolivia (Fig. 9 A; Tovar et al. 2013). They are the longest and widest cool region in the tropics, occupying an elevation range from around 700 m up to 6768 m a.s.l., Mt. Huascarán in Peru. The Tropical Andes are primary composed by parallel high mountain chains (two in Venezuela, Ecuador, South Peru and Bolivia, and three in Colombia) with a large number of snow-capped peaks, and a vast mountain plain, the Peruvian-Bolivian Altiplano (Josse et al. 2011).

The Andes are the result of the Cenozoic (i.e. ~ 65.5 million years ago) tectonic shortening of the South American plate margin caused by the subduction of oceanic crust, the Nazca plate (Fig. 9 B; Sobolev and Babeyko 2005, Capitanio et al. 2011). While the compression of the western rim of the South American plate is the primary cause of the Andes rise, volcanic activity (as a result of subduction of the Nazca plate), is also a significant phenomenon in the building of the Andes (see Fig. 10 for the different types of cordilleras found in the tropical Andes; Stern 2004). Indeed, the Andes are the world’s second highest orogenic belt and include at least 200 active Quaternary volcanoes, occurring in four separate segments referred to as the Northern, Central, Southern, and Austral Volcanic Zones (Fig. 9 B; Bourdon et al. 2003, Stern 2004).

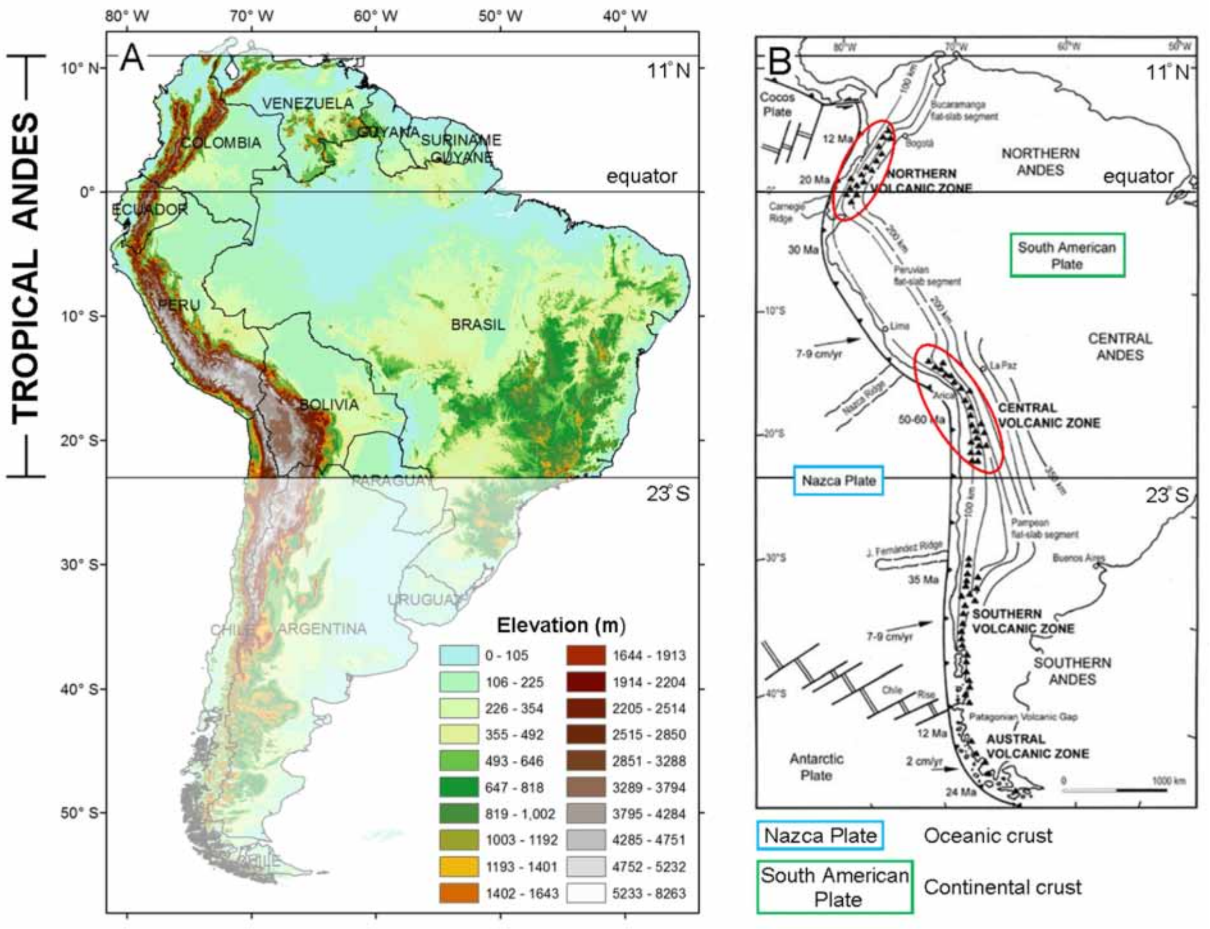


Figure 9: **A.** Elevation map of South America. The tropical Andes extend between 11º N to 23º S from western Venezuela to north Chile, and Argentina, encompassing Colombia, Ecuador, Peru and Bolivia. A 30 arc-second digital elevation model was taken from http://www.arcgis.com/features/. The map was made using ArcGis (10.0). **B.** Geological map of South America. Tropical Andes include two volcanic zones: the northern and central one. Modified from Stern (2004).

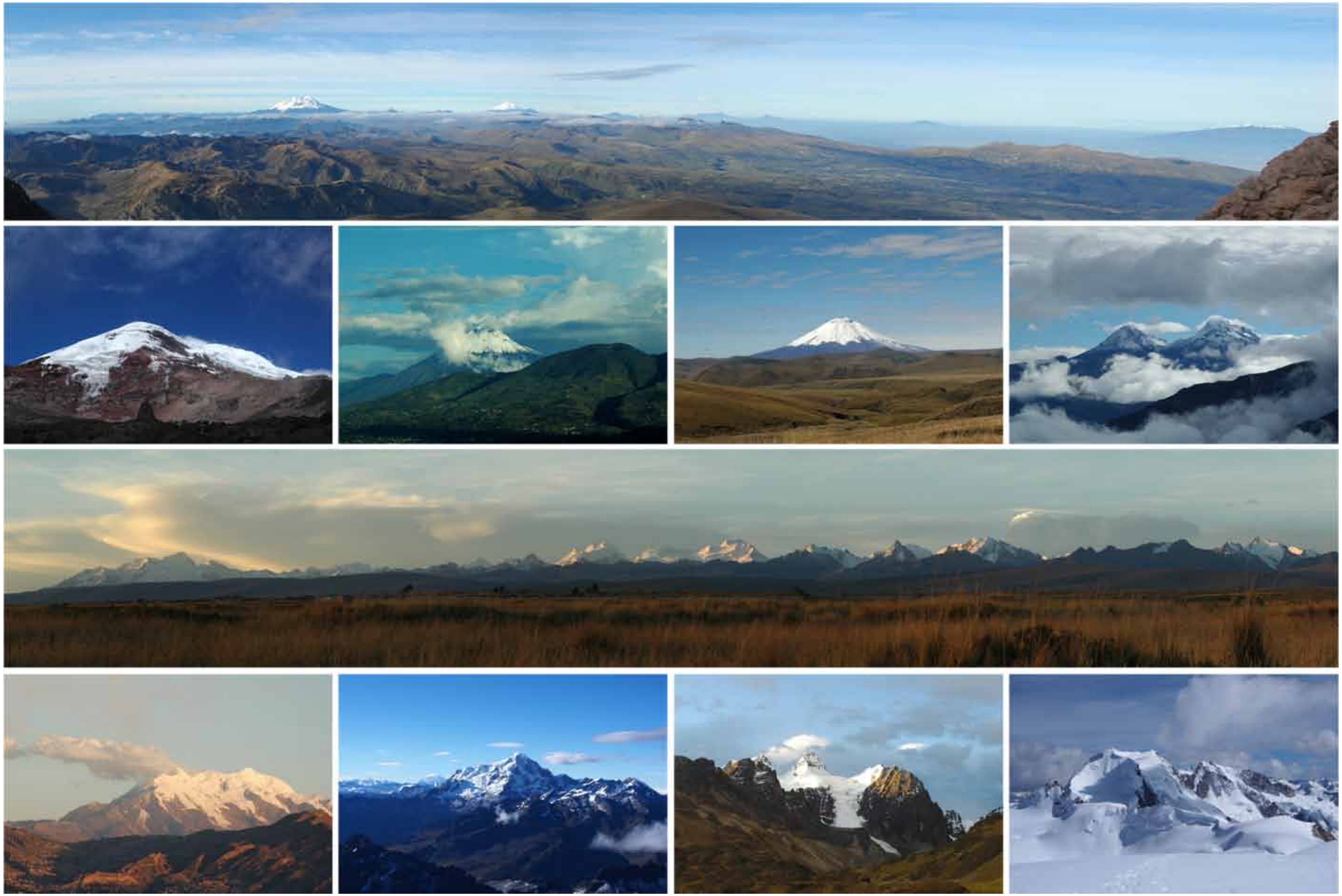


Figure 10: 1st line: Panoramic of the Ecuadorian Cordillera Real (volcanoes chain). 2nd line from left to right: Ecuadorian Volcanoes: Chimborazo, Tungurahua, Cotopaxi, and Los Illinizas. 3rd line: Panoramic of the Bolivian Cordillera Real (mountain chain). 4th line from left to right: Bolivian Mountains: Illimani, Huayna Potosi, Condoriri, and Chearoco.

4.1.2. Climate setting and implication for glaciers mass balance

From a climatological viewpoint, the tropical zone can be divided into two zones with different characteristics: the inner tropics, with more or less continuous precipitation throughout the year, and the outer tropics characterized by a dry season from May to September, and by a wet season from October to March (Troll 1941). For both inner and outer tropics, air temperatures are homogeneous throughout the year with a slight seasonality in the outer tropics. In the inner tropics, incident solar radiation is constant throughout the year, while it presents seasonality in the outer tropic due to the pronounced cloud seasonality. Indeed, in the inner tropics, humidity remains almost unchanged throughout the year, whereas the outer tropics are characterized by pronounced seasonality of specific humidity, cloud cover and precipitation (Rabatel et al. 2013). In the tropical Andes, precipitation mainly results from an easterly flow of moisture from the Amazon Basin (Garreaud et al. 2003, Vizy and Cook 2007).

Thus, in the inner tropic, as there is no seasonality of temperature and precipitation, accumulation and ablation occur simultaneously throughout the year, and the ELA remains at the same altitude. While, in the outer tropics accumulation occurs mostly during the wet season, and ablation at the end of the dry season (Kaser 2001, Jomelli et al. 2009). Thus within the inner tropic, diurnal flow variation caused by glacier melting occur throughout the year in glacier-fed streams (Fig. 5; Favier et al. 2008). Moreover, in tropical regions, there is neither permanent nor seasonal snow cover outside the glaciers because the 0℃ isotherm is located above the glacier snouts throughout the year (Vuille et al. 2008, Rabatel et al. 2013). In addition, previous studies have evidenced the significant effect of the tropical Pacific sea surface temperature on the glacier mass balance, and thus the important role of the El Niño-Southern Oscillation (ENSO) phenomenon in dictating the inter-annual glacial mass balance variability (Francou et al. 2004, Vuille et al. 2008). Climate in the tropical Andes is strongly influenced by the ENSO, with La Niña years tending to be wet and cold, and El Niño years warm and dry (Vuille et al. 2000, Vuille and Keimig 2004). Therefore, El Niño years usually induced negative mass balance, while la Niña events producing a nearly balanced or even slightly positive mass balance on glaciers (Rabatel et al. 2013).

4.1.3. Natural ecosystems and human activities

The Tropical Andes shelter around 45000 plant and 3400 vertebrate species (excluding fishes), of which almost half is endemic (Myers et al. 2000, Herzog et al. 2011). This high biodiversity is mostly due to the region's complex topography, coupled with altitudinal and latitudinal gradients, and local climate resulting in varied environmental conditions that create unique habitats and barriers for species movement (Anderson et al. 2011). Indeed, Josse et al. (2009) recognized 133 different ecosystem types for the tropical Andes, that can be grouped into nine major categories: 1) *Páramo,* > 3000 m, from Venezuela to northern Peru, consists in a high elevation humid shrublands; 2) *Humid Puna*, 2000-6000 m, from northern Peru to northern Argentina, dominated by grasses, shrubs, and cacti, replacing *Páramo* to the south where precipitation is lower; 3) *Dry Puna*, 2000-6000 m, from southern Peru to northern Argentina, consists in desert-like vegetation with low spiny shrubs; 4) *High Andean/Superpáramo*, > 4500 m, throughout the tropical Andes, composed by very small stature plants, lichens, and mosses; 5) *Cloud Forest*, 1000-3500 m, throughout the tropical Andes, consists in very humid forests with high epiphyte loads receiving a significant amount of precipitation in the form of cloud-borne mist that is intercepted by trees; 6) *Seasonal Andean Forest*, 800-3100 m, especially in Peru and Bolivia, characterized by medium stature forests partly composed by deciduous trees experiencing 3-5 month dry seasons and reduced precipitation; 7) *Dry Andean Forest*, 800-4100 m, in Inter-Andean valleys in Ecuador, Peru, and Bolivia, characterized by forests with low stature trees, thick stems and leaves for water storage and abundant spines and chemical defenses; 8) *Inter-Andean Valleys*, 1900-3500 m, throughout the tropical Andes, consist in landscapes heavily altered by humans characterized by shrublands with seasonal herbs with adaptations to dry periods; 9) *Aquatic Habitats*, > 800 m, throughout the tropical Andes, composed by lakes, wetlands, cushion bogs, streams, and rivers (see Fig. 3 in Josse et al. 2009, Josse et al. 2011, Young et al. 2011).

The tropical Andes are inhabited since more than 10000 years, and host today more than 40 million people depending on these ecosystems as a source of fresh water, food, and many other ecosystem goods and services (Josse et al. 2009). Tropical Andean landscapes have been intensely fragmented by long-term human influences, mainly related to agricultural practices that have transformed the region into a complex mosaic of cultivated fields (Young 2009). In addition, because of the benign climate in the tropics, human settlements, agriculture, and other anthropogenic activities can extend up to relatively high elevations. Thus, tropical high altitude ecosystems can be affected by organic pollution, agrochemicals, sedimentation, and mining wastes. In particular, altitude streams are threatened by dams and water abstraction (Jacobsen 2008).

4.2. The Antisana volcano

4.2.1. Geographical and geological settings

The Antisana is an active volcano covered by glaciers, located in the Eastern Cordillera of the northern Andes, in Ecuador (0° 29’19’’S, 78° 08’10’’W), i.e. in the inner tropics (Fig. 11). With an elevation of 5758 m, it is one of the highest Ecuadorian volcanoes (the fourth). It is situated in the Napo and Pichincha Provinces, 50 km south-eastern of Quito, the capital of Ecuador. The Ecological Reserve Antisana (ERA), closed to visitors (previously), was built in 1993 to protect the regional flora and fauna; it includes the volcano and its surroundings, covering about 120000 ha (i.e. 1200 km^2), and ranging from 1200 m to 5758 m (Boyla and Estrada 2005). Because of the restricted access of the ERA and its proximity from Quito, several research projects were conducted in the ERA during the last 20 years by the French Institute for Development (IRD – glaciology, hydrology, soil science, aquatic and terrestrial ecology, and paleoecology), the University of Copenhagen (UC – freshwater ecology), the *Pontificia Universidad Católica del Ecuador* (PUCE – botany), the *Empresa Pública Metropolitana de Agua Potable y Saneamiento* (water company EPMAPS – water quality and supply), the *Instituto Nacional de Meteorología e Hidrología* (INAMHI – meteorology) and the *Escuela Polytechnica National* (EPN – hydrology). As a consequence, unlike most tropical glaciers (Francou et al. 2000), climatic and hydraulic data as well as series of glacier mass balance are available for this site.

Figure 11: The Antisana volcano

The Antisana volcano is constructed upon the Eastern Cordillera basement, ranging between 3000 and 4000 m, and composed of old Tertiary volcanic rocks lying upon Mesozoic granites and metasedimentary rocks (Litherland et al. 1994). It is a Quaternary stratovolcano constituted of two edifices (Fig. 12). The oldest one, at the southeastern part, is composed of numerous volcanic breccia deposits, lava and pyroclastic flows, and is dominated by two calderas. This old edifice has been strongly destroyed by the two caldera events and intense glacial erosion. The recent edifice, situated on the northwestern flank of the complex, is a regular cone composed of the piling of numerous similar recent lava flows (Holocene) probably originating from the summit. The last volcanic eruptions related to the Antisana, the *Antisanilla* and *Potrerillos* lava flows date from the beginning of the nineteen century and are located a few kilometers away to the north from the main edifice (Bourdon et al. 2002, Bourdon et al. 2003). Antisana lavas display geochemical characteristics intermediate between adakites rocks, i.e. rocks derived from the partial melting of the subducting oceanic crust (Defant and Drummond 1990), and calc-alkaline rocks, i.e. rocks derived from partial melting of the mantel (Bourdon et al. 1999, Bourdon et al. 2002). This suggests that Antisana lavas were generated in an enriched mantle that was heterogeneously metasomatized by oceanic crust melts (Bourdon et al. 2003).

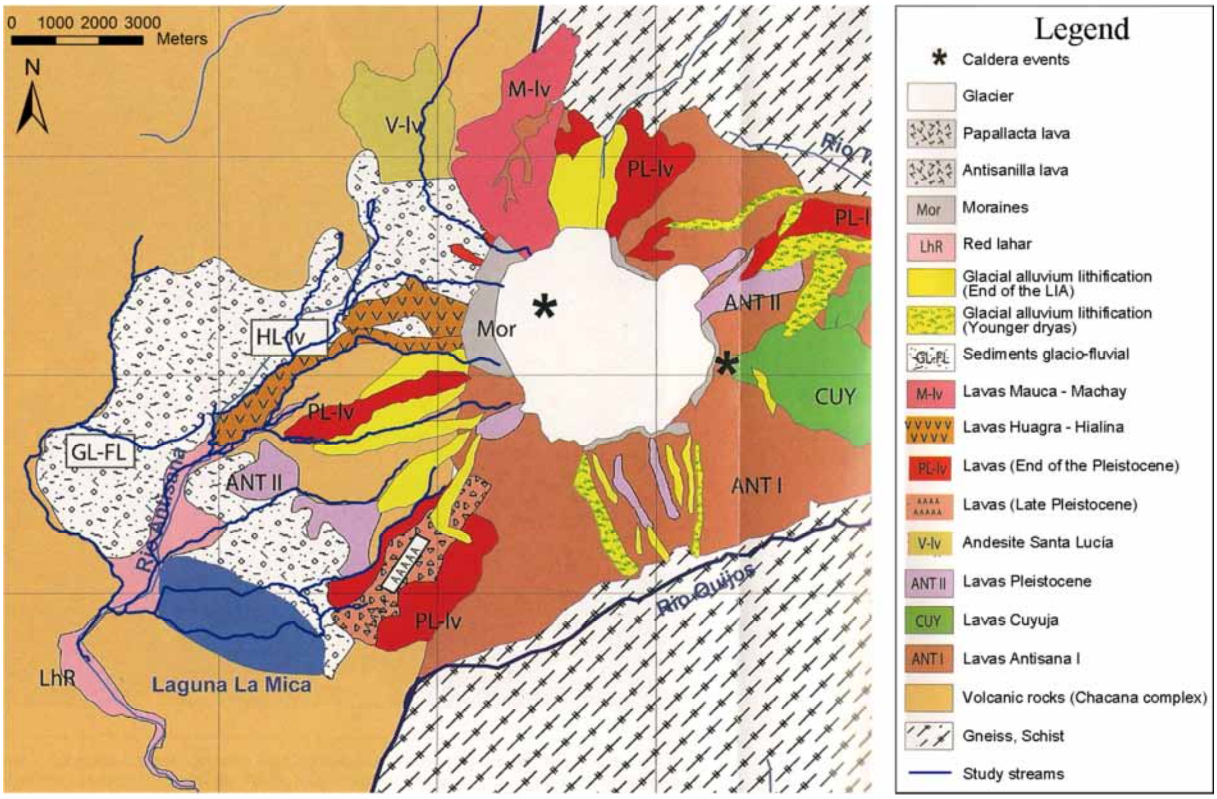


Figure 12: Geological map of the Antisana volcano. Image was taken from Hall et al. (2012), georeferenced and modified in ArcGis (10.0). Study streams were added in blue.

4.2.2. Climate setting and glacier retreat

Antisana glaciers consist in a small ice cap and 17 slope glaciers (Hastenrath 1981). They covered an area of about 14 km^2 in 2004, and extended until 4700 m on the eastern flank and 4800 m on the western one (Cáceres et al. 2006) because the east face receives more precipitations from the adjacent Amazonian basin (Maisincho et al. 2007). The Antisana area is representative of the Eastern Cordillera by being directly exposed to moist easterly winds from the Amazon basin. Precipitation falls year-round, generally with an increase from February to June, but each month receives a minimum of 50 mm w.e. (Francou et al. 2004). Mean daily temperatures do not display any significant seasonal variations. At 4850 m in 2009, mean monthly temperature ranged from 0.66 and 2 ˚ C (Cáceres et al. 2012). On the contrary, winds exhibit a seasonal pattern with strong and almost constant easterly winds between April and September, and weak and intermittent winds and from October to March (Francou et al. 2004).

Two Antisana glaciers have been continuously monitored since 1999: the glacier 12, *Los Crespos*, and the glacier 15 (including 2 tongues α and β, Fig. 13). The loss in surface area of those glaciers was estimated at 33% for the period 1979-2007 with an increase since the 1990s (Rabatel et al. 2013). From 1956 to 1965 the average deficit of those glaciers was estimated to be 251 kg m^{-2} yr^{-1}. It was reduced to 146 kg m^{-2} yr^{-1} during the 1965-1993 period but then accelerated dramatically in the next 5 years, 1993-1998, to reach 600 kg m^{-2} yr^{-1} (Fig. 14, Francou et al. 2000). Since 1956, glacier terminus lost more than 400 m and 0.32 km^2 (Basantes 2010). However, despite this general retreating trend Antisana glacier display a strong inter-annual variability in glacial masse balance due to the opposite phases of ENSO (Francou et al. 2004, Rabatel et al. 2013).

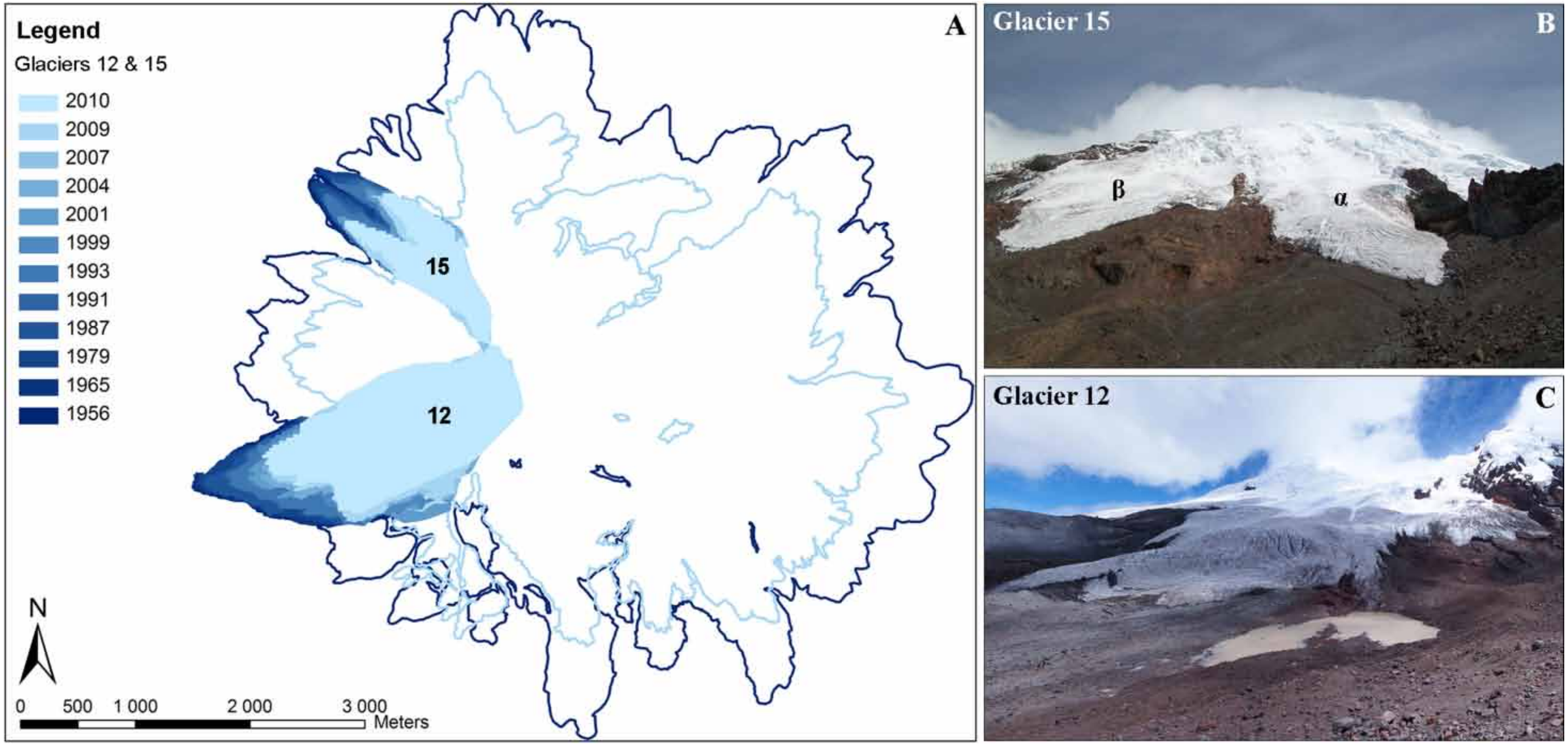


Figure 13: A. Map of the retreat of Antisana's glaciers since 1956. Total glacier outlines were represented for the years 1956 and 2009. Outlines of glacier 12, *Los Crespos*, and glacier 15 α and β were represented for 12 years between 1956 and 2010. Glacier outlines were computed from satellite images by Ruben Basantes and Maëlle Collet (see also Rabatel et al. 2013). Map was made using ArcGis (10.0). **B**. Glacier 15 α and β. **C.** glacier 12, *Los Crespos.*

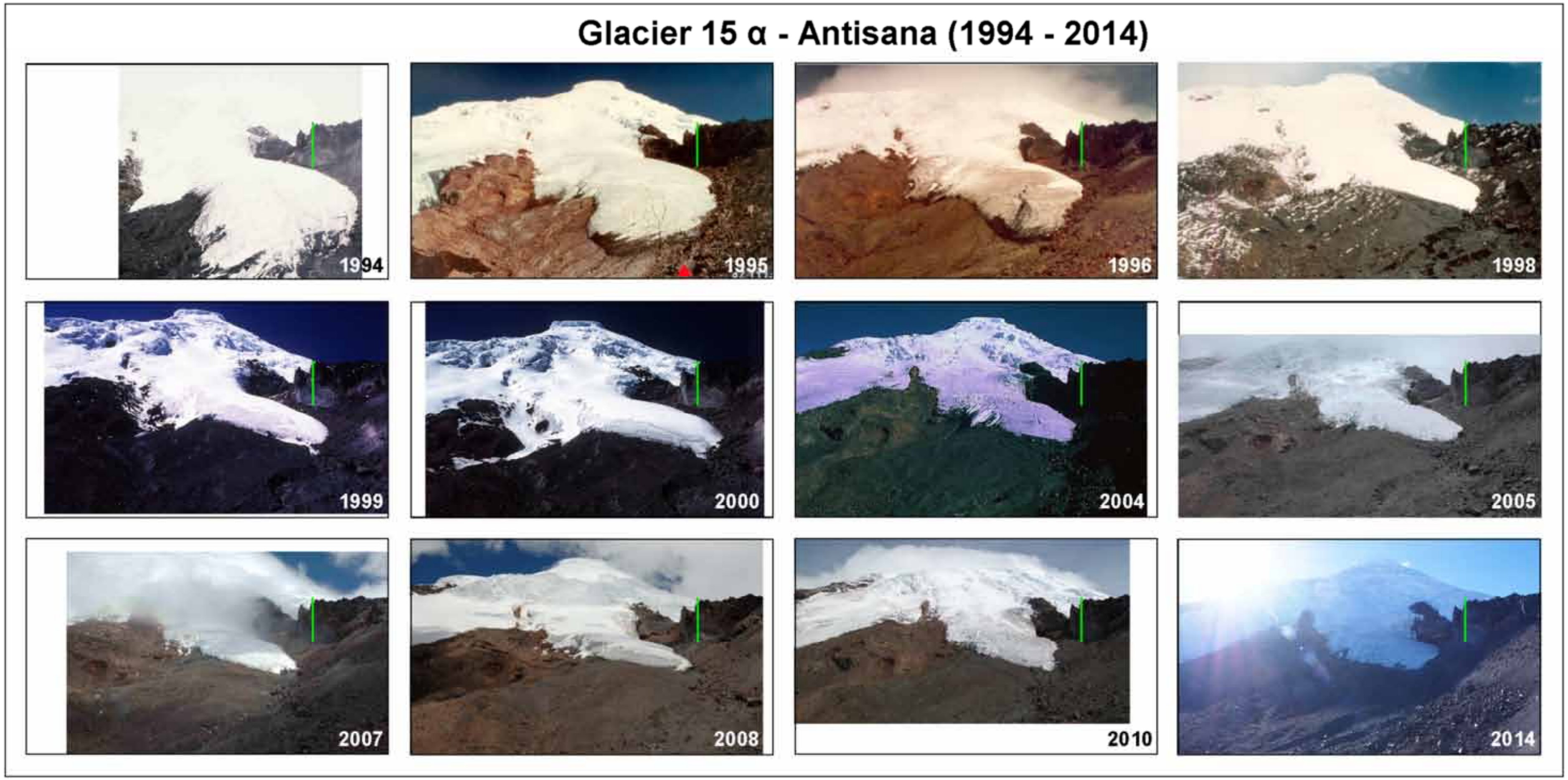


Figure 14: Glacier retreat of Antisana glacier 15 α. Pictures were taken by Bernard Francou from 1994 to 2008. © Sophie Cauvy-Fraunié for pictures in 2010 and 2014.

4.2.3. Natural ecosystems and human activities

The Antisana reserve includes Andean forests below the tree line at 3000 m and *Páramos* above (Sklenář and Jørgensen 1999). The *Páramos* display an altitudinal pattern with three distinct zones (Luteyn and Churchill 1999): 1) *sub páramo*, 3000-3500 m, characterized by shrubs and small scattered trees, 2) *grass páramo*, 3500-4200 m, characterized by continuous vegetation, dominated by tussock and bunchgrasses and punctually dominated by cushion species in areas with high soil moisture, and 3) *super páramo* or *desert páramo*, 4200-4800 m, characterized by scarce and scattered vegetation with cushions, basal rosettes and tussock grasses as dominant growth forms (Fig. 15; Sklenář and Ramsay 2001, Sklenář and Balslev 2005). The Antisana reserve shelters native wild fauna (Fig. 16), e.g., the Andean fox (*Pseudalopex culpaeus*), the white-tailed deer (*Odocoeileus virginianus)* including rare and threatened species such as the Andean Condor (*Vultur gryphus*), the spectacled bear (*Tremarctos ornatus*; Williams et al. 2001, Peralvo et al. 2005, Dangles et al. 2010), but also introduced species (e.g. the rainbow trout *Oncorhynchus mykiss*).

Inside the reserve, scarce crop fields and habitations are present until 3700 m. Cows, sheep, and llamas are reared extensively (cow density ~ 1 ind km^{-2}, sheep density ~ 2.5 ind km^{-2}, and llama density < 0.1 ind km^{-2}) at higher altitude and can be found occasionally until 4800 m (especially llamas). Besides, a water reserve of 3.72 km^{2}, was built in 1999 at 3910 m, southwest of the Antisana volcano, by the drinking water company EPMAPS. This water reserve, *La Mica*, supplies a large portion of potable water to Quito and neighboring cities and villages (600000 people in 2005, Boyla and Estrada 2005). The Antisana reserve has been recently open to the public (2013) for bird watching, climbing, and fishing at the lake *La Mica*, but the access close to the volcano area (i.e. all around the volcano from 4000 m) remains restricted.

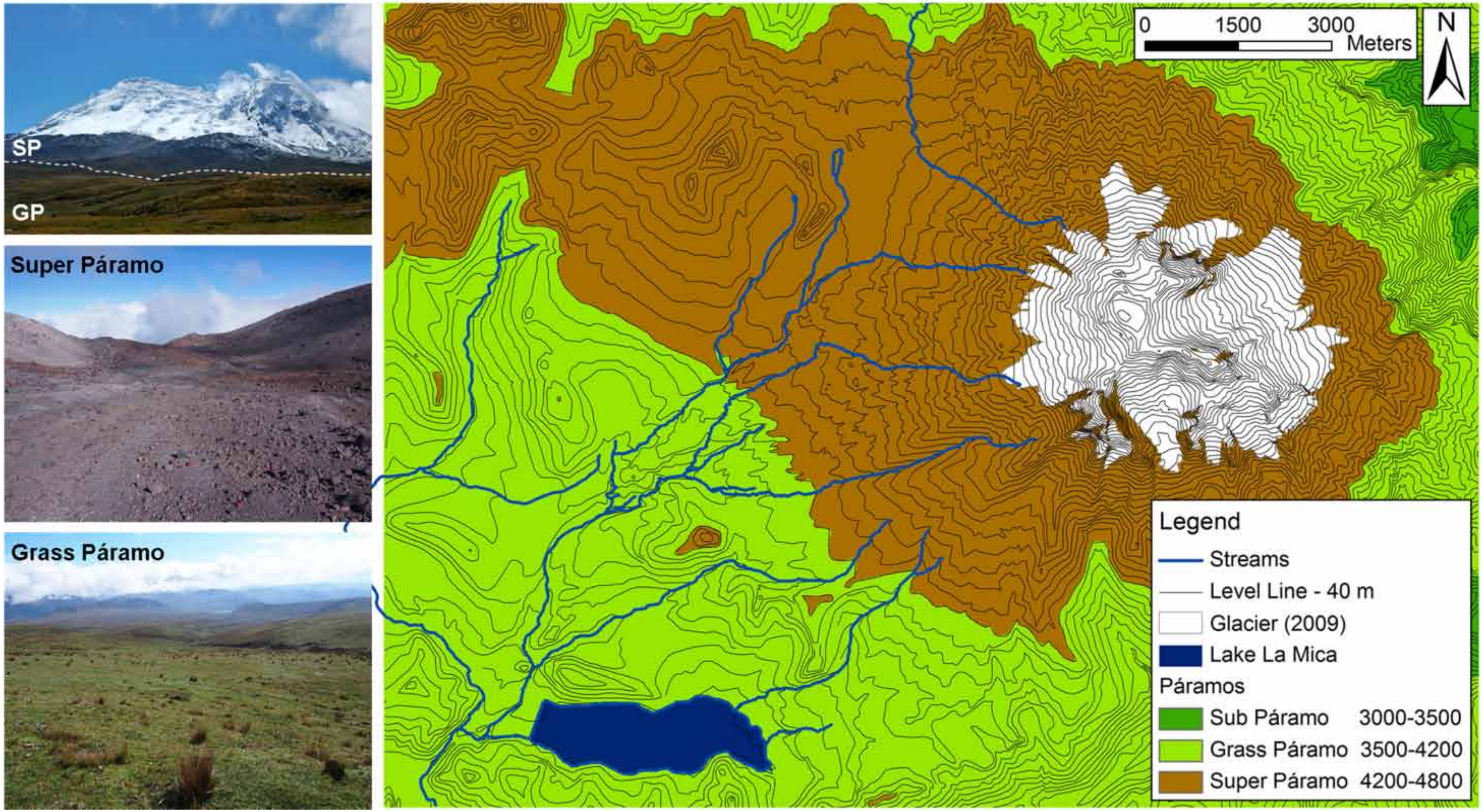


Figure 15: Ecological map of the Antisana showing the altitudinal pattern of *Páramos*. Level lines (40m) were taken from the Ecuadorian Military Geographical Institute (http://www.igm.gob.ec/site/index.php). Glacier outline was calculated based on a satellite image from 2009 by Ruben Basantes. The map was made using ArcGis (10.0). Pictures on the left show the two types of *Páramos* present in our study area: *Super Páramo* (SP) and *Grass Páramo* (GP).









Figure 16: Example of flora and fauna present in the Antisana reserve. Fauna on the left side from the top to the bottom: Andean Condor (*Vultur gryphus*), Andean fox (*Pseudalopex culpaeus*), white-tailed deer (*Odocoeileus virginianus*), llamas (*Lama lama*). Flora on the right side: *Chuquiraga jussieui*, *Huperzia crassa*, *Arenaria dicranoides*, *Azorella aretioides*, *Xenophyllum rigidum*.

4.3. The study glacierized catchment

The study was performed in 115 km^2 watershed (watershed outlet at site 33, see Fig. 17) where we identified and monitored 51 stream sites in the Ecological Reserve of Antisana, on the southwest of the Antisana volcano (Fig. 17). Study stream sites were located between 3886 and 4835 m. The study area is influenced by four glaciers: glacier 12 (*Los Crepos*), 13, 14, and 15, covering in 2010 an area of about 1.81, 0.78, 0.45, and 0.60 km^2, respectively. Among the first order streams, four originated from glaciers above 4800 m and 11 were groundwater streams. As there is no permanent snow cover in the tropics, there were no snowmelt streams. Among the 51 stream sites, 11 were located along the four glacier-fed streams before any confluence with non-glacial streams, 16 along the four glacier-fed streams after at least one confluence, and 24 were located in groundwater streams (or rainfall) with no glacial influence. Glacially-influenced stream sites were located at distances of 15 m - 15.2 km from the glacier snouts. Study stream sites will be described in details in each chapter.

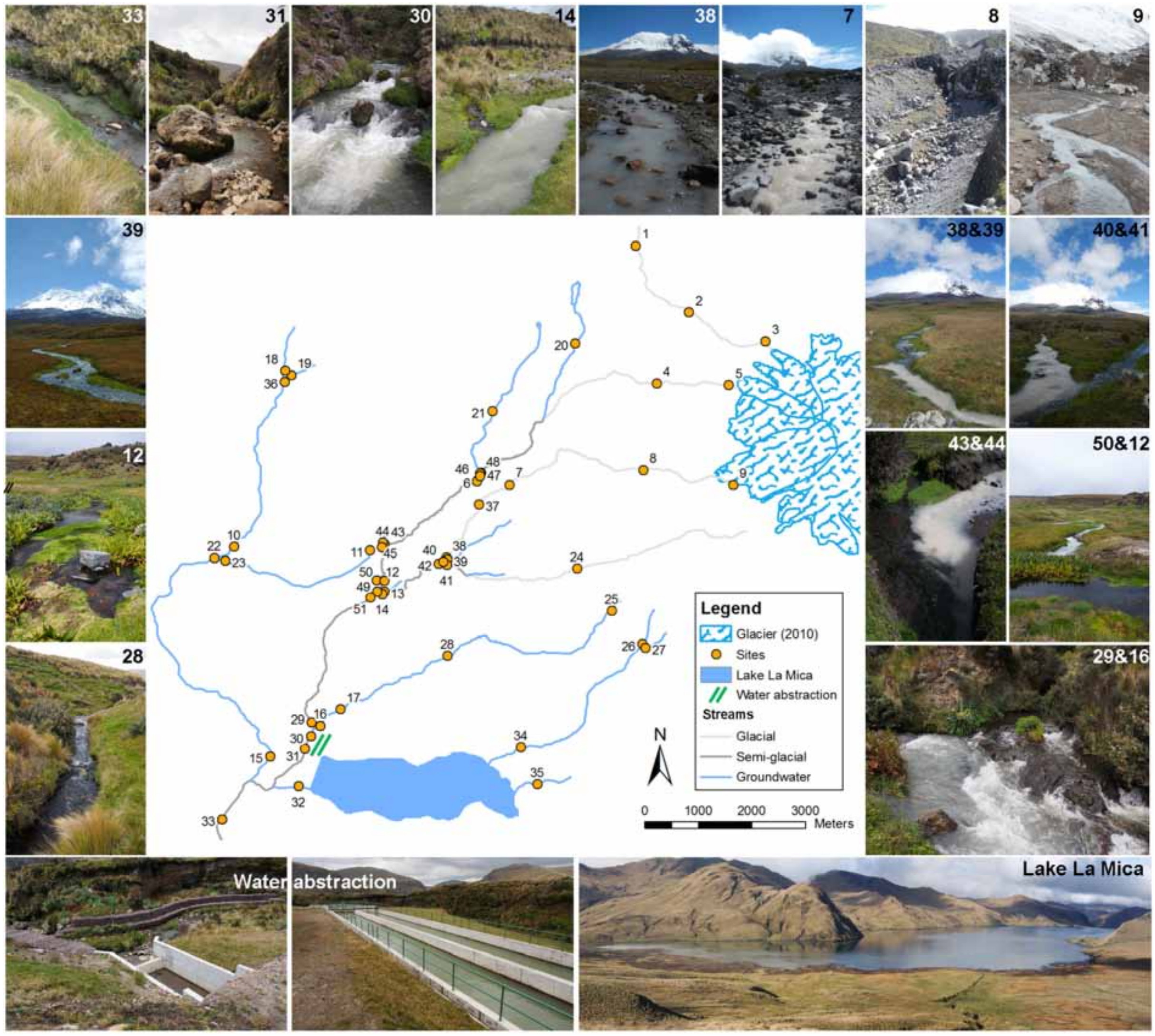


Figure 17: Map of the study area. Study stream sites are represented by orange circles. First order streams originated from glacier are represented in light grey. Groundwater streams are represented in blue. Stream segments resulting from the union of glacier-fed and groundwater streams are represented in dark-grey. Glacier outline was calculated based on a satellite image from 2010 by Maëlle Collet. Map was made using ArcGis (10.0). Pictures on the top show stream sites (9, 8, 7, 38, 14, 30, 31, and 33) located along the glacier-fed stream originated from the glacier "*Los Crespos*". Pictures on the left side show three groundwater stream sites (39, 12, and 28). Pictures on the right side show five confluences between glacier-fed streams and groundwater streams (38 & 39, 40 & 41, 43 & 44, 50 & 12, and 29 & 16). Pictures on the bottom show the infrastructure built for water abstraction and the lake *La Mica*.

5. Objectives

5.1. *Hydroecology as a scientific framework*

Freshwater ecosystems are among the most diverse ecosystem types worldwide because they exhibit a wide gradient in environmental conditions such as temperature, salinity, availability of light, dissolved gases, and nutrient. This high variability in environmental conditions, along with biogeographic processes (e.g. isolation) explains in large part the high diversity of life in aquatic ecosystems (Geist 2011). However, freshwater ecosystems may be the most endangered ecosystems in the world (Gleick 2014); because threatened by global environmental changes and climatic shifts superimposed upon overexploitation, water pollution, habitat degradation, flow alterations, and invasions by exotic species (Dudgeon et al. 2006). Thus, understanding the factors which govern aquatic biodiversity is crucial for effective and sustainable conservation (Geist 2011). Hydroecology is an interdisciplinary research approach at the interface between hydrology and ecology (Hannah et al. 2007). It aims to study the link between hydraulic conditions and ecosystems, i.e. to determine the bi-directional nature of hydrological-ecological interactions at a bench range of spatial and temporal scales (Hannah et al. 2007, Wood et al. 2007). As alpine streams in glacierized catchment exhibit a strong environmental gradient from harsh conditions in glacier-fed streams close to the glacier to benign conditions in groundwater streams, they provide thus a perfect model system to explore trends of aquatic community structure along environmental gradients (Jacobsen and Dangles 2012). Moreover, another important factor that influences aquatic biodiversity is flow disturbance, i.e. floods or droughts (Boulton and Lake 2008, Death 2008). They are defined by their intensity, frequency, predictability, spatial extent, timing and temporal duration (Lake 2000). They usually change the nature of habitats and deplete organisms and their resources. Therefore, disturbance can act as a filter to set the stage for subsequent colonization and succession, and thus may play a central role in regulating species assemblage (Lake 2008). However, the response of organisms is not only related to the strength of the disturbance but also to the organism's resistance (its capacity to withstand a disturbance), and resilience (its capacity to recover from disturbance; Lake 2000). As glacier-fed streams display high flow events (glacial flood) during the ablation season of the glaciers and drought events when glacial meltwater freeze, they provide an excellent study model to explore the effect of disturbance on aquatic communities but also the temporal variability in community composition after disturbance events. Therefore this thesis is set in a global context of hydroecology science, which is to improve our knowledge about the effect of hydraulic conditions on freshwater ecosystems in order to assess the ecosystem sensitivity to hydrological changes under both climate change and anthropogenic pressure (Hannah et al. 2007).

5.2. *Objectives and the scale issue*

With this conceptual background in mind, the overall objective of this thesis was to evaluate the effect of glacial meltwater contribution to alpine streams on aquatic biodiversity in an equatorial glacierized catchment. More specifically, our objectives were to 1) quantify the glacial influence and its impact on the hydraulic and environmental stream conditions, 2) determine the effect of different ecologically-relevant aspects of glacial influence on aquatic communities, and 3) anticipate the possible consequences of glacial meltwater alteration caused by the accelerated glacial shrinkage under global warming on aquatic biodiversity.

Those objectives were addressed throughout the thesis at different spatial scales, from stream reaches to the entire glacierized catchment and at different temporal scales from diurnal to *seasonal* time-scale. Ecological patterns and processes are usually dependent on the spatio-temporal scale of observation (Tisseuil et al. 2012, Heino and Peckarsky 2014) and ecologists long ago recognized the importance of considering both spatial and temporal scale to understand ecological phenomena (Wiens 1989, Levin 1995). However, most studies focused only on a single level of organization or a single spatio-temporal scale (Keil et al. 2011). Under a context of global climate change, this scale-dependence matter is even more relevant and thus continue to attract considerable attention (e.g. the Gordon Research Conferences "Unifying Ecology Across Scales" hold in July 2014) as linking ecological processes across scales is necessary for determining organism's and ecosystem's response to climate change (Storch and Marquet 2007). Therefore, at the stream reach scale, we studied the effect of the hydraulic and physico-chemical stress caused by glacial meltwater on macroinvertebrate communities; while at the catchment scale, we examined the effect of the variability in glacial meltwater contribution to stream flow on the community variation among stream sites. We also studied the effect of both the diurnal variability in hydraulic stress and the *seasonal* change in diurnal flow variability (e.g. intensity) on macroinvertebrate communities. Thus at each spatial and temporal scale, we used different metrics to characterize the glacial influence.

Determining the effect of glacial meltwater alteration on aquatic communities ideally requires long term abiotic and biotic time series. However, in our case due to the lack of long term macroinvertebrate data, we used the space-for-time substitution approach to anticipate aquatic community responses to glacier retreat. This method allows using the contemporary link between spatial species distribution and environmental gradients to predict the temporal change in species assemblage in response to change in environmental conditions under the ongoing climate change (Blois et al. 2013).

5.3. *Thesis organization*

This thesis is divided into three parts, each of them corresponding to a given spatial scale: the stream reach scale in chapter 1, the watershed scale (i.e. 15 stream sites) in chapter 2, and the regional scale (i.e. the entire glacierized catchment, 51 stream sites) in chapter 3 (Fig. 18).

- ***Response of macroinvertebrate communities to diurnal flow variation at the stream reach scale***

The aim of this chapter was to determine the effect of temporal variability in hydraulic stress generated by diurnal flow variation in glacier-fed streams on aquatic macroinvertebrates at the stream reach scale. Within the stream reaches, we thus examined the temporal variability in macroinvertebrates assemblage at the diurnal time-scale. More specifically, our objectives were (1) to quantify the change in hydraulic stress caused by the diurnal flow variation, (2) to determine the impact of hydraulic stress variation on macroinvertebrate communities, and (3) to envisage the ecological response of these communities to potential hydrological shifts (i.e. reduction in hydraulic stress) caused by glacial meltwater reduction. For this, we measured the near-bed turbulence (Boundary Reynolds number), and sampled macroinvertebrates (using a 125 cm^2 Surber net) at 30 random points in two glacier-fed stream sites at two different times during the days: in the morning for base-flow conditions and in the afternoon for high flow conditions. We performed those measurements at two different dates presenting variable high flow intensities (Fig. 18).

- ***Impact of the spatio-temporal variability in glacial influence on macroinvertebrates assemblage at the watershed scale***

The second chapter of this thesis aims to determine the effect of the spatio-temporal variability in glacial influence on macroinvertebrates assemblage at the watershed scale. This chapter is divided into three parts.

In the first part, we developed a new method based on the diurnal flow variation as a quantitative measure of glacial influence. For this, we performed water level measurements using water pressure loggers at 30 min time steps over 10 months at 15 stream sites presenting different combination of water sources contribution, i.e. different glacial influence. We performed wavelet analyses on water level time series to identify the diurnal flow variation and determine three wavelet-based glacial indices to quantify the glacial influence and identify its fluctuation throughout the year.

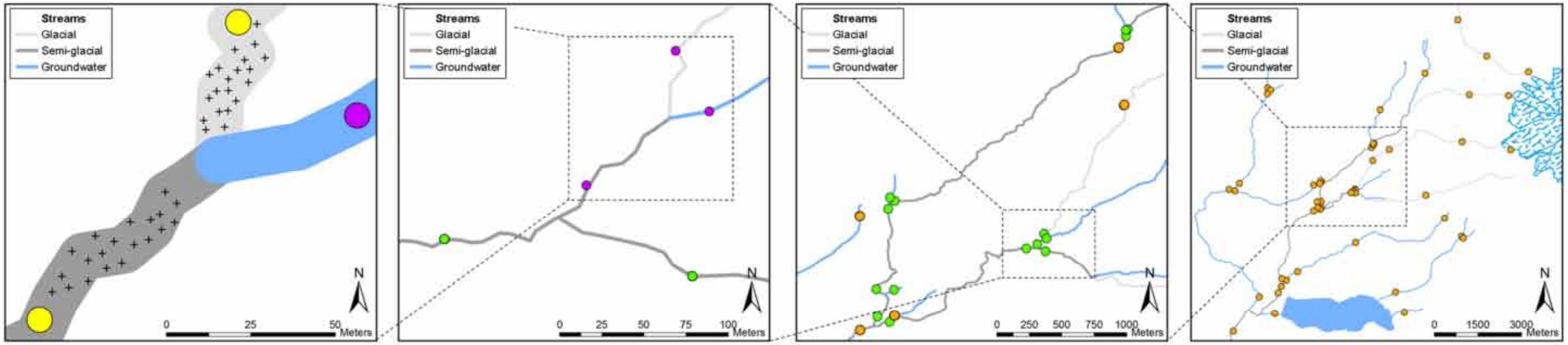
In the second part, we tested the relevance of the new wavelet-based glacial indices as predictors of macroinvertebrate communities, and we determined the relationships in spatial variability between macroinvertebrate communities and glacial influence at the catchment scale. For this, in the same 15 stream sites as previously, we sampled macroinvertebrates (5 samplings for each site with a 500 cm^2 Surber net) in addition to the water level measurements.

In the last part, we examined the effect of temporal variability in flow in glacier-fed streams on macroinvertebrates assemblage. In three stream sites of different glacial influence, we performed water level measurements at 30 min time steps over 29 months, and sampled aquatic macroinvertebrates at 14 different dates spread over the 29 months (5 samplings for each date with a 500 cm^2 Surber net).

- ***Glacier meltwater influence on macroinvertebrate metacommunity structure and dynamics in an Andean stream network***

This last chapter aims to assess the effect of glacial meltwater contribution to alpine streams within the entire catchment on the macroinvertebrate metacommunity structure. More specifically, our objectives were (1) to test whether the local environmental conditions resulting from the combination of different water sources contribution to stream flow explain macroinvertebrates spatial distribution within the glacierized catchment, (2) to test whether glacial meltwater limits macroinvertebrates dispersion, and (3) to anticipate the potential effect of the alteration of glacial meltwater contribution to stream flow on the metacommunity structure within the catchment. For this, we performed abiotic measurements (e.g., temperature, conductivity, turbidity) and sampled macroinvertebrates (5 samplings for each date with a 500 cm^2 Surber net) at 51 stream sites within a wide range of glacial influence.

Figure 18: Sampling design of all studies performed in this thesis. In chapter 1, study was conducted in two stream sites. Punctual environmental measurements (water level, near-bed velocity, substratum size and roughness) and macroinvertebrates samplings were performed, for each stream site, at 30 random points, two times (before and during a daily glacial flood) at two different dates. In chapter 2 (part 3), study was conducted in three stream sites. At each stream site, continual measurements of water level were performed during 29 months and macroinvertebrates were sampled 14 times. In chapter 2 (part 1 and 2), study was conducted in 15 stream sites. At each site, continual measurements of water level were performed during 10 months and macroinvertebrates were sampled once. In chapter 3, study was conducted in 51 stream sites. For all sites, punctual environmental measurements (temperature, conductivity, turbidity, pH, water level, width, slope, substrates) and macroinvertebrates, benthic detritus and epilithic algae samplings were performed. Pictures on the bottom illustrate the fields work and show our team work (Sophie Cauvy-Fraunié, Patricio Andino, Olivier Dangles, Dean Jacobsen and Rodrigo Espinosa).



● **2 Stream sites** **CHAP 1**

Punctual Measurements
Twice at 2 dates in 2010

At 30 random point (+)
Macroinvertebrates (1/4 Surber)
Water level
Near-bed velocity
Substratum size & roughness

● **3 Stream sites** **CHAP 2**

Continual Measurements
29 months: Dec 2009 to July 2012
Water level

14 dates in 2010-2012
Macroinvertebrates (5 Surbers per site & per date)

● **15 Stream sites** **CHAP 2**

Continual Measurements
10 Months: Jan to Oct 2010
Water level

Punctual Sampling (1 date in 2010)
Macroinvertebrates (5 Surbers per site)

● **51 Stream sites** **CHAP 3**

Punctual Measurements (1 date in 2009-2010)
Macroinvertebrates (5 Surbers per site)
Benthic detritus
Temperature
Conductivity
Water level
Substrates
Epilithic algae
pH
Turbidity
Width
Slope

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CHAPTER 1

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

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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

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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

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dependent changes in the relative influence of ice-melt, snowmelt, rainfall, rainstorms, and groundwater (Malard *et al.*, 2006; Hannah *et al.*, 2007). Despite such complexity, glacial stream discharge in temperate zones can be roughly characterized by two seasonal flow regimes: a minimum base-flow in winter and higher flows with irregular peaks in summer (Schütz *et al.*, 2001; Smith *et al.*, 2001). Contrastingly, hydrographs of glacial streams in equatorial mountains do not reveal such marked seasonal pattern due to (1) the absence of persistent snow cape and (2) the regular ablation and melting of equatorial glaciers throughout the year, both variables being driven by aseasonality (Favier *et al.*, 2008). Consequently, the main variation in discharge of equatorial glacier-fed streams occurs on a daily basis as a result of diurnal melting and nocturnal freezing (see Jacobsen *et al.*, 2010). However, the amplitude of these diel cycles is highly variable from day to day, depending on air temperature (which influences melting), occasional snowfall (which increases glacier albedo), and wind (which increases sublimation) (Favier *et al.*, 2004). Due to these particular hydrological characteristics, we expect that the response of freshwater fauna to flow variability in tropical glacier stream may differ from that documented in recast.

In tropical glacier-fed streams, although the benthic fauna is poorly known (see Jacobsen *et al.*, 2010 for the first quantitative study), the few available data indicate that accelerated glacier shrinking has strong negative effects on glacial stream biodiversity, with 11–38% of the regional species pools, including endemics, expected to be lost following the complete disappearance of glaciers in a catchment (Jacobsen *et al.*, 2012). However, glacier melting impact on the stream biota is likely to occur before the total disappearance of ice-melt water contribution, for example through changes in the regime of glacial runoff, which may alter in-stream physical habitat characteristics. While several factors (e.g. water temperature, conductivity, transported sediment, and channel stability) affect benthic fauna in glacier-fed streams, stream flow regime and resulting hydraulic conditions represent key integrative variables describing the overall abiotic conditions of these systems (Lancaster and Hildrew, 1993; Rempel *et al.*, 2000; Snook and Milner, 2001; Snook and Milner, 2002). In turn, hydraulic conditions are expected to strongly influence the spatial distribution of benthic macroinvertebrates (Füreder *et al.*, 2001; Brooks *et al.*, 2005).

In this paper, we studied the distribution of benthic macroinvertebrates in relation to hydraulic habitats in an equatorial glacier-fed stream in the tropical high Andes (4100 m). The Andean region is particularly relevant for this purpose as (1) most of tropical glaciers (> 99%) are located in the Andes (Vuille *et al.*, 2008), and (2) the highest increases in air temperature are predicted to occur in the tropical high mountains (Bradley *et al.*, 2006). Our 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 km^2, 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 ($\leq 15\ \mu\mathrm{S\ cm}^{-1}$), 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

	High glacial site	Low glacial site
Coordinates	0°30’25"S, 78°12’19"W	0°30’28"S, 78°12’21"W
Wetted width (m)	<1.50[a]	<1.50[a]
Depth (cm)	<12[a]	<27.5[a]
Mean discharge ($\mathrm{l\,s}^{-1}$)	59	103
Mean temperature (°C)	7.6 (0.0–19.8)	8.4 (2.0–19.9)
Conductivity ($\mu\mathrm{S\ cm}^{-1}$)	9 (1–15)	125 (30–187)
pH	7.85 (6.92–8.42)	7.64 (6.52–7.99)
O_2 ($\mathrm{mg\,l}^{-1}$)	7.19 (1.62–10)	8.23 (5.65–14.63)
PO_4^{3-} ($\mathrm{mg\,l}^{-1}$)	<0.01	0.8
NO^{2-} ($\mathrm{mg\,l}^{-1}$)	<0.001	<0.001
NO^{3-} ($\mathrm{mg\,l}^{-1}$)	0.8	0.2
SO_4^{2-} ($\mathrm{mg\,l}^{-1}$)	1.3	34.2

[a] base-flow conditions

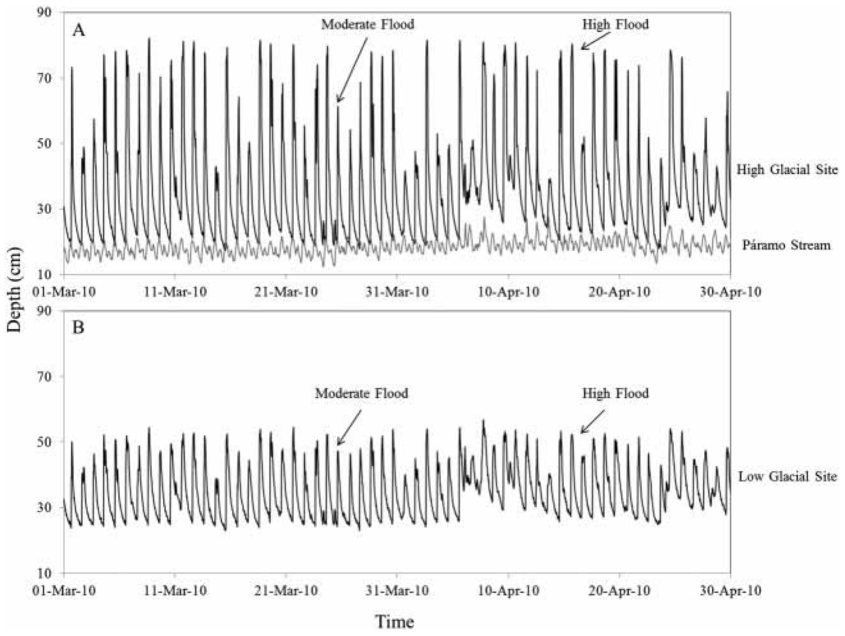

Figure 1. Water depth patterns of the high glacial (A) and low glacial site (B) from 1st March to 30th April 2010. Data were obtained using HOBO Water Level data-loggers (HOBO U20-001-04, 13 Foot Depth, U.S.A.) recording pressure to an accuracy of 3 mm every 30 min over the study period. For comparison, water depth patterns of rain- and groundwater fed stream (referred to as the 'páramo stream' in the figure) running at close proximity to the high glacial stream was added to panel A

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, Kempter, 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; χ^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× 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 sites (2009–2010; using Hobo water pressure loggers, U20, Onset Computer Corp., United States of America (U.S.A.)), we calculated that the two flood events Q_3 and Q_4 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 Q_1, Q_2, Q_3, and Q_4 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/m^2) 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

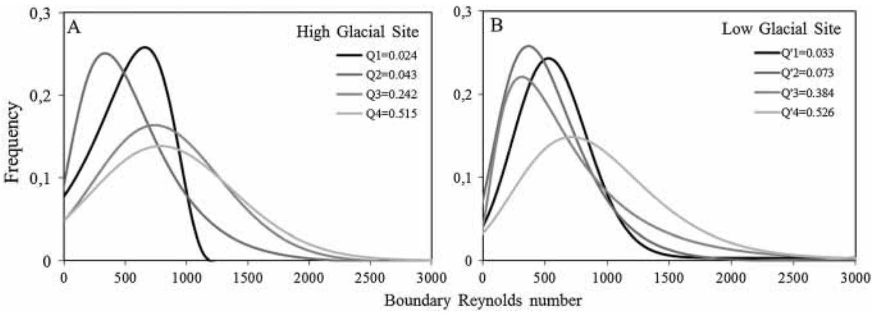

Figure 2. Frequency distribution of boundary Reynolds number values for the four discharges observed during the study. For both high glacial (A) and low glacial (B) sites, two discharges corresponding to base-flow conditions (Q_1, Q_2 and Q'$_1$, Q'$_2$ for high glacial and low glacial site, respectively) and two others: one corresponding to a moderate glacial flood pulse (Q_3 and Q'$_3$ for high glacial and low glacial site, respectively) and one corresponding to a high glacial flood pulse (Q_4 and Q'$_4$ for high glacial and low glacial site, respectively). Each flood event corresponds to one date

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.

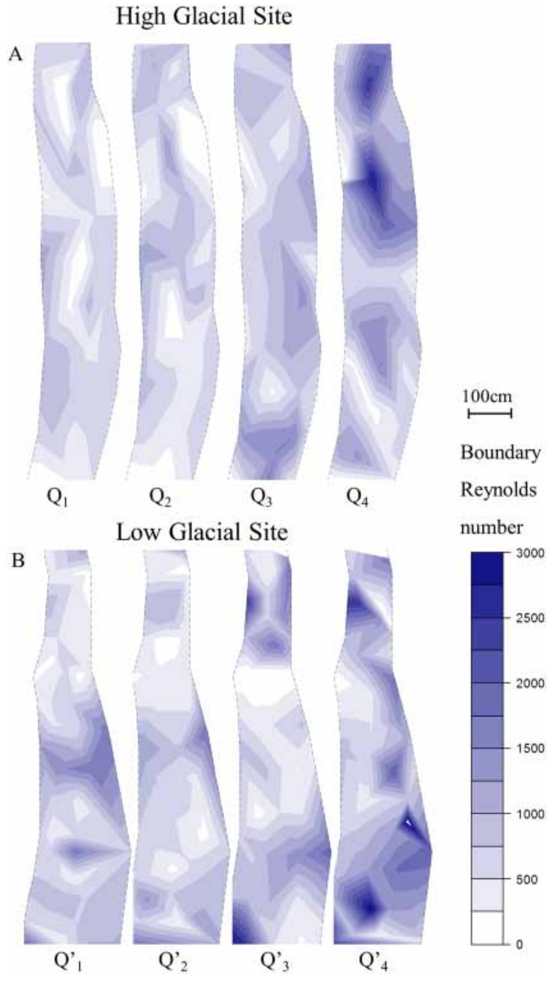

Figure 3. Boundary Reynolds number spatial distribution in the streambeds among both high glacial (A) and low glacial (B) sites for the four discharges. Each flood event corresponds to one date

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

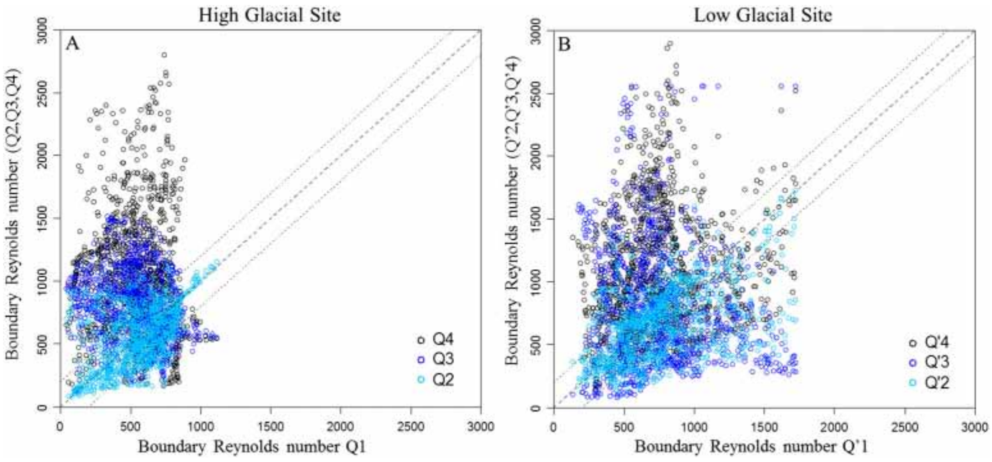

Figure 4. Scatter plot of boundary Reynolds number values during the highest discharges (Q_2, Q_3, Q_4 and Q'_2, Q'_3, Q'_4 for high glacial (A) and low glacial (B) site, respectively) *versus* boundary Reynolds number values during the lowest discharge (Q_1 and Q'_1 for the high glacial and low glacial site, respectively)

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. (Hyallelidae) (> 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 Q_2 were significantly smaller than for Q_1 and Q_4 and the mean values for Q_4 significantly higher than for Q_3. At the low glacial

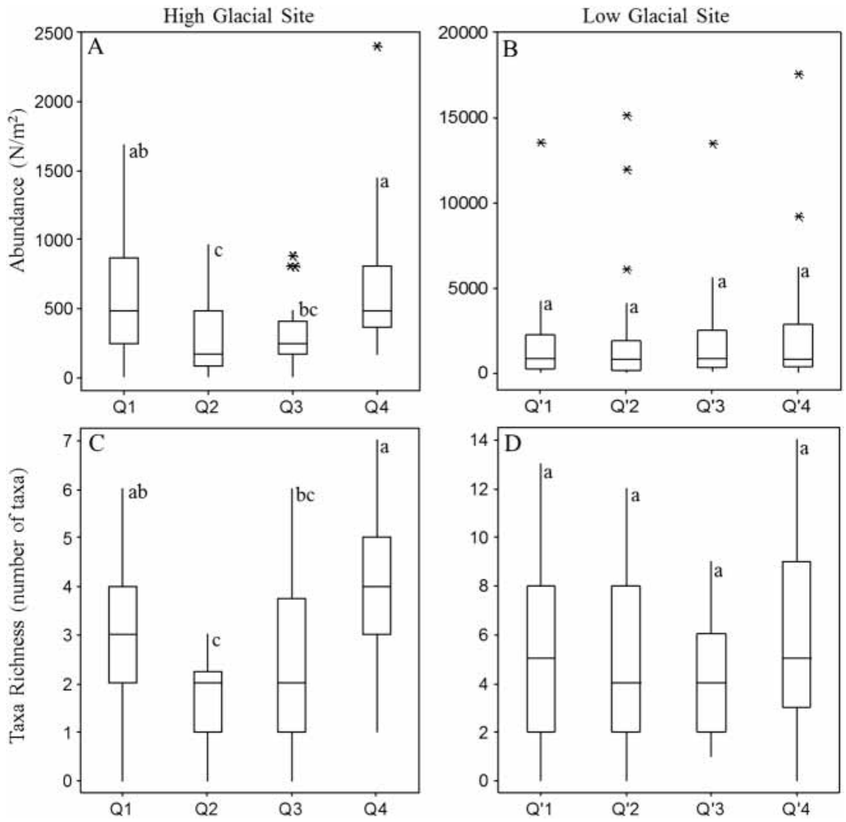

Figure 5. Box plot of abundance: total of individuals in one square meter (A, B) and taxa richness: number of taxa (C, D) *versus* discharge. Both high glacial (A, C) and low glacial (B, D) sites were represented. Mean values followed by different superscript letters are significantly different between zones (p-value < 0.001). Each flood event corresponds to one date

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 Re* values at the high glacial site (Spearman rank test, $p > 0.05$, Figure 6A and C), they significantly increased with increasing 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 Re* (ANOSIM, $p > 0.05$, Figure 7A). However, at the low glacial site, we found that macroinvertebrate assemblages occurring in habitats with Re* > 1000 differed significantly from those found in other Re* habitats (ANOSIM, $p < 0.05$, R = 0.019, Figure 7B).

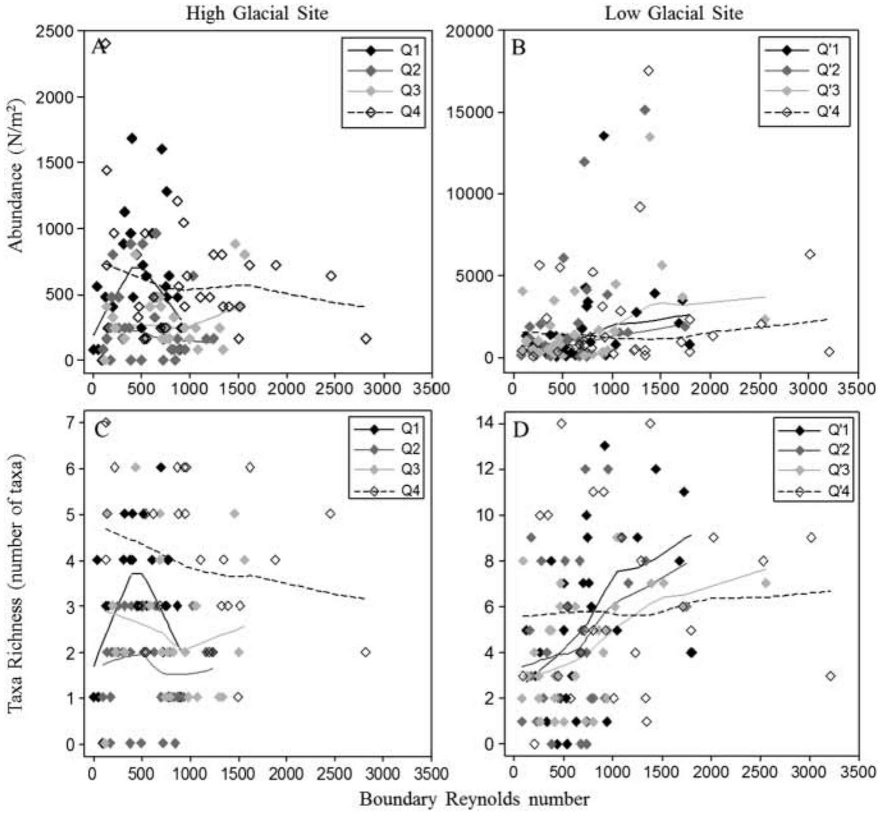

Figure 6. Scatter plot of abundance: total of individuals in one square meter (A, B) and taxa richness: number of taxa (C, D) *versus* boundary Reynolds number values at each sampling points, fitted by a non-parametric curve LOWESS. In high glacial (A, C) and low glacial (B, D) sites, all discharges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

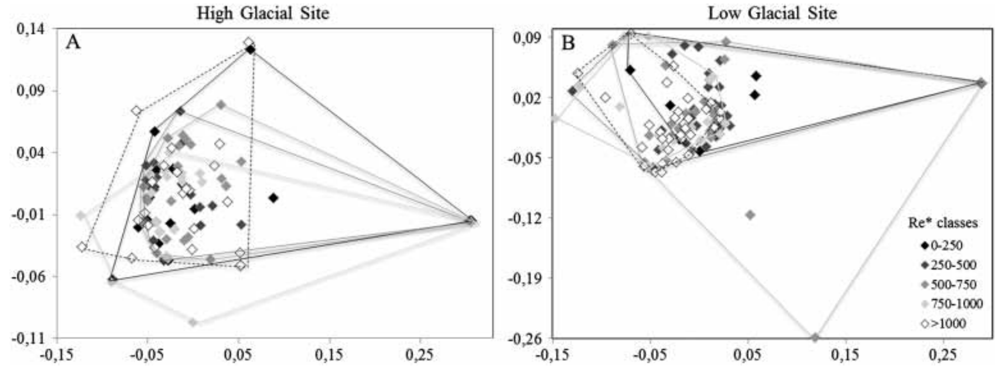

Figure 7. Non-metric multidimensional scaling ordination of log-transformed macroinvertebrate community data in the both high glacial (A) and low glacial (B) sites. The five different classes of boundary Reynolds number are shown (stress = 0.3622 and 0.3058 for high glacial and low glacial site, respectively)

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 8C and D). 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

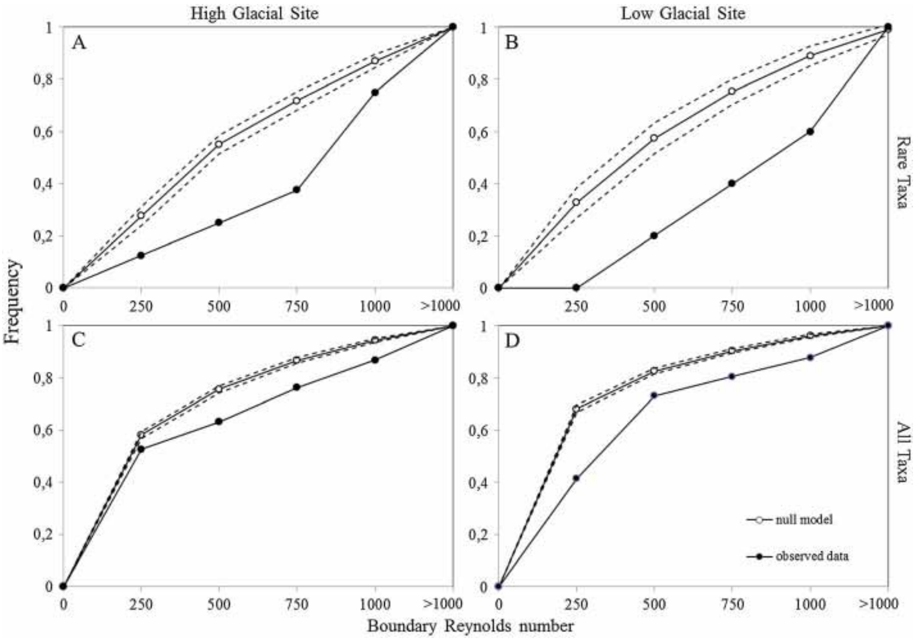

Figure 8. Frequency of taxa (rare taxa (A, B), and all taxa (C, D)) *versus* boundary Reynolds number classes. For high glacial (A, C) and low glacial (B, D) sites, observed data were represented with black rounds and the null model with white rounds (solid line for the taxa richness average of the 100 null matrixes and dotted line for the Interval of confidence 95%)

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/trait-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 $> 5\,\mathrm{m}^3\,\mathrm{s}^{-1}$, 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 *Blephariceria 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.

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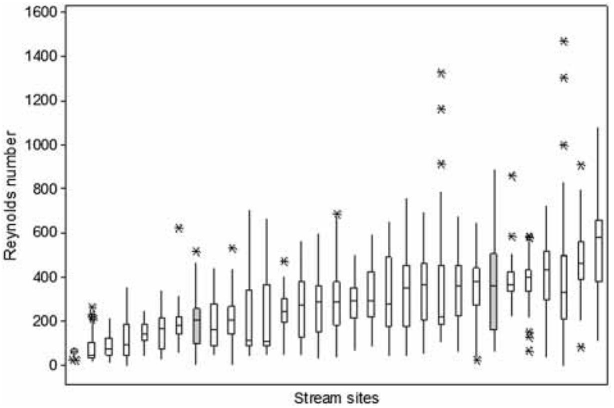
APPENDIX 1



Box plot of Reynolds number values, Re (see Statzner, 1988 for formule details) calculated in 31 stream sites located in our studied catchment. Re was calculated using data from Jacobsen and Dangles (2012), in which substratum and water levels were measured ten times along five transects for each site and slope was measured once for each site (see Jacobsen et al., 2010 for slope measuring method explanation). Stream site are ranked in increasing order of Re values. Our two study sites (grey box plots) present hydraulic conditions representative of other stream sites in the studied hydrological network.

CHAPTER 2

PART 1

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Technical Note: Glacial influence in tropical mountain hydrosystems evidenced by the diurnal cycle in water levels

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Abstract. Worldwide, the rapid shrinking of glaciers in response to ongoing climate change is modifying the glacial meltwater contribution to hydrosystems in glacierized catchments. Determining the influence of glacial runoff to streams is therefore of critical importance to evaluate potential impact of glacier retreat on water quality and aquatic biota. This task has challenged both glacier hydrologists and ecologists over the last 20 yr due to both structural and functional complexity of the glacier–stream system interface. Here we propose quantifying the diurnal cycle amplitude of the streamflow to determine the glacial influence in glacierized catchments. We performed water-level measurements using water pressure loggers over 10 months at 30 min time steps in 15 stream sites in 2 glacier-fed catchments in the Ecuadorian Andes (> 4000 m a.s.l.) where no perennial snow cover is observed outside the glaciers. For each stream site, we performed wavelet analyses on water-level time series, determined the scale-averaged wavelet power spectrum at 24 h scale and defined three metrics, namely the power, frequency and temporal clustering of the diurnal flow variation. The three metrics were then compared to the percentage of the glacier cover in the catchments, a metric of glacial influence widely used in the literature. As expected, we found that the diurnal variation power of glacier-fed streams decreased downstream with the addition of non-glacial tributaries. We also found that the diurnal variation power and the percentage of the glacier cover in the catchment were significantly positively correlated. Furthermore, we found that our method permits the detection of glacial signal in supposedly non-glacial sites, thereby revealing glacial meltwater resurgence. While we specifically focused on the tropical Andes in this paper, our approach to determine glacial influence may have potential applications in temperate and arctic glacierized catchments. The measure of diurnal water amplitude therefore appears as a powerful and cost-effective tool to understand the hydrological links between glaciers and hydrosystems better and assess the consequences of rapid glacier shrinking.

1 Introduction

In view of the accelerated glacier shrinking worldwide (Lemke et al., 2007; Rabatel et al., 2013; Sakakibara et al., 2013), coupling glacier and glacier-fed hydrosystem dynamics is a timely research thematic (Bradley et al., 2006;

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Jacobsen et al., 2012). While at the early stages of glacier retreat the reduction in ice volume would yield a significant increase in annual runoff (see the conceptual model presented by Baraer et al., 2012), after a critical threshold (depending on the glacier size) the annual discharge would decrease up to the end of the glacial influence on outflow (Huss et al., 2008). Worldwide, glacial river discharges have shown both increasing and decreasing trends, depending on ice cover in the catchment, the study region, and where the glacier stands along the deglaciation trajectory (Fleming and Clarke, 2003; Stahl and Moore, 2006; Casassa et al., 2009; Moore et al., 2009; Dahlke et al., 2012; Fleming and Weber, 2012). In this context, a growing number of studies have quantitatively explored the potential future impacts of various climate change and glacier recession scenarios upon water resources, using modern glaciological and hydrological modeling techniques (e.g., Schaefli et al., 2007; Huss et al., 2008; Stahl et al., 2008; Villacis, 2008; Jost et al., 2012; Yao et al., 2013). Such studies have demonstrated that glacier change effects are likely to be hydrologically substantial, even in relatively lightly glacierized basins. Modifications in water regimes may have significant consequences on water quality, aquatic biota and water security for human populations (Barnett et al., 2005; Brown et al., 2010; Kaser et al., 2010).

In this context, detecting the influence of glacial runoff to stream discharge has become a key challenge for a broad community of researchers, including glaciologists, hydrologists, water managers and ecologists (Brown et al., 2010; Baraer et al., 2012; Cauvy-Fraunié et al., 2013). To measure glacial meltwater influence on mountain streams, most approaches have focused on determining the water source contribution in glacierized river basins (e.g., glacial melt, snowmelt, rain, and groundwater) using methods ranging from thermal and discharge balances to stable isotope analyses (Huss et al., 2008; Kaser et al., 2010; Dahlke et al., 2012) or hydro-glaciological model (Condom et al., 2012). “Glacier indices” have also been developed such as (1) the glacial index (Jacobsen and Dangles, 2012) calculated from glacier size and distance from the glacier terminus, (2) the percentage of glacier cover in the catchment (Rott et al., 2006; Füreder, 2007; Milner et al., 2009), (3) the Alpine River and Stream Ecosystem classification (ARISE, Brown et al., 2009) based on hydrochemical analyses of water samples and statistical mixing models, and (4) the “glaciality index” (Ilg and Castella, 2006) based on four physico-chemical habitat variables (water temperature, channel stability, conductivity, and suspended sediment concentration).

However, a major challenge for these methodologies is the need to incorporate the high spatiotemporal variability of the different water source contributions in glacierized catchments (Brown et al., 2009). In this respect, existing glacier indices suffer from several limitations. First, although commonly used, the estimation of glacier cover in the catchment may be neither an easy nor a reliable approach. For example, in the upper reaches of mountain catchments where accumulation zone of different glacier tongues can be connected, the accurate delimitations of each individual glacier can be difficult, mainly due to the lack of information on the bedrock topography under the glacier and on the ice-flux directions. Likewise, catchment delimitation can be hazardous in places with complex topographies dominated by flats (as in South American plateaux) and short-scale steep altitudinal gradients (Verbunt et al., 2003). Second, it may be complicated to determine glacial influence on stream locations as the apparent absence of glacier cover may not be a reliable indicator of an absence of glacial influence on streamflow (Favier et al., 2008). Indeed, in glaciers located on terrains with complex geology and groundwater reservoirs (e.g., volcanoes, karstic areas), meltwater infiltrations are more often the rule than the exception (Bazhev, 1973; Bengtsson, 1982; Favier et al., 2008; Finger et al., 2013). Third, there is growing evidence that water chemical signatures may not be so reliable in detecting ice melt influence on streamflow as they can be modified by many factors such as climate, bedrock substrates and altitude (Nelson et al., 2011; Zhu et al., 2012). In particular, when glacial meltwater infiltration occurs, water chemistry is likely to be considerably modified during the underground flow routing, depending on the residence time underground, the distance of the underground flow routing and the bedrock substrates (Hindshaw et al., 2011; Nelson et al., 2011). Finally, incorporating the high spatiotemporal variability of the different water sources contributions in glacierized catchments requires extensive measurement campaigns (e.g., glacier area measurement, water sampling, and stream habitat measurements), the building of water monitoring structures (e.g., hydrological and climatological stations) or costly analyses (e.g., water chemistry over long time periods). While these factors may not appear as major constraints in temperate regions where many monitoring field stations have been established over the last 50 yr, most glacierized catchments in the world (e.g., subtropical and tropical mountains) remain poorly studied due to the difficulties in accessing and monitoring costs over long time periods (Baraer et al., 2012). In this context, we were interested in developing a new cost-efficient method for detecting the glacial influence in mountain catchments.

During the ablation period, glacier-fed streams are characterized by diurnal flood events (Milner et al., 2009) with discharge depending on the portion of glacier exposed to melting conditions (Favier et al., 2004). In this article, we proposed using the diurnal cycle amplitude as a quantitative measure of glacial influence in hydrosystems located in glacierized catchments. To identify the diurnal flow variation caused by the diurnal glacier melting, we propose using wavelet analyses on water-level time series. Indeed, contrary to Fourier transform and autocorrelogram approaches commonly used for time-series analyses (Chatfield, 1989; Bloomfield, 2004; Andreo et al., 2006), wavelet analysis is a time-dependent spectral analysis that decomposes a data series in time–frequency space and enables to identify

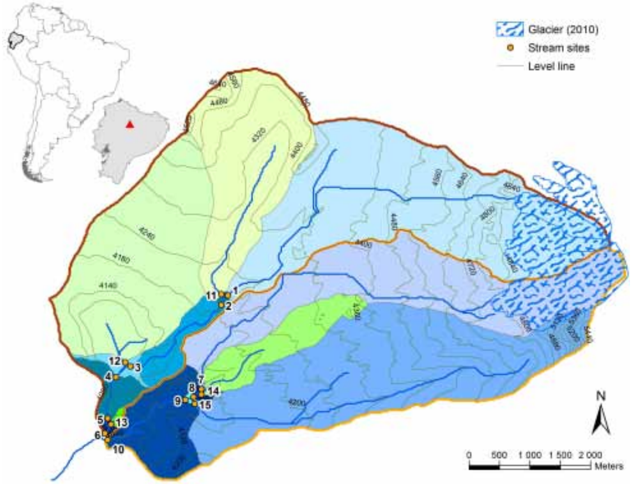

Fig. 1. Study area at the Antisana volcano, Ecuador. Stream sites are represented by orange circles. Catchment basins of all stream sites are represented by blue (glacier-fed stream sites) and green (supposedly non-glacial tributaries) polygons. Map was made using ArcGIS (10.0), and catchment basins were defined using SAGA (2.0.8). The location of the Antisana volcano is indicated on the map of Ecuador by a red triangle. The catchments "Los Crespos" (including the catchments of stream sites 7 to 10, 14, and 15) and "Antisana 14 Glacier" (including the catchments of stream sites 1 to 6, and 11 to 13) are delimited by an orange and brown contour line, respectively.

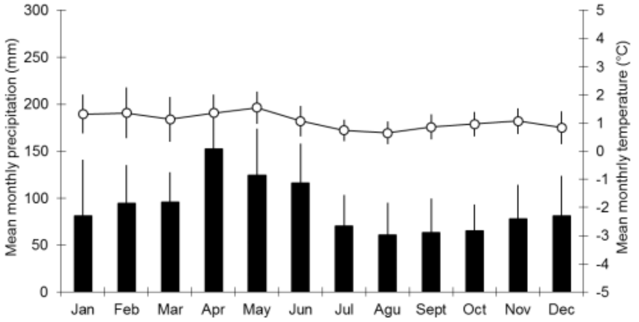

Fig. 2. Mean monthly precipitation (bars) and temperatures (dots) over 1 yr at the Antisana volcano, Ecuador. The weather station is located on the proglacier margin of Glacier 15 at 4850 m. Mean values and standard deviations were calculated over 6 yr (2005–2010).

repeated events at different temporal scales (Lafreneire and Sharp, 2003). This method has a long tradition in climatology and hydrology (e.g., Smith et al., 1998; Mathevet et al., 2004; Labat, 2005; Jiang et al., 2007), but, surprisingly, only a handful of studies used wavelet analyses on glacier-fed stream discharge time series, with, to our knowledge, only one study (Lafreneire and Sharp, 2003) using wavelet transforms on discharge time series to identify the seasonal and inter-annual variability in the relative contributions of different water sources (e.g., glacial ice, snow, rain and groundwater).

In our study, we used wavelet analyses on water-level time series from 15 stream sites in two glacierized catchments in the tropical Andes of Ecuador to determine the glacial influence in alpine hydrosystems and to identify the fluctuation of this glacial influence throughout the year. We further propose three metrics to quantify the power, the frequency, and the temporal clustering of the diurnal flow variation based on the scale-averaged wavelet power spectrum at 24 h scale. Our goals were (1) to test whether our method was reliable using water-level time series instead of discharge time series; (2) to verify that the diurnal flow variations were only caused by the glacial meltwater; (3) to describe the glacial influence in two well-studied catchments in the tropical Andes using wavelet analyses on water levels; and (4) to test the information provided by the three wavelet metrics (i.e., power, frequency, and temporal clustering of the diurnal flow variation) with regards to one of the most widely used index, the percentage of glacier cover in the catchment.

2 Study sites

2.1 Climatic, glaciological and hydrological settings

The study was conducted in the Ecological Reserve of Antisana, Ecuador (0°29′06″ S, 78°08′31″ W; Fig. 1). From a climatological viewpoint, the Antisana volcano belongs to the inner tropics (sensu Troll, 1941) with more or less continuous precipitation and homogeneous temperature conditions throughout the year (Fig. 2). The Antisana's precipitation regime is complex. Although substantial precipitation is observed year-round, there is always a period with heavy precipitation between February and June. The beginning of this wet season is however quite variable, and another period between September and November generally shows high a amount of precipitation. These features reflect the different origins of precipitation at the Antisana. First, Antisana receives precipitation from the Amazon Basin. The eastern slopes of the Andes are the first obstacles encountered by air masses coming from the east, pushed by the trade winds from the Atlantic (Vuille et al., 2000), creating an ascent of the air and an adiabatic cooling leading to heavy precipitation. Second, the site is located in a border zone with the inter-Andean plateau; thus on Antisana, the precipitation regime of the Amazon regions (a single maximum between June and July and a minimum in February) is mixed with the inter-Andean valley regime (with two wet seasons in February–May and October–November; Vuille et al., 2000). At inter-annual timescales, there is a general agreement that a significant fraction of the variability of precipitation is related to the El Niño–Southern Oscillation (ENSO) phenomenon, with El Niño years (warm phase of ENSO) tending to be warmer and drier than the average, while La Niña years (ENSO cold

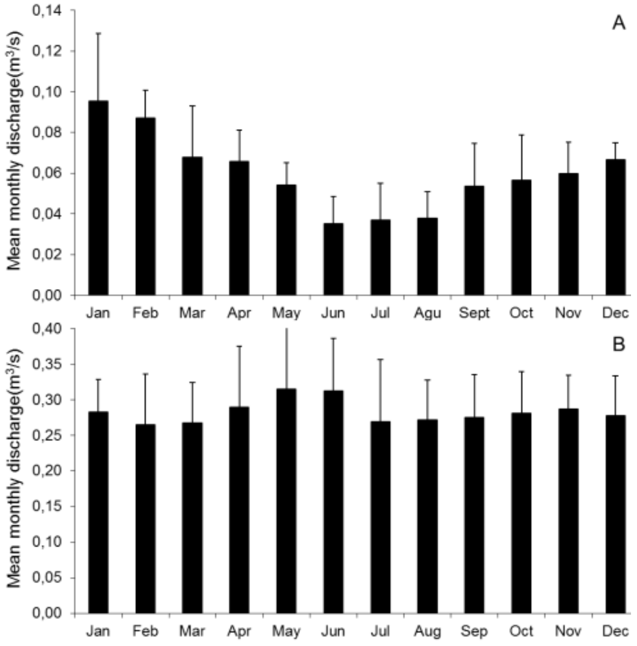

Fig. 3. Mean monthly discharge data at two gauging stations with high (**A**, Los Crespos station, 54.5 % of glacier cover in the catchment) and low glacial influence (**B**, Humboldt station, 8.6 % of glacier cover in the catchment) over 1 yr in the Antisana volcano catchment, Ecuador. Mean values and standard deviations for **(A)** and **(B)** were calculated over 5 (2006–2010) and 11 yr (2000–2010), respectively.

phase) are associated with colder and wetter conditions (e.g., Vuille et al., 2000).

From a glaciological point of view, both ablation and accumulation occur all year round on Ecuadorian glaciers (Favier et al., 2004; Francou et al., 2004; Rabatel et al., 2013). Moreover, in such tropical regions, there is neither permanent nor seasonal snow cover outside the glaciers due to a combination of two characteristics. First, the 0 °C isotherm is located around 4950–5000 m a.s.l. throughout the year as there is no seasonality in temperature in Ecuador (see Fig. 2; Vuille et al., 2008). Second, glacier snouts are located at about 4850–4900 m a.s.l. (Rabatel et al., 2013). Thus, precipitation outside the glaciers is almost exclusively liquid, except during exceptionally cold conditions during strong La Niña events.

From a hydrological viewpoint, the three main components of streamflow are direct superficial runoff, snow and ice melting, and groundwater. The mean monthly discharge ranges from 0.04 to 0.1 m^{3} s^{-1} at Los Crespos station (1.6 km from the glacier snout of the "Crespo" glacier) and from 0.25 to 0.3 m^{3} s^{-1} at Humboldt station (8 km from the glacier snout; see Fig. 3). The differences in absolute values of outflows are due to the different drainage areas with 2.4 and 14.2 km^{2}, respectively. Two different patterns in the monthly outflows variations can be observed. The mean monthly discharge for the Los Crespos station shows a perennial flow with the lower values observed between June to August and higher values from October to May. The high discharge values are a consequence of important glacier melting resulting from strong shortwave radiation absorption (i.e., low surface albedo, resulting from liquid precipitation over the lower part of the glacier). Low discharge values are a consequence of higher wind velocity that enhances mass losses through sublimation instead of melting. The correlation between the precipitation and the outflows is weak, and the regime is mainly controlled by glacier melting (Favier et al., 2004). The flow at the Humboldt station shows low seasonal variations in accordance to the pluviometric regime with glacier contribution during the months of lower precipitation.

2.2 Stream sites

The study was conducted in 15 stream sites belonging to two glacier-fed catchments in the Ecological Reserve of Antisana. These sites were selected because detailed long-term climatic and hydrological data were available in this area. For example, work on the geology and water chemistry of these catchments (see Favier et al., 2008; Villacis, 2008) has detected glacial meltwater infiltrations and resurgences, which were of great interest to test the relevance of our method (see Introduction).

To assess the wavelet signals of a broad range of glacial contributions, 10 of the 15 stream sites (no. 1–10; Fig. 1) were localized along two glacier-fed streams and five on their respective tributaries (no. 11–15; Fig. 1). Among the studied tributaries, four stream sites (no. 11–14) were considered non-glacial as they had no glacier cover in their catchment (see Fig. 1) and did not present physico-chemical features generally observed in glacier-fed streams (Brown et al., 2003), e.g., high turbidity (> 30 NTU), low conductivity (< 10 µS cm^{-1}) (see Table 1), and one site (no. 15) was partially fed by glacial meltwater (glacier cover in the catchment = 1.0 %). The two glacier-fed streams originated at 4730 m a.s.l.: one from the snout of the "Crespos" Glacier, which covered an area of about 1.82 km^{2} at the time of the study in 2010, and the second from the snout of the Glacier "14", which covered an area of about 1.24 km^{2} (Rabatel et al., 2013). Stream sites were all located between 4040 and 4200 m a.s.l., between 5.9 and 9.6 km away from the glacier snouts. At the glacier snout, both streams had high turbidity (> 285 NTU) and low conductivity (< 9 µS cm^{-1}), which decreased and increased downstream, respectively, in particular after confluences with tributaries (see Jacobsen et al., 2010; Kuhn et al., 2011, for details). Contrastingly, non-glacial tributaries presented high conductivity (> 60 µS cm^{-1}) and low turbidity (< 10 NTU, see Table 1 for details on the physico-chemical characteristics of each stream site).

Table 1. Physico-chemical attributes of the study stream sites (see location of the sites on Fig. 1). Conductivity, turbidity, and temperature are means with min-max values given in brackets ($n = 2$ to 10 for conductivity and temperatures; $n = 1$ to 3 for turbidity). Stream sites no. 11 to 15 have no visible connection to the glacier. GCC = glacier cover in the catchment. UTM coordinates refer to stream site coordinates in UTM-WGS84 zone 17S expressed in meters.

Sites	UTM coordinates		Altitude	Distance from	%	Conductivity	Turbidity	Temperature
	X (long.)	Y (lat.)	(m a.s.l.)	glacier (m)	GCC	(µS cm^{-1})	(NTU)	(°C)
1	811 725	9 945 452	4195	5932	17	16.7 (14.6–20)	144 (133–155)	8.5 (4.9–11.8)
2	811 710	9 945 398	4193	6157	11.3	22 (19–24.6)	131	9.1 (7.3–11.4)
3	809 927	9 944 126	4093	8282	10.7	42.5 (35.9–53.6)	92	9.8 (6.8–12.1)
4	809 877	9 944 066	4095	8597	7.5	126.1 (93.7–165.3)	32	9.9 (9.2–11)
5	809 783	9 943 444	4056	9352	7.3	99.1 (49.9–138)	62	9 (6.9–11.2)
6	809 793	9 943 234	4050	9648	7.3	106.5 (88.6–142)	17	8.4 (7.1–9.9)
7	811 078	9 943 872	4109	6512	23.2	18.2 (7.1–55.6)	284	11.5 (5.6–17)
8	811 025	9 943 792	4105	6695	18.5	163.8 (68.7–248)	103 (95–111)	12.8 (7.5–16.7)
9	810 941	9 943 760	4093	6848	9.5	117.3 (81.4–167.2)	40 (36–44)	10.4 (7.4–13.4)
10	809 888	9 943 190	4042	8493	8.6	143.6 (82.4–308)	41.6 (37–46.1)	10.1 (6.9–11.8)
11	811 707	9 945 446	4202	–	0	72.4 (58.5–108)	4	8.3 (5.8–12.2)
12	809 890	9 944 154	4090	–	0	175.6 (144.9–209)	10	10.2 (9.6–11.7)
13	809 919	9 943 238	4050	–	0	137.2 (90.4–274)	1.3 (1–1.9)	7.5 (7.1–9.9)
14	811 098	9 943 836	4101	–	0	244.2 (191.1–313)	7 (5–9)	13.1 (7–17)
15	811 088	9 943 738	4108	–	1	106.1 (67.8–157.4)	6 (5–7)	9.3 (7–11.7)

2.3 Field measurements

The location of each stream site was measured using the UTM-WGS84 coordinate system with a GPS (Garmin Oregon 550, Garmin International Inc., Olathe, USA). In January 2010, 15 water pressure loggers were installed (Hobo water pressure loggers, Onset Computer Corp., USA) in the water at each stream site and recorded water pressure every 30 min over 10 months (i.e., from January to October 2010). Water pressure loggers were previously protected in plastic tubes placed vertically on the stream side where the sections were deep enough to avoid overflowing during the glacial flood and with homogeneous shapes among stream sites. Water level and height between the stream bottom and the Hobo sensor were measured twice, when the loggers were installed and removed. One more logger was fixed on a rock at 4100 m a.s.l. to measure the atmospheric pressure and the air temperature every 30 min over the same 10-month period. In addition, at the Los Crespos hydrological runoff gauging station (close to site 7), discharge was recorded every 30 min during the entire year of 2010 (Fig. 4). Precipitation was also recorded every 30 min at the weather station, located on the glacier foreland of Antisana 15 Glacier, within our catchment area.

3 Materials and methods

3.1 Wavelet transform analyses on water-level time series

Our method proposes using wavelet transform analyses on water-level time series to detect the hydrological signal originating from glacier melting. As glacial runoff exhibits repeated cyclic fluctuations at the daily timescale during the ablation period (Hannah et al., 1999, 2000), we aim to detect corresponding variations in water level at 24 h scale.

Previous work has reviewed in detail the concepts of wavelet analysis for different applications (Daubechies, 1990; Torrence and Compo, 1998; Cazelles et al., 2008). Here we list some important concepts with special attention to properties used in this study. The wavelet transform analysis is a time-dependent spectral analysis that decomposes a data series in time–frequency space. The wavelet transforms therefore express a time series in a three-dimensional space: time (x), scale/frequency (y), and power (z). The power matches the magnitude of the variance in the series at a given wavelet scale and time. Various types of wavelet functions (e.g., Morlet, Mexican hat, Paul) can be used for the signal transform, depending on the nature of the time series and the objectives of the study. Here, we chose the Morlet wavelet, a nonorthogonal, continuous, and complex wavelet function (with real and imaginary parts), because it is particularly well adapted for hydrological time-series analyses (Torrence and Compo, 1998; Labat et al., 2000; Lafreneire and Sharp, 2003). Nonorthogonal continuous wavelet transforms are indeed more robust to noise than other decomposition schemes

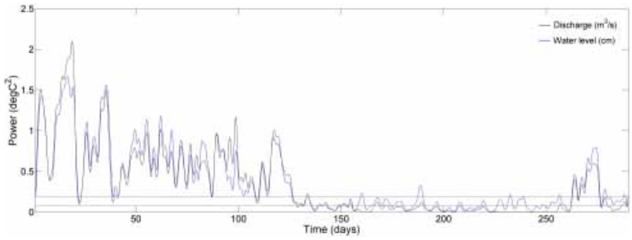

Fig. 4. Comparison of the wavelet analysis output (scale-averaged power spectrum over 24 h scale) between discharge (black line) and water-level time series (blue line) at site 7 (Los Crespos station). Dashed black and blue lines indicate the corresponding 95 % confidence levels for the red-noise spectrum for discharge and water-level time series, respectively.

and are robust to variations in data length (Cazelles et al., 2008). Moreover, complex wavelet functions are well suited for capturing oscillatory behavior, whereas real wavelet functions do better at isolating peaks or discontinuities (Torrence and Compo, 1998). Finally, the Morlet wavelet function has a high resolution in frequency compared to other continuous wavelets (Cazelles et al., 2008), which was fundamental in our method as we intended to detect the repeated water-level variations at 24 h scale.

The continuous wavelet transform $W_n(s)$ of a discrete time series x_n (n being the time position) at scale s is defined as the convolution of x_n with a scaled and translated version of the wavelet function $\psi(t)$:

$$W_n(s) = \sum_{n'=0}^{N-1} x_{n'} \psi * \left[\frac{\left(n' - n\right)\delta t}{s}, \right] \tag{1}$$

where N is the number of points in the time series, $\psi * (t)$ the complex conjugate of wavelet function (the Morlet wavelet in our case) at scale s and translated in time by n, and δt the time step for the analysis (Torrence and Compo, 1998). The Morlet wavelet is defined as

$$\psi(t) = \pi^{-1/4} e^{i w_0 t} e^{-t^2/2}, \tag{2}$$

where t is a nondimensional "time" parameter, and w_0 the nondimensional frequency. w_0 must be equal to or greater than 5 to satisfy the wavelet admissibility condition (Farge, 1992; Cromwell, 2001): the function must have zero mean and be localized in both time and frequency space to be "admissible" as a wavelet (Santos et al., 2001). In the present application, we use $w_0 = 6$, a value commonly used for geoscience applications (Torrence and Compo, 1998, Labat, 2005; Si and Zeleke, 2005; Schaefli and Zehe, 2009). For $w_0 = 6$, the Morlet wavelet scale was almost identical to the corresponding Fourier period of the complex exponential, and the terms "scale" and "period" may conveniently be used synonymously (Torrence and Compo, 1998; Torrence and Webster, 1999; Maraun and Kurths, 2004). Thus the left axis in Figs. 5 and 6 is the equivalent Fourier period corresponding to the wavelet scale.

To visualize the magnitude of the variance in the series at a given wavelet scale and location in time, we determined the local wavelet power spectrum (Torrence and Compo, 1998), defined as the squared absolute value of the wavelet transform ($|W_n(s)|^2$) and calculated as follows:

$$|W_n(s)|^2 = W_n(s)\, W_n^*(s), \tag{3}$$

where $W_n * (s)$ is the complex conjugate of $W_n(s)$.

To examine fluctuations in power over a range of scales (a band), we calculated the scale-averaged wavelet power spectra $\overline{W_n^2}$, defined as the weighted sum of the wavelet power spectrum (over two scales s_1 to s_2), over the whole measurement period.

$$\overline{W_n^2} = \frac{\delta j \delta t}{C_\delta} \sum_{j=j_1}^{j_2} \frac{\left|W_n(S_j)\right|^2}{S_j}, \tag{4}$$

where δj is the spacing between discrete scales, δt the time step of the time series, and C_δ the reconstruction factor (Anctil and Coulibaly, 2004; Coulibaly and Burn, 2004; Markovic and Koch, 2005; White et al., 2005).

3.2 Glacial signal determination

As glacier-fed streams are characterized by diurnal flood events, with discharge depending on the portion of glacier exposed to melting conditions (Favier et al., 2004; Villacis, 2008), we calculated the scale-averaged wavelet power spectrum over scales around 24 h over the whole time series, which permitted visualizing the fluctuation of the diurnal flow variation power throughout the year.

The significance of the wavelet power spectrum was tested against a background (or noise) spectrum, which is either white noise (constant variance across all scales or frequencies) or red noise (increasing variance with increasing scale or decreasing frequency; Schiff, 1992). When the wavelet power of the time series exceeds the power of the background (at the chosen confidence level), the time-series variance can be deemed significant (see Torrence and Compo, 1998; Lafreneire and Sharp, 2003, for background spectrum calculation details). Assuming a random process, we chose here the red-noise spectrum (at 95 % confidence level; see Lafreneire and Sharp 2003, Schaefli et al., 2007, for a justification on red-noise choice).

To express the main features of the scale-averaged wavelet power spectrum quantitatively over time, allowing a comparison of glacial influence among sites, we defined three metrics: (1) the diurnal variation power, (2) the diurnal variation frequency, and (3) the diurnal variation temporal clustering. The scale-averaged wavelet power at 24 h scale is considered significant when above the 95 % confidence level curve (see Torrence and Compo, 1998; Markovic and Koch, 2005).

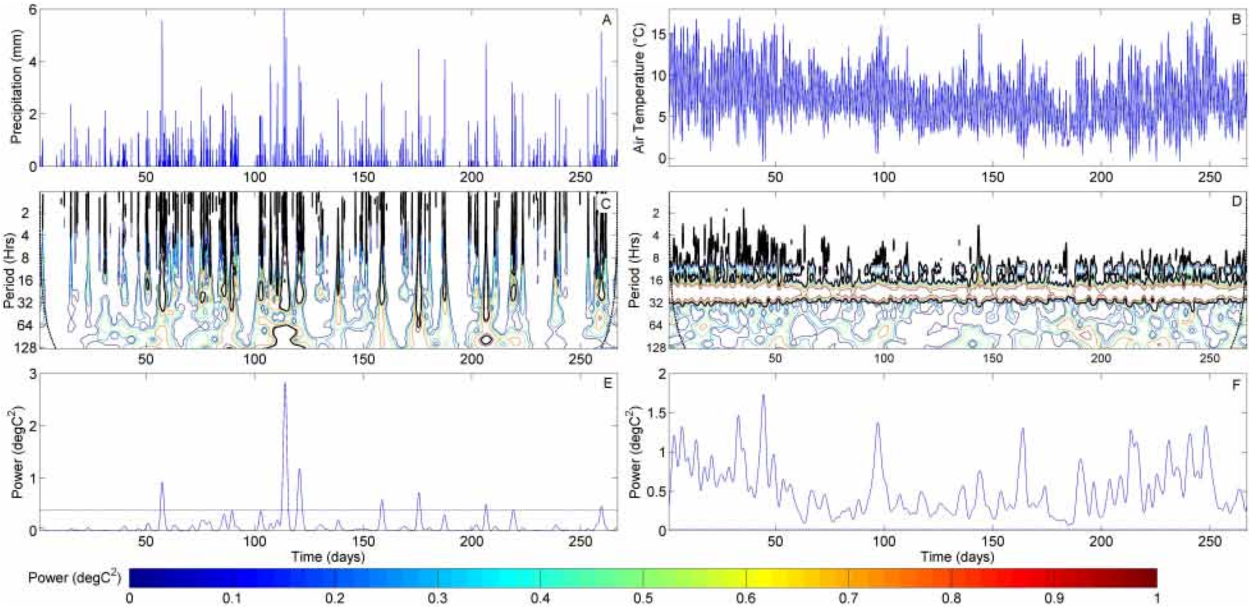

Fig. 5. Wavelet analysis outputs for rainfall (**A**, **C**, and **E**) and air temperature time series (**B**, **D**, and **F**): **(A–B)** averaged normalized rainfall **(A)**, and air temperature **(B)** time series. **(C–D)** local wavelet power spectrum normalized by their standard deviations. The black line delineates the areas where the power is significant (i.e., exceeds the 95 % confidence level of a red-noise process). The dashed black line delineates the cone of influence that delimits the region not influenced by edge effects. **(E–F)** normalized scale-averaged wavelet power spectra at 24 h. The dashed blue line shows the corresponding 95 % confidence level for the red-noise spectrum. In each panel, day one corresponds to the 1 January 2010. The color bar shows the legend for the different colors: blue and red for low and high wavelet power, respectively.

We calculated the *diurnal variation power* as the integration of the corrected scale-averaged wavelet power curve (i.e., divided by its corresponding 95 % confidence level value). Note that we calculated the area under the curve above the "$y = 1$" line (see Torrence and Compo, 1998). Higher values of diurnal variation power correspond to higher power of the variance in water levels at 24 h scale. The *diurnal variation frequency* was calculated as the frequency of days with significant diurnal flow variations in the time series. A diurnal variation frequency equal to 0 means no significant diurnal flow variation over the study period while when equal to 1 it corresponds to a significant diurnal flow variation every day. Concerning the *diurnal variation temporal clustering* (sensu De Vos et al., 2010; Hsu and Li, 2010), we first defined two "hydrological states" corresponding to days with and without significant diurnal flow variation. We then calculated the number of hydrological state changes and divided it by the total number of days in the time series minus one (the maximum number of possible state modifications). If the diurnal variation temporal clustering is equal to 1, there is no hydrological state shift (i.e., there is never/or every day significant diurnal flow variations). On the contrary, if it is equal to 0, the hydrological state of the stream changes every day.

3.3 Application

3.3.1 Local and scale-averaged wavelet power spectrum

To determine the glacial influence based on water-level time series, we first transformed water pressure values, obtained from the 15 stream sites, into water-level values by subtracting the atmospheric variations from the water pressure data. Time series were centered on their means and normalized by their standard deviations prior to wavelet transform calculation to allow across-site comparison of our results. We then developed a code inspired by C. Torrence and G. Compo (available at http://paos.colorado.edu/research/wavelets) that we ran in MATLAB, version R2009a (The MathWorks Inc., Natick, MA, USA). This code allowed producing three types of figures: (1) the averaged normalized water-level time series, which presents the water-level variations throughout the year; (2) the local wavelet power spectrum (normalized by their standard deviations), which gives the magnitude of the variance in the series at a given wavelet scale and location time; and (3) the scale-averaged wavelet power spectrum, which presents the fluctuation in power over 24 h scale over a whole year. For illustrative purposes, Fig. 6 presents the outputs of our wavelet analyses for three stream sites with contrasting time-series patterns resulting from different glacial influences: a glacier-fed stream site without tributaries (no. 7, Fig. 6a, d and g) and two groundwater-fed

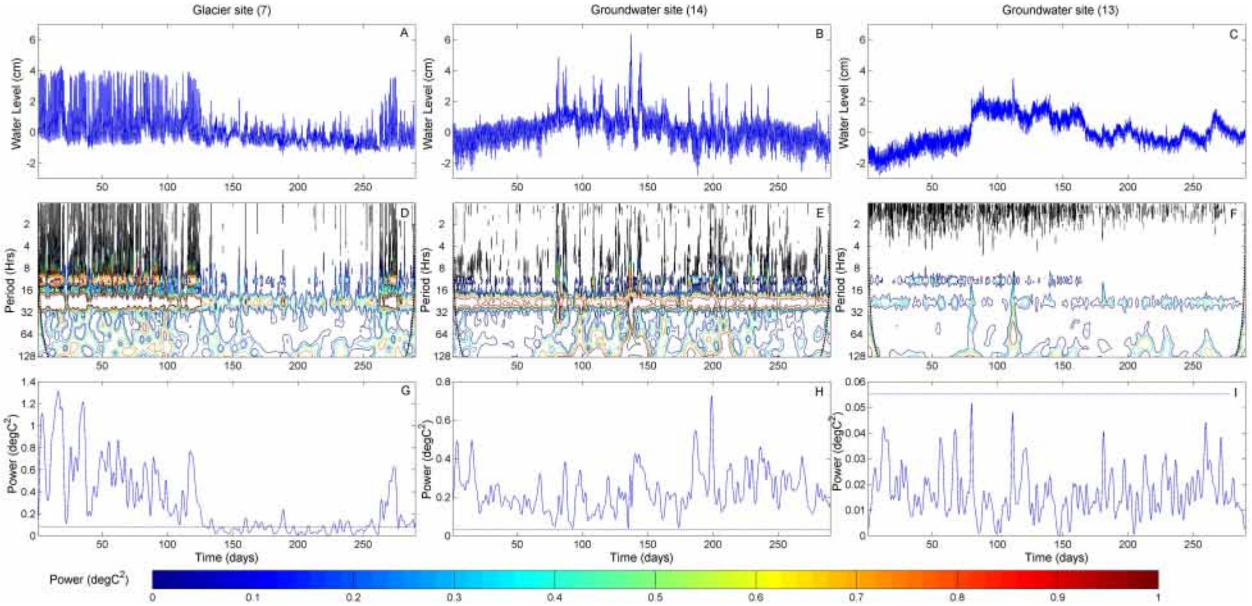

Fig. 6. Wavelet analysis outputs at three stream sites (7, 13, 14) with contrasting glacial influence (site 7 is glacier-fed while site 13 and 14 have no superficial connection to the glacier – but site 14 has glacial resurgence as indicated by significant diurnal flow variation). **(A)**, **(B)**, **(C)**: averaged normalized water-level time series. **(D)**, **(E)**, **(F)**: local wavelet power spectrum normalized by their standard deviations. The black line delineates the areas where the power is considered significant (i.e., exceeds the 95 % confidence level of a red-noise process); the dashed black line delineates the cone of influence that delimits the region not influenced by edge effects. **(G)**, **(H)**, **(I)**: normalized scale-averaged wavelet power spectra at 24 h. The dashed blue line shows the corresponding 95 % confidence level for the red-noise spectrum. In each panel, day one corresponds to the 1 January 2010. The color bar shows the legend for the different colors: blue and red for low and high wavelet power, respectively.

stream sites (no. 13 and 14, Fig. 6b, c, e, f, h, and i). For all stream sites we then calculated from the scale-averaged wavelet power spectrum the three metrics defined above (diurnal variation power, diurnal variation frequency, and diurnal variation temporal clustering).

To test whether our method was reliable using water-level time series instead of discharge time series, we compared wavelet outputs of water-level time series at site 7 and those from discharge time series at the Los Crespos hydrological station (Fig. 4). Moreover, to exclude the rainfall as contributor of diurnal flow variation, we plotted the precipitation and air temperature time series (Fig. 5a and b), their corresponding local wavelet power spectrum (Fig. 5c and d), and scale-averaged wavelet power spectrum at 24 h scale (Fig. 5e and f).

3.3.2 Glacier metrics vs. glacier cover in the catchment

As the percentage of glacier cover in the catchment is commonly used to estimate the potential influence of a glacier on a stream (e.g., Hari et al., 2005; Thayyen and Gergan, 2010; Jacobsen et al., 2012), we were interested in assessing how our three wavelet metrics at each stream site would behave as a function of glacier cover in the catchment.

To measure the percentage of glacier cover in the catchment, we first created the channel network, and the catchment area was calculated with the SAGA GIS software (System for Automated Geoscientific Analyses, version 2.0.8). Briefly, SAGA derives a channel network based on gridded digital elevation model (DEM) with the specification of the target cells (gauge station), for which the upslope contributing area is identified. The catchment delimitation is based on the multiple flow direction model (Tarboton, 1997), and the extraction of the drainage network uses the algorithm described in O'Callaghan and Mark (1984). We created the hydraulic channel network of our two study catchments using a 40 m resolution DEM in SAGA GIS. The DEM was created using 40 m resolution contour line from the Ecuadorian Military Geographical Institute (available at http://www.igm.gob.ec/site/index.php) in ArcGIS (10.0). We verified each created channel with our GPS point measurements and field observations, and determined for each stream site the corresponding catchment using SAGA GIS (Olaya and Conrad, 2009). Hereafter we named “Los Crespos” and “Antisana 14 Glacier” catchments as the area of all small catchments they contain: Los Crespos catchment includes catchments of stream sites 7 to 10, 14, and 15; and Antisana 14 Glacier catchment includes catchments of stream sites 1 to 6, and 11 to 13 (see Fig. 1).

Glacier outlines were first automatically extracted from LANDSAT satellite images (30 m pixel size) using the common Normalized Difference Snow Index (NDSI). The glacier outlines were then manually checked and adjusted by overlaying the glacier outline shapefile on the satellite images for which a spectral band combination associating the shortwave infrared, the near infrared, and the green bands had been applied (such a combination facilitates the distinction between snow, ice and rock; see Fig. 4 in Rabatel et al., 2012). We finally merged the glacier outlines and catchment contours shapefiles using ArcGIS 10.0. This enabled computing the percentage of the glacier cover in the catchment basin of each stream site by dividing the glacier area by the total catchment basin area. The three metrics (diurnal variation power, diurnal variation frequency, and diurnal variation temporal clustering) were plotted against the percentage of glacier cover in the catchment. The strength of the glacier cover in the catchment vs. the three metrics correlation was measured using Spearman correlation coefficients and associated p values.

4 Results and discussion

4.1 Water-level vs. discharge time series

To verify whether our method was reliable using water-level time series, we compared our wavelet analysis outputs on discharge time series (in "Los Crespos" hydrological station) vs. those obtained with water-level time series at site 7. We found a very good match between both curves (Fig. 4), and all significant diurnal flow variations on discharge data were also detected on water-level data. This indicates that our method for detecting and characterizing glacial influence can be applied on both stream discharge and water-level time series. This is an interesting result as using water-level data instead of stream discharge presents at least two main advantages. First, water-level data are easily obtained using staff gauges or pressure transducers, whereas discharge data additionally require detailed velocity measurements under a range of conditions to generate a rating curve. Second, discharge is usually inferred from stage measurements using a rating curve, which is subject to error. However, water-level data can be used only if the stage–discharge relationship is not too strongly non-linear, and if the shape of the cross sections remains unchanged throughout the measurement period, which was the case in our study.

4.2 Sorting out the contribution of rainfall and snowmelt to diurnal flow variation

To verify that diurnal flow variations were mainly caused by glacier or snow melting, we first performed wavelet analyses on air temperature time series. The local wavelet power spectra of air temperature time series show that most of the variance in temperature time series indeed occurred at 24 h scale (Fig. 5d and f). We then performed wavelet analyses on precipitation time series to rule out the potential influence of diurnal rainfall events (e.g., convective storm activity) on diurnal flow variation. We only found seven significant peaks over 2010 in the scale-averaged wavelet power spectrum at 24 h scale (Fig. 5e), which corresponded to a total of only 19 rainy days with significant diurnal variation. This supports the fact that, in our case, the diurnal variation of the streamflow could be employed as an indicator of meltwater influence (Favier et al., 2004). Note that if the local wavelet spectrum for precipitation data had significant power at 24 h scale all year round (which was not the case in our study), a wavelet coherence spectrum analysis on the two time series could then be run (Torrence and Compo, 1998; Maraun and Kurths, 2004), and would allow determining whether or not the water-level–precipitation cross spectrum mimics the general pattern observed in the wavelet spectrum of water-level time series.

In the inner tropics, the absence of snow cover outside the glaciers (see study site section) ensures that glacier melting is the main cause of diurnal flow variations. Note, however, that in other regions, our method would not allow identifying the relative contribution of ice melt and snowmelt on streamflow variation, and should therefore be employed as an indicator of seasonal or multi-annual storage of water in the form of snow or ice.

4.3 Local and scale-averaged wavelet power spectrum to detect glacial influence

Most of the variance in the local wavelet spectra of stream sites 1 to 10 was concentrated at the 24 h period (Fig. 6d). This diurnal wavelet power represented the diurnal glacial flood (see also Lafreneire and Sharp, 2003), resulting from the diurnal fusion of the ice (see above). At all sites along the two glacier-fed streams, the power of the local wavelet spectra at the 24 h period was statistically significant over the 10 months (Fig. 6d). Indeed, glacial floods occur all year round in equatorial glacier-fed streams due to the lack of thermal seasonality in the inner tropics (Favier et al., 2008; Vuille et al., 2008; Jacobsen et al., 2010). However, we found that, for all stream sites from 1 to 10, the scale-averaged wavelet power at 24 h scale was continuously significant between January and May while it was seldom significant after May (e.g., site 7, Fig. 6g). This phenomenon is related to strongest ablation rates of the glaciers during this period (January to May). Indeed, Rabatel et al. (2013) showed that during the period from January to April 2010 the Antisana glaciers experienced high ablation rates related to El Niño conditions (see Fig. 9 in Rabatel et al., 2013), which favored glacier melting. Contrastingly, ablation is generally reduced under La Niña conditions (Francou et al., 2004).

As expected, the three non-glacial tributaries (sites 11, 12, and 13) did not present any significant power at 24 h scale (Fig. 6f). The scale-averaged wavelet power spectrum was below the 95 % confidence level curve during the entire study period (Fig. 6i). Surprisingly, significant glacial signal was identified at one supposedly non-glacial site (site 14, Fig. 6e). While this site presented no glacier cover in its catchment as well as non-glacial characteristics (turbidity < 9 NTU, conductivity $> 90\,\mu\mathrm{S\,cm^{-1}}$; Fig. 1 and Table 1), our wavelet analysis revealed a significant glacial influence (Fig. 6e and h). However, the unexpected spectrum at site 14 confirms the presence of glacial water resurgence, as previously detected by Villacis (2008) and Favier et al. (2008) (see study site section). Site 14 was a spring with a substantial discharge (around $20\,\mathrm{L\,s^{-1}}$, similar to that of site 7) revealing the presence of an aquifer with meltwater alimentation and underground flow transfer. The scale-averaged wavelet power spectrum at 24 h scale allowed identifying such infiltrations using only data of water levels, making the diurnal flow variation analysis a good method for understanding glacial influence. This is an important result as catchments with complex geological structure containing groundwater reservoirs and meltwater infiltrations are common throughout the world, in particular in volcanic regions (Favier et al., 2008).

4.4 Relationship between wavelet metrics and glacier cover in the catchment

As expected, we found an overall significant positive relationship between the diurnal variation power and the percentage of glacier cover in the catchment (Spearman rank test, $r = 0.71$, $F = 13.12$, $p < 0.01$). The diurnal variation power generally decreased as moving downstream, and this decrease was more pronounced at sites located after a confluence with a groundwater tributary (except for site 14), a pattern already observed by Jacobsen and Dangles (2012) using their glacier index. Figure 7a also highlights the particularity of site 14, whose diurnal variation power was far above the regression line. Note that removing site 14 from the relationship between the diurnal variation power and percentage of glacier cover in the catchment increased markedly the correlation coefficient ($r = 0.93$, $F = 76.14$, $p < 0.001$). This confirms that analyzing the diurnal flow variation may be a much better alternative to the percentage of glacier cover in the catchment as the latter does not permit the detection of glacial meltwater reemergence.

We found a high diurnal variation frequency (> 0.45, i.e., the diurnal flow variation was significant about half of the year) for all sites that had at least part of their catchment covered by glacier. Interestingly, while we found a significant positive relationship between the diurnal variation frequency and percentage of glacier cover in the catchment in the Antisana 14 Glacier catchment ($r = 0.98$, $F = 194.98$, $p < 0.001$, Fig. 7b), this was not the case for the Los Crespos catchment (no significant relationship). This suggests that the two catchments have different hydrological behaviors, which may be related to the different origin of the tributaries of the main glacier-fed stream. Indeed, while the Los Crespos stream had several tributaries with glacial influence (e.g., site 14, 15), the Antisana 14 Glacier catchment had only non-glacial tributaries (see Fig. 1).

Stream sites with no glacier cover in their catchment had diurnal variation temporal clustering values equal to 1 as they were always in the same hydrological state of no significant diurnal flow variation (full clustering; Fig. 7c). All other stream sites (e.g., with glacier cover in the catchment $> 0\,\%$) had also high temporal clustering values (> 0.85) meaning that the two possible hydrological states (days presenting either significant or non-significant diurnal flow variation) did not alternate frequently but were rather clustered over the year (i.e., the ablation process concentrates at specific periods of the year). For these stream sites, we found a significant positive relationship between the diurnal variation temporal clustering and the percentage of glacier cover in the catchment ($r = 0.76$, $F = 12.33$, $p < 0.01$, see Fig. 7c). This suggests a decreasing number of switches between the two hydrological states as percentage of glacier cover in the catchment increases. Due to the high diurnal variation frequency measured in glacier-fed sites (see above), the probability of having alternative hydrological states decreases closer to the glacier, where significant diurnal flow variations are more frequent. Note that both diurnal variation frequency and temporal clustering do not have an absolute meaning, but they give substantive additional temporal information to characterize the glacial influence, and are used to compare signals among sites.

The three metrics obtained with our wavelet analyses are complementary and do not convey the same information on the hydrology of the watersheds. Indeed each metric presented a different relationship with the percentage of glacier cover in the catchment (Fig. 7a, b, and c). Even though the diurnal variation power was sufficient to detect, quantify and compare the glacial influence among sites, it did not give any information about the variation over time of this glacial influence. Both diurnal variation frequency and temporal clustering revealed that the temporal dynamics of water regimes differed between the two study catchments, and that the high flow/low flow regime shift could be a relevant index of glacier behavior. As the variance in hydrological regime of glacier-fed streams in the tropics has been proposed to be a good indicator of the state of glacier retreat (Baraer et al., 2012), further applications of the diurnal variation temporal clustering index may be relevant.

5 Conclusions

Our study is the first to propose the analysis of diurnal flow variation as an indicator of glacial influence in mountain catchments. Opting for wavelet analyses as a methodological framework had several advantages as it allowed a full description of the glacial influence over time. We showed that our method (1) is relatively simple and cost-effective as it can be used with water-level data instead of discharge

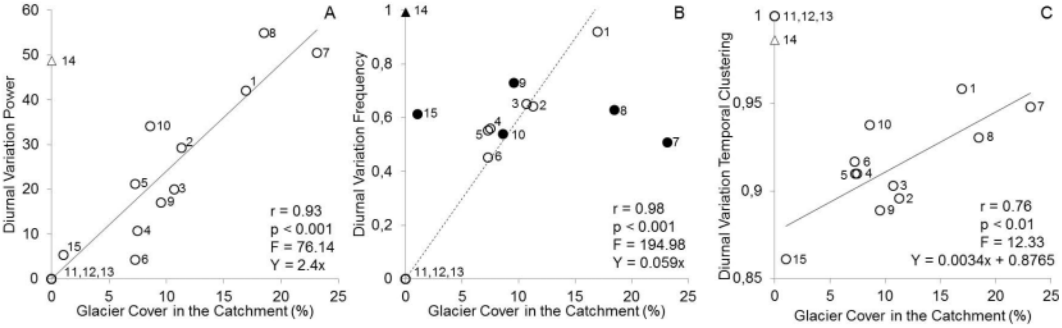

Fig. 7. Scatter plot of **(A)** diurnal variation power, **(B)** diurnal variation frequency, and **(C)** diurnal variation temporal clustering vs. the percentage of glacier cover in the catchment. In **(B)** black dots represent stream sites located in the Los Crespos catchment and open dots stream sites in the Antisana 14 Glacier catchment. The full regression line excludes site 14 in **(A)**, sites localized in the Los Crespos catchment (i.e., excludes black dots) in **(B)** and sites with no glacier cover in the catchment (i.e., excludes sites 11 to 14) in **(C)**. Sites numbers are indicated in the three panels.

data; (2) can sort out the potential influence of other water sources to detect the glacial signal; (3) reliably quantifies the glacial influence and can therefore be used as a substitute of the percentage of glacier cover in the catchment; (4) allows detecting the influence of glacial meltwater in resurgence; and (5) allows providing a detailed description of temporal patterns in flow variations over time thereby making possible quantitative comparisons of the glacial influence among sites. Taking all these aspects in consideration, we think that our method represents a significant improvement when compared to existing methods, as it overcomes most of their limitations (see Introduction).

Several issues however require further investigation. In particular, it would be interesting to study whether our method could be used on continuous stream discharge time series to quantify (in terms of volume) the glacier contribution of different water sources at a given stream site. Another important issue is to what extent this method may be applicable in other regions of the world. On the one hand, as diurnal glacial floods always occur during the ablation season in any glacier-fed streams worldwide – e.g., in the tropical Andes (Rabatel et al., 2013), the Himalayas (Sorg et al., 2012), the European Alps (Schutz et al., 2001), the North American Rockies (Lafreneire and Sharp, 2003), and the Arctic (Dahlke et al., 2012) – the core of our approach should be valid. On the other hand, several refinements would be needed to account for the specificities of temperate and arctic regions such as the presence of snow cover outside the glacier or the potential interference of rainfall with diurnal cycles, and strong annual cycle. Despite these limitations, our hope is that our method may provide a testable and applicable methodological framework to understand better the complex interactions between glacier and glacier-fed hydrosystems in a warming world.

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PART 2

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Relationships between stream macroinvertebrate communities and new flood-based indices of glacial influence

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SUMMARY

1. As glacier shrinkage is accelerating due to climate change, it is important to understand the effect of changes in glacier runoff on downstream aquatic communities. The overall goal of this study was to test the relevance of recently developed wavelet-based metrics of flow variations caused by glacial melting cycles to deepen our knowledge about the relationship between glacial influence and aquatic biodiversity.
2. In an equatorial glacierised catchment, we selected 15 stream sites covering a gradient of direct contribution from glacial runoff. At each site, we recorded water level time series for 10 months and sampled benthic macroinvertebrates. Wavelet analyses on the water level time series were used to calculate three indices: glacial flood intensity, frequency and temporal clustering. We then examined how these three indices were related to macroinvertebrate community composition using generalised additive models.
3. While macroinvertebrate density decreased significantly with glacial flood intensity, we found a significant hump-shaped relationship between local taxon richness and glacial flood intensity, a pattern that was not produced simply by overlapping broad taxon distributions from either end of the environmental gradient. These results suggest that glacial meltwater contribution creates local peaks in macroinvertebrate richness and enhances regional diversity in the catchment.
4. The significant relationships between faunal metrics and the new glacial influence indices suggest the latter are valuable for assessing the effects of altered meltwater contributions on aquatic communities of glacier-fed rivers. Relationships differed depending on the feature of the glacial disturbance considered (glacial flood intensity, frequency, temporal clustering). We anticipate that these distinctions may help disentangle the mechanisms driving aquatic biodiversity in glacierised catchments, especially in terms of identifying resistance and/or resilience as key processes in glacial macroinvertebrate communities.

Keywords: benthic macroinvertebrates, daily glacial floods, glacierised catchments, tropical mountains, wavelet analyses

Introduction

Global warming is causing glacial retreat and thinning, resulting in an altered glacial meltwater contribution to stream flow in glacierised catchments (Sorg *et al*., 2012; Grah & Beaulieu, 2013; Rabatel *et al*., 2013). The reduction in ice volume should yield a significant increase in annual glacial runoff in the early stages of glacial retreat

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(Baraer *et al.*, 2012), but after a critical threshold (depending on the glacier size), annual glacial runoff should decrease until the complete disappearance of the glacier when glacial influence on outflow will be non-existent (Rees & Collins, 2006; Huss *et al.*, 2008). Alpine headwater streams originate from snow-melt, ice-melt, rainwater runoff and ground water (Ward *et al.*, 1999; Füreder *et al.*, 2001). Glacier-fed streams are generally characterised by low water temperature (but see Jacobsen *et al.*, 2010), low channel stability, high turbidity (i.e. suspended sediment), low conductivity and high temporal variability (Milner *et al.*, 2001). Glacierised catchments thus encompass a range of streams with contributions from different water sources, from meltwater to groundwater-dominated streams (i.e. high to low glacial influence). This high spatiotemporal environmental heterogeneity gives rise to high aquatic biodiversity, including endemic species (Milner, Brown & Hannah, 2009; Jacobsen *et al.*, 2012). Therefore, in the context of global warming, it is important to develop, test and adopt tools to measure the effect of glacial influence on aquatic biodiversity to better understand and predict aquatic community responses to glacial retreat (Brown, Milner & Hannah, 2010; Jacobsen *et al.*, 2012).

Several indices of glacial influence on the stream environment have been developed and used to investigate the effect of glacial meltwater contribution on aquatic biodiversity. These have been based on percentage of glacier cover in the catchment (Rott *et al.*, 2006; Füreder, 2007; Milner *et al.*, 2009), glacier size and distance from the glacier terminus (Jacobsen & Dangles, 2012), percentage of meltwater contribution (Milner, Conn & Brown, 2006; Brown, Hannah & Milner, 2007) or physicochemical habitat variables (Ilg & Castella, 2006). All of these studies found that richness of macroinvertebrates and benthic algae decreased monotonously with increasing glacial influence. However, compiling extensive data sets from three continents, Jacobsen *et al.* (2012) recently demonstrated that local macroinvertebrate richness peaked at intermediate levels of glacial influence. These apparently conflicting findings, which suggest that mechanisms driving aquatic biodiversity in glacierised catchments are still far from completely understood, may be due to differences in data density, methods for analysing patterns and the variable used to quantify glacial influence. In this context, a key, yet poorly considered, characteristic of glacier-fed streams is that their flow shows daily flood pulses created by the ablation of the glacier, usually during the afternoon (Hannah, Gurnell & Mcgregor, 1999, 2000). Recently, Cauvy-Fraunié *et al.* (2013b) used wavelet analyses on water level time series to develop new glacial indices based on diurnal flow variation (hydrological data). The method allowed three metrics to be calculated to quantify the intensity, frequency and temporal clustering of diurnal flow variation, providing a more detailed and thorough description of glacial influence (i.e. intensity and fluctuation throughout time).

In this study, we applied these new wavelet-based metrics to explore relationships in spatial variability between macroinvertebrate communities and glacial influence in an equatorial glacierised catchment in the tropical Andes. More specifically, our objectives were (i) to test the relevance of the three glacial indices (i.e. components of glacial influence) as predictors of macroinvertebrate communities and quantify their explicative power for different faunal metrics, (ii) to reveal taxon distribution patterns producing the observed taxon richness versus glacial influence relationships and (iii) to assess the contribution of glacial influence to aquatic biodiversity within a equatorial glacierised catchment. We hypothesised (i) that this new approach would prove valuable for assessing the effects of glacial influence on macroinvertebrate communities, (ii) that we would find a hump-shaped relationship between local taxon richness and glacial influence, in agreement with Jacobsen *et al.* (2012) from the same study region, without any *a priori* expectation on the distribution of taxa producing such a pattern and (iii) that glacial influence would generate environmental heterogeneity within the glacierised catchment enhancing regional diversity. We discuss the relevance and advantages of this new method to predict the ecological response of these communities within the context of the currently ongoing glacial shrinkage.

Methods

Study site

The study was conducted in 15 stream sites belonging to two glacier-fed catchments in the Ecological Reserve of Antisana, Ecuador (0° 29′ 06″S, 78° 08′ 31″W). Ten of the 15 sites (1–10; Fig. 1) were located along the two main glacier-fed streams and five on their tributaries (11–15; Fig. 1). The two glacier-fed streams originated at 4730 m a.s.l., one from the ‘Crespo’ glacier, which covered an area of about 1.82 km^2 at the time of the study in 2010, and the second from ‘glacier 14’, covering an area of about 1.24 km^2 (Rabatel *et al.*, 2013). Study sites were all between 4040 and 4200 m a.s.l., at distances of 5.9–9.6 km from the glacier snouts.

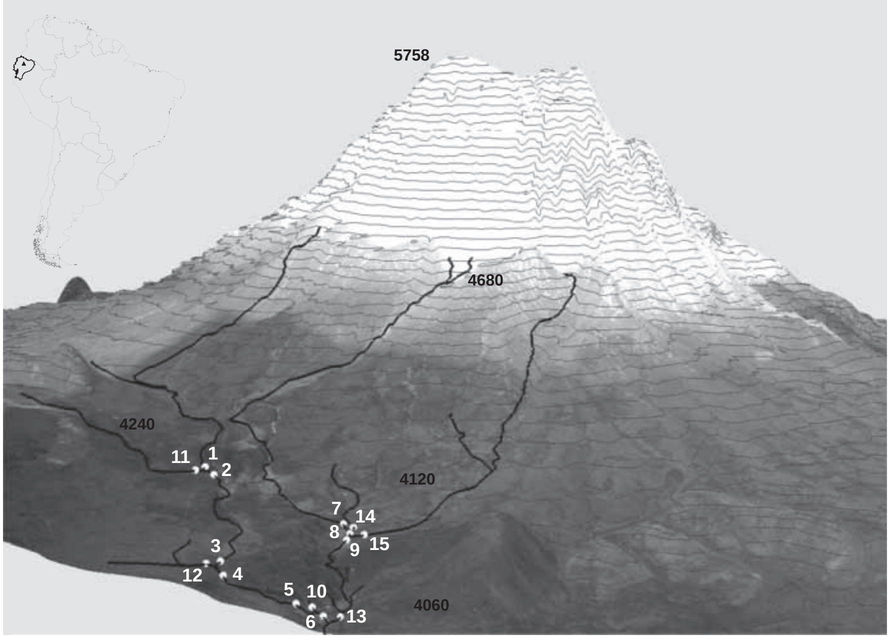

Fig. 1 Three-dimensional map of the study area at Antisana Volcano, Ecuador, based on a 1993 photo. Stream sites are represented by white circles. Contours (every 40 m) are represented by grey lines. The location of Antisana is indicated on the map of South America by a black triangle. Only study streams are shown.

Hydrological measurements

The location of each stream site was determined using the UTM-WGS84 coordinates system with a GPS (Garmin Oregon 550, Garmin International Inc., Olathe, CO, U.S.A.). To measure water levels, 15 water pressure loggers (Hobo water pressure loggers, Onset Computer Corp., Bourne, MA, U.S.A.) were installed in the water at each stream site in 2010 and left to record water pressure every 30 min for 10 months. Before deployment, water pressure loggers were protected in plastic tubes placed vertically on the stream side where the sections were deep enough to avoid overflowing during the glacial flood and with homogeneous shapes among stream sites. Water level and height between the stream bottom and the Hobo sensor were measured twice, when the loggers were installed and removed. One more logger was placed in the air at 4100 m a.s.l. to correct for variation in atmospheric pressure.

Macroinvertebrate sampling

Five quantitative Surber samples (0.05 m^2; mesh size 200 μm) were collected randomly from pebble–cobble substratum at each site. 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 magnification. No subsampling was applied. Invertebrates were identified under a microscope at 10× magnification to morphospecies, genus or (sub) family, according to Fernández & Domínguez (2001).

Determination of the glacial influence metrics: intensity, frequency and temporal clustering

To calculate the intensity, frequency and temporal clustering of glacial influence at each stream site, we applied a recently developed method based on wavelet analyses on water level time series. This method is presented in detail by Cauvy-Fraunié *et al.* (2013b); here, we only list the most important steps.

We first transformed water pressure values, obtained from the 15 stream sites, into water level values by subtracting the atmospheric variations from the water pressure data. Water level time series were centred on their means and normalised by their standard deviations to allow across-site comparison of our results. We then performed wavelet analysis on the water level time series to identify the pattern of diurnal flow variation.

The wavelet transform analysis is a time-dependent spectral analysis that decomposes a data series in time–frequency space. The continuous wavelet transform $W_n(s)$ of a discrete time series x_n (n being the time position) at scale s is defined as the convolution of x_n with a scaled and translated version of the wavelet function $\psi(t)$:

$$W_n(s) = \sum\nolimits_{n'=0}^{N-1} x_{n'} \psi^* \left[\frac{(n'-n)\delta t}{s} \right] \tag{1}$$

where N is the number of points in the time series, $\psi^*(t)$ is the complex conjugate of wavelet function (the Morlet wavelet in our case, see Cauvy-Fraunié *et al.*, 2013b for justification and formula) at scale s and translated in time by n, and δt is the time step for the analysis (Torrence & Compo, 1998). The local wavelet power spectrum $|W_n(S)|^2$, defined as the squared absolute value of the wavelet transform, permits visualisation of the magnitude of the variance in the series at a given wavelet scale and location in time. The scale-averaged wavelet power spectra $\overline{W_n^2}$, defined as the weighted sum of the wavelet power spectrum (over two scales s_1 to s_2), over the whole measurement period, are:

$$\overline{W_n^2} = \frac{\delta j \delta t}{c_\delta} \sum_{j=j_1}^{j_2} \frac{|W_n(S_j)|^2}{S_j} \tag{2}$$

where δj is the spacing between discrete scales, δt the time step of the time series and C_δ the reconstruction factor (Anctil & Coulibaly, 2004; Coulibaly & Burn, 2004; Markovic & Koch, 2005; White, Schmidt & Topping, 2005); this permits examination of fluctuations in power over a range of scales (a band).

The scale-averaged wavelet power spectrum over scales around 24 h permits visualisation of the temporal variability of diurnal flow variation power (Cauvy-Fraunié *et al.*, 2013b). We considered that daily glacial flood occurred when the scale-averaged wavelet power at the 24-h scale was significant (i.e. when above the 95% confidence level; see Torrence & Compo, 1998; Markovic & Koch, 2005; Schaefli, Maraun & Holschneider, 2007 for 95% confidence level calculation details). We determined glacial flood intensity as the integration of the scale-averaged wavelet power at the 24-h scale corrected by its corresponding 95% confidence level (see Cauvy-Fraunié *et al.*, 2013b for details). Glacial flood frequency was calculated as the frequency of days with significant diurnal flow variations in the time series. Concerning the temporal clustering (*sensu* De Vos, Rientjes & Gupta, 2010; Hsu & Li, 2010), we first defined two 'hydrological states' corresponding to days with and without significant diurnal flow variation. The temporal clustering was calculated as one minus the number of hydrological state changes divided by the total number of days in the time series minus one. Thus, values near 1 indicate that daily glacial floods were clustered, while values near 0 indicate that daily glacial floods were scattered in time.

Note that glacial flood intensity, frequency and temporal clustering correspond to the diurnal flow variation power, frequency and temporal clustering determined in the study of Cauvy-Fraunié *et al.* (2013b), respectively. The calculation of the three metrics was performed in MATLAB, version R2009a (The Mathworks Inc., Natick, MA, U.S.A.). Figure 2 illustrates the calculation of the three glacial influence metrics.

Data analysis

To describe macroinvertebrate communities at each of the 15 stream sites, we calculated (i) density, defined as the total number of individuals observed in the five Surbers divided by the total area of the five Surbers, (ii) local taxon richness (α-diversity) determined as the number of taxa found in the five Surbers, (iii) dominance (1 – evenness), calculated using the probability of interspecific encounter (see Hurlbert, 1971) and (iv) β-diversity, defined here as the Sørensen dissimilarity index between all possible pairs of two sites. Note that we have chosen to work with taxon density, instead of a theoretical measure of 'taxon abundance' for the entire locality. Indeed, we were interested in how glacial floods affect taxon density, in part through the effect on density of individuals in the assemblage (i.e. the number of taxa potentially interacting ecologically within a standardised spatial scale).

To determine the effect of glacial influence on the macroinvertebrate communities, we first plotted, independently, density (previously log-transformed), local taxon richness and dominance against glacial flood intensity, frequency and temporal clustering, and fitted quadratic regression models in R (Development Core Team, version 3.0.2, Vienna, Austria). We then analysed the effects of the three glacial influence metrics and their interaction on the same three faunal metrics using generalised additive models (GAMs) in the R package *MGCV*. The interactions permitted us to test whether the combined effect of two glacial influence metrics affected the macroinvertebrate communities.

The distribution patterns of individual taxa along gradients of the three glacial influence metrics were examined by plotting taxon occurrences, assuming continuous ranges (i.e. from lowest to highest observation).

Results

The three glacial indices as predictors of macroinvertebrate communities

Macroinvertebrate density ranged from 232 m^{-2} (at site 7) to 11 188 m^{-2} (at the groundwater-fed site 44). Log-transformed density decreased significantly with glacial flood intensity ($r^2 = 0.51$, $F = 6.31$, $P < 0.05$, Fig. 3a). The GAM on log-transformed data revealed significant effects of glacial flood intensity and the interaction of intensity and temporal clustering on macroinvertebrate density, and marginally significant effects ($P < 0.10$) of frequency (Fig. 3d) and the interaction of frequency and temporal clustering on macroinvertebrate density

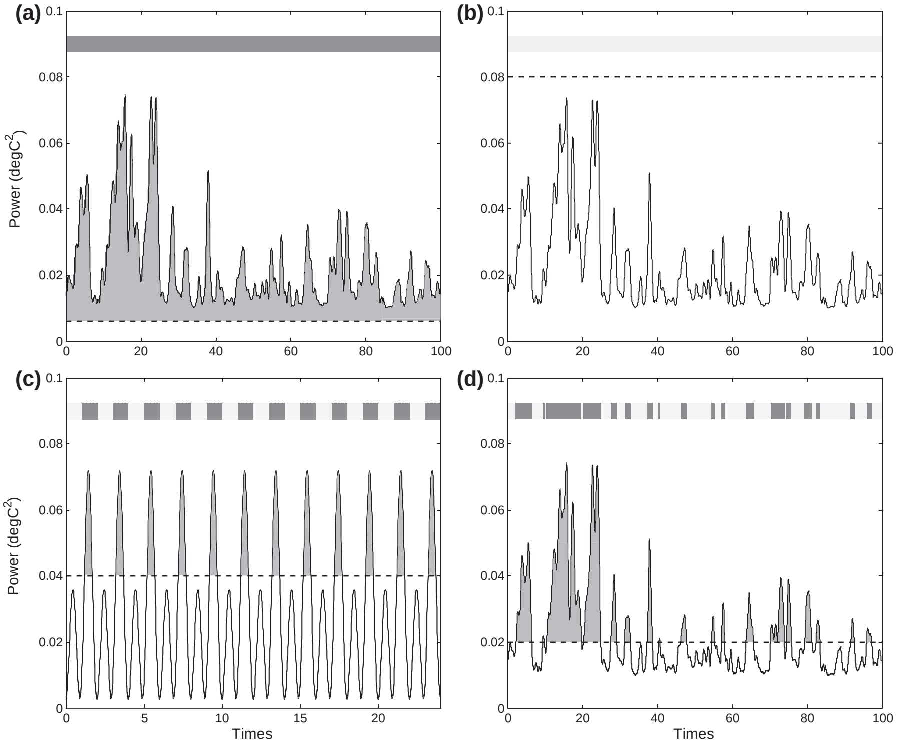

Fig. 2 Theoretical illustration of calculations of the glacial influence metrics. Black lines represent the scale-averaged wavelet power spectrum at the 24-h scale. Dashed lines represent the 95% of confidence level. The grey bands, at the top of each panel, indicate the hydrological state: dark grey corresponds to days with significant daily glacial flood (i.e. when the scale-averaged wavelet power spectrum at the 24-h scale curve is above the 95% confidence level line) and light grey corresponds to days without significant daily glacial flood (i.e. when the scale-averaged wavelet power spectrum at the 24-h scale curve is below the 95% confidence level line). Intensity is calculated as the area between the scale-averaged wavelet power spectrum curve and the 95% of confidence level line (the area is shaded in grey). At panel (a), daily glacial floods occur every day; frequency = 1 and temporal clustering = 1. At panel (b), there is not a single day with significant diurnal flow variation; frequency = 0 and temporal clustering = 1. At panel (c), daily glacial floods occur every second day; frequency = 0.5 and temporal clustering = 0. Panel (d) presents an example where daily glacial floods occur more than half of the time; frequency > 0.5 and temporal clustering >0.5.

(Table 1). The interactions of intensity and frequency with temporal clustering had stronger effects on macroinvertebrate density than the unique variables intensity and frequency. The adjusted R^2 of the GAM was 0.57 with 75.2% variance explained.

In total, 56 macroinvertebrate taxa were found at our 15 stream sites, and local richness ranged from 15 to 35 taxa per site. The highest α-diversity was found at site 3, a mixed stream site (i.e. fed by ice-melt and ground water, Fig. 1), and the lowest at site 7, the only entirely glacier-fed site in our study area (Fig. 1). Figure 3b showed a significant hump-shaped relationship between local taxon richness and glacial flood intensity ($r^2 = 0.56$, $F = 7.59$, $P < 0.01$). In the GAM, local taxon richness was significantly explained by glacial flood intensity (Table 1). GAM adjusted R^2 was 0.47 with 69.8% variance explained. There was no significant effect of glacial flood frequency and temporal clustering (Fig. 3e,f), but we found a marginally significant effect of the intensity and temporal clustering interaction (Table 1). Thus, the interaction of intensity and temporal clustering explained less taxon richness than the unique variable intensity.

Macroinvertebrate dominance ranged from 0.13 to 0.38 at site 7 and 44, respectively (Fig. 3c). Dominance was significantly explained by glacial flood frequency and by the interaction of frequency and temporal clustering (GAM, Table 1, Fig. 3f,i); however, the unique variable intensity better explained dominance than the interaction of frequency and temporal clustering. The adjusted R^2 of the GAM was 0.47 with 69.6% variance explained.

Taxon distribution patterns producing the observed hump-shaped relationship

For each glacial influence metric, we found a higher number of taxa occurring exclusively at the intermediate level of glacial influence: seven, fifteen and eight for glacial flood intensity, frequency and temporal clustering, respectively (Fig. 4). We found 21 taxa occurring exclusively at sites with some glacial influence (e.g. *May-*

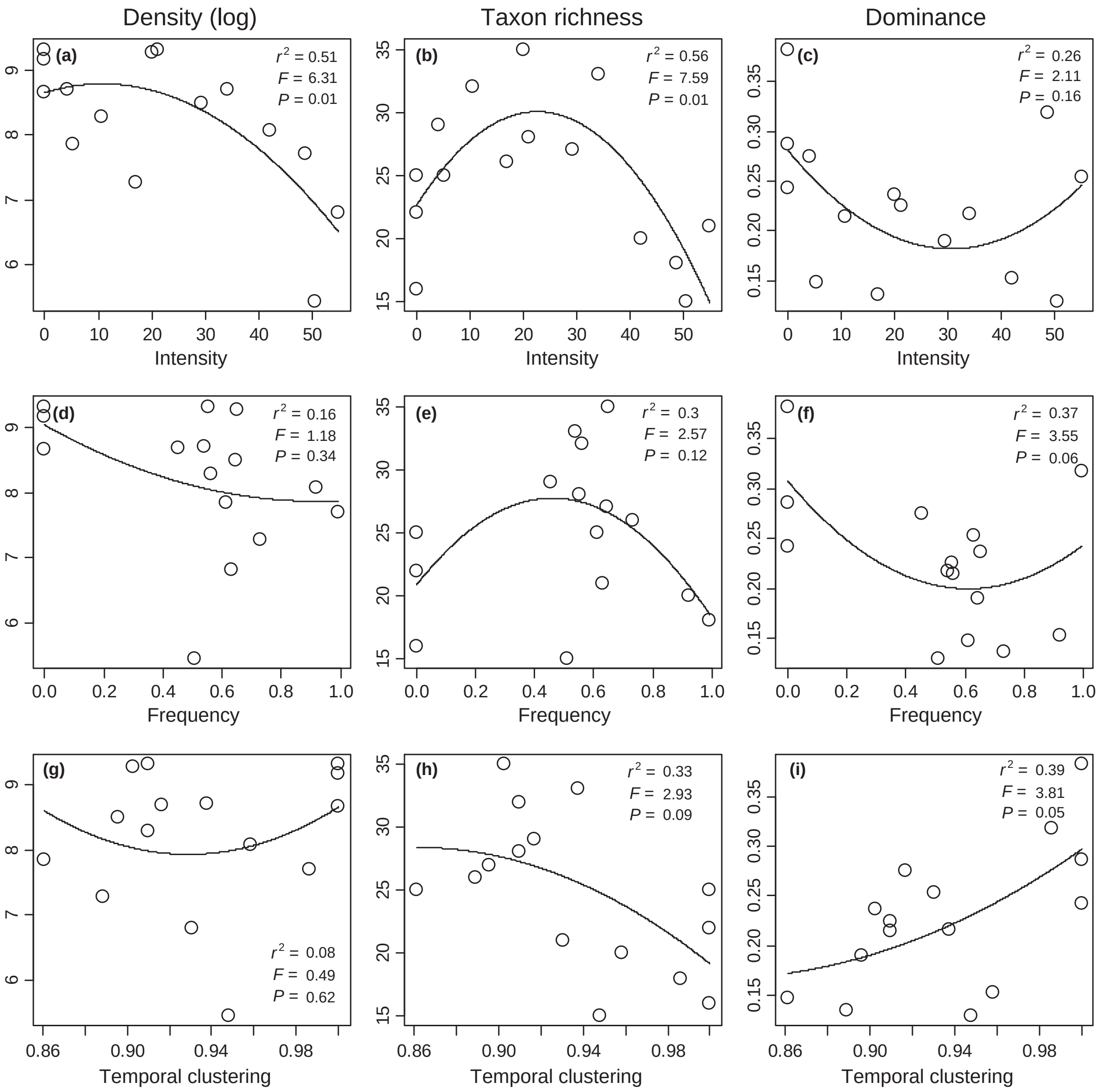

Fig. 3 Scatter plot of density (log-transformed) (a, d, g), local taxon richness (b, e, h) and dominance (c, f, i) relative to glacial flood intensity (a–c), frequency (d–f) and temporal clustering (g–i). Black lines are predictions of quadratic regression (i.e. second degree polynomial) models, for each macroinvertebrate metric separately.

atrichia Hydroptilidae, *Prionocyphon* sp3 Scirtidae and *Molophilus* sp2 Limoniidae at sites 1–10, 14 and 15, Fig. 1), and only two taxa exclusively occurring at non-glacial stream sites (i.e. Curculionidae sp2 and Podonominae sp2 Chironomidae at sites 11–13, Figs 1 & 4).

Discussion

The three glacial indices as predictors of macroinvertebrate communities

We used a recently developed method based on the diurnal flow variation (see Cauvy-Fraunié *et al.*, 2013b) to characterise glacial influence on stream sites. Although these indices are calculated from diurnal flow variation caused by glacial floods (Cauvy-Fraunié *et al.*, 2013b) and thus describe a hydrologic stress (Rempel, Richardson & Healey, 2000; Lancaster *et al.*, 2006; Cauvy-Fraunié *et al.*, 2013a), they integrate other environmental factors that might also affect macroinvertebrate communities, such as decreases in conductivity and water temperature and an increase in turbidity (Brown, Hannah & Milner, 2004; Malard *et al.*, 2006).

This method quantifies the temporal dimension of glacial influence (frequency and temporal clustering) and allows us for the first time to study the effect of different

Table 1 Generalised additive models, explaining (a) density (log-transformed), (b) local taxon richness and (c) dominance by the glacial influence intensity, frequency and temporal clustering and their interactions. The adjusted R^2 of the models and percentage deviance explained are 0.57 and 75.2%, respectively, for the density model; 0.47 and 69.8% for the local taxon richness model; and 0.47 and 69.6% for the dominance model

	d.f.	*F*	*P*-value
(a) Density (log)			
Intensity	1	7.756	**0.0237**
Frequency	1	4.490	0.0669
Temporal clustering	1	0.574	0.4703
Intensity × Frequency	1	0.580	0.4683
Intensity × Temporal clustering	1	8.608	**0.0189**
Frequency × Temporal clustering	1	4.945	0.0569
(b) Taxon richness			
Intensity	1	5.321	**0.0499**
Frequency	1	1.922	0.2030
Temporal clustering	1	0.027	0.8734
Intensity × Frequency	1	1.163	0.3123
Intensity × Temporal clustering	1	5.034	0.0551
Frequency × Temporal clustering	1	2.503	0.1523
(c) Dominance			
Intensity	1	1.096	0.3257
Frequency	1	5.837	**0.0421**
Temporal clustering	1	3.482	0.0990
Intensity × Frequency	1	3.502	0.0982
Intensity × Temporal clustering	1	1.559	0.2471
Frequency × Temporal clustering	1	5.537	**0.0465**

Bold indicates significant relationship ($P < 0.05$).

components of glacial disturbance dynamics and to sort out their effects on aquatic macroinvertebrate communities. We found that glacial flood intensity best accounted for local macroinvertebrate communities. Thus, we found a significant effect of glacial flood intensity on density and taxon richness, but no significant effect of glacial flood frequency or temporal clustering on these two faunal metrics. However, this might be due to the lack of glacial stream sites with low frequency of flooding (i.e. <0.45, see Cauvy-Fraunié *et al*., 2013b) and the limited range in the temporal clustering covered in our study area.

In addition, biotic responses to disturbance depend on both the resistance (ability to withstand a disturbance) and resilience (ability to recover from disturbance) of organisms (Death, 2008; Milner *et al*., 2012; Anderson & Ferrington, 2013). Previous studies have found that macroinvertebrates that make up communities in these streams have species traits that potentially offer high resilience or resistance to the harsh and fluctuating environmental conditions of glacier-fed streams (Snook & Milner, 2002; Ilg & Castella, 2006; Füreder, 2007). However, while the effect of disturbance intensity is expected to be most directly tied to species resistance, the disturbance frequency effect should relate more to species resilience (Grimm & Fisher, 1989; Dole-Olivier, Marmonier & Beffy, 1997). Indeed, if species resilience is the principal persistence mechanism, taxon richness should decrease with disturbance frequency (Allison & Martiny, 2008; Datry *et al*., 2014). On the other hand, if species resistance is more important, then taxon richness should not be affected by disturbance frequency but rather by disturbance intensity (Allison, 2004; Fritz & Dodds, 2004). In our study, where glacial floods occur year-round, the results (i.e. no effect of frequency and temporal clustering but a significant effect of glacial flood intensity) suggest a dominance of resistance traits in the glacial macroinvertebrate communities (see Cauvy-Fraunié *et al*., 2013a). As resilience occurs only after the disturbance has ceased (Lake, 2013), temporal clustering provided additional information to assist in identifying processes involving species resilience. Thus, the three glacial metrics together should allow better predictions of the type of traits (resistance and/or resilience) more likely to be exhibited by species in glacier-fed streams.

Taxon distribution patterns producing the observed hump-shaped relationship

Contrary to most previous studies, which found that local diversity decreased monotonously with increasing glacial influence (Snook & Milner, 2001; Brown *et al*., 2007; Brown *et al*., 2010; Finn, Rasanen & Robinson, 2010)**,** we found a hump-shaped relationship between local taxon richness and glacial flood intensity. This pattern has previously been reported by Jacobsen *et al*. (2012), using percentage glacial cover in the catchment as the independent variable. We rule out the possibility that the diversity peak was purely due to overlapping broad taxon ranges from either end of the glacial flood intensity gradient, because most taxa were actually generalists with distribution ranges spanning most of the gradients. Instead, we found seven taxa occurring exclusively at intermediate levels of glacial flood intensity. We suggest that the peaked relationship might be caused by exclusion of some species by high dominance of competitively superior species at low level of glacial influence, and by environmental harshness at a high level of glacial influence (Milner *et al*., 2009). This explanation of high competition at low levels of glacial influence is supported by (i) the higher density and dominance at low level of glacial flood intensity and (ii) by the absence of 21 taxa (i.e. 37.5% of the total number of taxa found) in stream sites without glacial influence. Moreover, some species appeared not to tolerate strong environmental harshness, as we found that 21

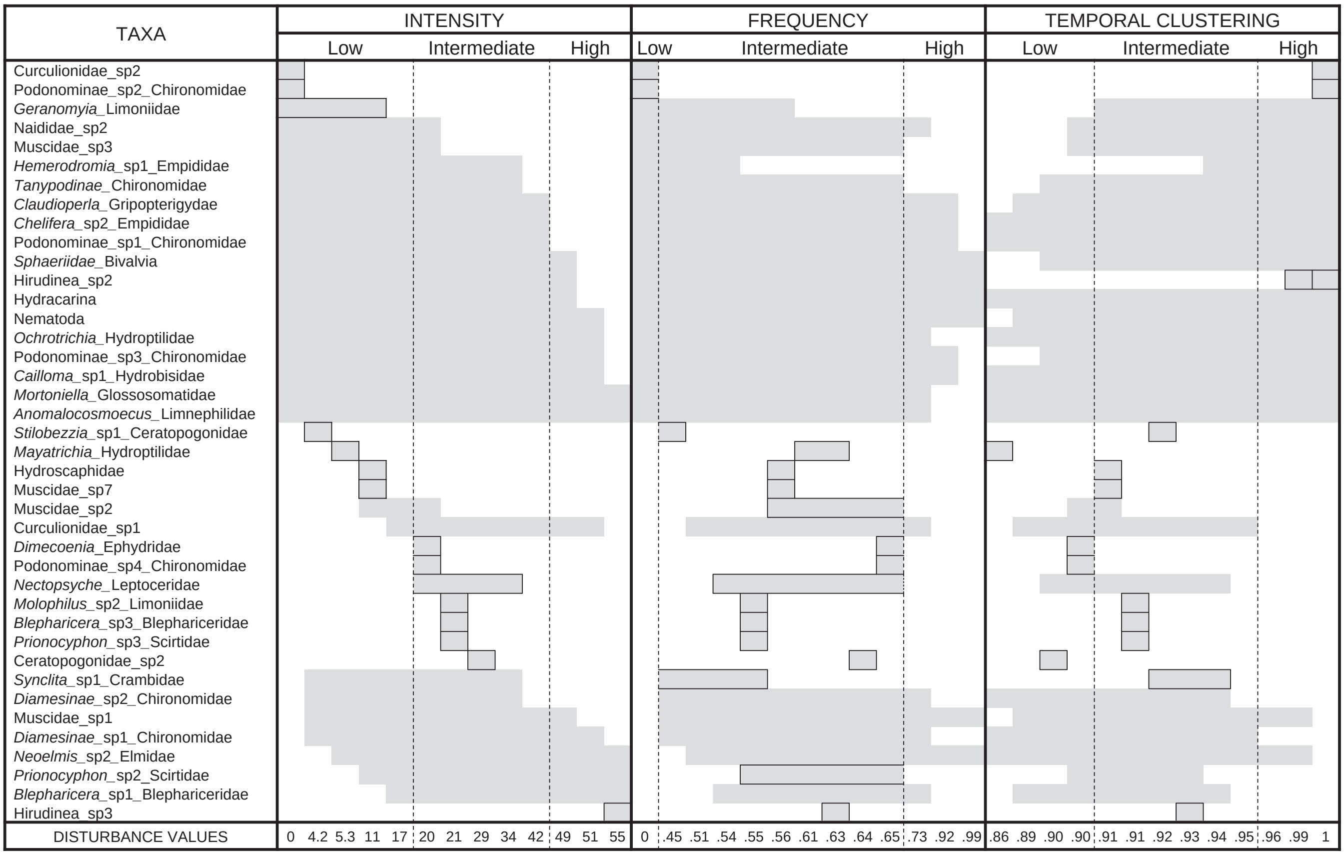

Fig. 4 Taxon ranges versus glacial flood intensity, frequency and temporal clustering. Each bar corresponds to one taxon. For each glacial influence metric, three levels of glacial disturbance were determined dividing the metric's range observed by three. Black contours show taxa occurring exclusively at low, intermediate or high levels of disturbance. Taxa occurring in a range including more than twelve stream sites for all glacial influence metrics are not shown.

taxa (37.5% of the total) did not occur at high levels of glacial flood intensity. Among the 21 taxa occurring only in glacier-fed stream sites, 13 (62% of taxa only found in glacial sites) did not occur at high levels of glacial flood intensity.

Glacial influence generates regional diversity in glacierised catchments

Our study indicates that under a scenario of complete disappearance of glaciers, current hotspots of local richness (α-diversity) will disappear and lead to a decrease in regional diversity (γ-diversity), a finding in agreement with Jacobsen *et al.* (2012). Among the 21 taxa exclusively occurring at our glacier-fed stream sites, 13 were found less than five times. Hence, vanishing glaciers will probably lead to increased rates of species extinction (Milner *et al.*, 2009). Moreover, glacial influence contributes strongly to environmental heterogeneity at the basin scale (Hannah *et al.*, 2007; Poff & Zimmerman, 2010; Marchetti *et al.*, 2011), thereby generating β-diversity (Brown *et al.*, 2007; Finn, Khamis & Milner, 2013) and enhancing regional diversity (Bunn & Arthington, 2002; Clarke *et al.*, 2008; Jacobsen & Dangles, 2012). We found species replacement along our intensity gradient, suggesting that environmental heterogeneity generated by glacial meltwater contribution in the catchment engendered species turnover. Moreover, seven taxa were only found at intermediate levels of glacial influence. Therefore, even before complete disappearance of glaciers, spatiotemporal heterogeneity can be expected to diminish and macroinvertebrate diversity would begin to decline.

Thanks to better characterisation of glacial influence (Cauvy-Fraunié *et al.*, 2013b), the new indices used here should not only permit testing macroinvertebrate resistance to glacial flood, but also allow us to examine macroinvertebrate resilience. Therefore, in the context of climate change, we believe these new glacial flood indices can improve our understanding of the mechanisms driving aquatic biodiversity and thus predictions of -species responses to glacier retreat.

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PART 3

Temporal scaling of flow disturbance effects on benthic fauna: insights from equatorial glacier-fed streams

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Running head: Flow variation and temporal β-diversity

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Abstract

We used equatorial glacier-fed streams as study models to investigate the relationships between flow disturbance and benthic fauna at different temporal scales. We measured water level at 30 min time steps during 29 months and sampled benthic macroinvertebrates 14 times during the entire study period. We performed wavelet analyses on water level time series to identify at which scale significant flow variation occurs and calculated three indices: the intensity, frequency and temporal clustering of the diurnal flow variation for time series from 2 to 50 days. We then determined the effect of temporal scaling (length of the time series considered) on relationships between community dissimilarity (using Sørensen and Bray-Curtis indices) and differences in flow indices among the 14 sampling dates. Temporal scaling affected flow index values, but had no effect on the relationship between flow indices and community dissimilarity. Community dissimilarity significantly increased with increasing difference in flow disturbance intensity. This dissimilarity was associated with a decrease in dominant taxa density and a taxa turnover along the temporal gradient in flow intensity. Although flow disturbances are very frequent and highly predictable in equatorial glacier-fed streams, macroinvertebrate communities exhibited a temporal variability in taxon assemblage linked to the flow disturbance intensity. We explain these patterns by downstream displacement during high flow events and upstream displacement during low flow periods, thereby highlighting the need of appropriately considering temporal scaling effects on benthic fauna to understand the ecological dynamics of lotic systems.

Introduction

Natural running waters exhibit a wide range of flow regimes depending, among others, on their geographical location (e.g. latitude, altitude), climatic conditions and water sources (e.g., groundwater, rainfall, meltwater, or mixture of different water sources; Hannah et al. 2000). Worldwide, natural flow regimes are strongly altered by human activities such as dam building, land-use modifications, river impoundments, and water abstraction (Moss 2010). Those anthropogenic modifications have direct impacts on both baselines flows and flow temporal variability (Poff and Zimmerman 2010). Additionally, ongoing global climate change (i.e. changes in temperature and precipitation patterns) also provokes strong alteration of stream flow regimes. For example, the acceleration of glacial shrinkage caused by global warming strongly affects glacier-fed stream flow regime (Sorg et al. 2012).

Many studies have already demonstrated negative effects of flow alteration on stream communities (Poff and Zimmerman 2010). The scientific discipline of "environmental flow assessment" has developed considerably over the last two decades in response to the recognition of the extent of flow alteration (Wathern 2013). It aims at assessing the quantity, timing, and quality of water flow required to sustain freshwater and estuarine ecosystems as well as the human livelihood and well-being that depend on these ecosystems (Wathern 2013). As a result, many hydrological metrics have been developed to describe the multiple characteristics of flow regime (Poff et al. 2009) and applied to characterize and quantify 'natural', semi-natural and anthropogenic modifications to river flow. In many cases, these methods have been combined with biological data to study the response of aquatic communities to flow alteration (Stewart-Koster et al. 2014). For example, Poff et al. (2009) proposed a new framework named "ecological limits of hydrologic alteration" (ELOHA), for assessing environmental flow needed for streams and rivers to foster both the development and implementation of environmental flow standards at the regional scale. Despite this bulk of studies, effects of flow regime alteration on aquatic ecosystems are still far from being well understood due to 1) the high variability in flow regime types, flow alteration, and the responses of organisms and ecosystems (Poff and Zimmerman 2010), and 2) a general lack of knowledge of the full range of natural flow regime types that species can cope with (Lytle and Poff 2004). Therefore, to be able to predict the response of aquatic organisms to flow alteration, it is of critical importance to improve our knowledge of the relationship between flow regime and freshwater biota (Turner and Stewardson 2014). In particular, the influence of time scales on flow-biota relationships, the temporal scaling effect, has been understudied compared to variation across space (Korhonen et al. 2010).

Most running waters display high temporal variability in flow patterns at different time scales: from short time-scale (e.g., abrupt increase caused by storm; Allan and Castillo 1995) to long time-scale (e.g., annual increase caused by glacial shrinkage; Sorg et al. 2012), with strong ecological consequences at time intervals ranging from hours (physiological effects) to millennia (evolutionary effects; Naiman et al. 2008; see also Denny and Benedetti-Cecchi 2012). The natural flow-regime paradigm postulates that the structure and function of riverine ecosystems, and the adaptations of their constituent riparian and aquatic species, are dictated by patterns of temporal variation in river flows (Lytle and Poff 2004). In ecological terms, the primary components of a flow regime are the magnitude, frequency, seasonal timing, predictability, duration and rate of change of flow (Lytle and Poff 2004). Extreme flow events, such as floods or droughts, are especially important as they usually change drastically the nature of habitats and deplete organisms and their resources (Lake 2000). While floods increased shear stress at the stream bed level, removing substrates, periphyton and organisms (Death 2008), drought events leads to changes in hydrological connectivity, deterioration in water quality, and eventually a total desiccation of the habitat (Lake 2008).

In this study, we used wavelet analyses to study the effect of past flow variability patterns (e.g., intensity, frequency) on benthic invertebrates assemblage at a given date. More specifically we aimed at (1) testing whether flow-biota relationships varied according to the duration of hydrological time series considered before sampling and (2) whether temporal flow variability could be involved in structuring benthic communities (temporal beta-diversity). We performed this study in glacier-fed streams as they exhibit relevant temporal variability in flow linked to the cycles of glacier melting.

Methods

Study site

The study was conducted in three stream sites in an equatorial glacierized catchment, in the Ecological Reserve of Antisana, Ecuador (0° 29′ 06″S, 78° 08′ 31″W). Stream sites were located at 4100 m a.s.l., at 6.5 km from the “Crespo” glacier, which covered an area of about 1.82 km^2 in 2010, and showed an average trend of the cumulative mass balance of - 0.6 m water equivalent yr^{-1} (Rabatel et al. 2013). Those equatorial glacier-fed streams exhibit an increase in flow variation at the diurnal time scale (Cauvy-Fraunié et al. 2013) caused by the daily ice melting in the ablation zone of the glacier (Hannah et al. 2000). Those daily glacial floods occur throughout the year because ablation of the glaciers happens all year round in the inner tropics due to the lack of pronounced seasonality (Rabatel et al. 2013). For generalization purpose, we selected three replicate stream sites covering a gradient of diurnal flow variation intensity and frequency with different fauna composition (our aim here is not to compare results among the three stream sites, see Cauvy-Fraunié et al. 2014b).

Hydrological measurements

During 29 months (from 24 December 2009 to 22 July 2012, but with a two-month gap) water pressure loggers (Hobo water pressure loggers, Onset Computer Corp., United States of America) were installed in the water at each stream site and left to record water pressure every 30 minutes. Water pressure loggers were previously protected in plastic tubes placed vertically on the stream side where the sections were deep enough to avoid overflowing during the glacial flood and with homogeneous shapes among stream sites. Water level and height between the stream bottom and the Hobo sensor were measured twice, when the loggers were installed and removed. One more logger was placed in the air at 4100 m a.s.l. to correct for variation in atmospheric pressure. Water pressure values were then transformed into water level values by subtracting the atmospheric variations from the water pressure data. Water level time series were centered on their means and normalized by their standard deviations to allow across-site comparisons.

Macroinvertebrate sampling

At each stream site, five quantitative Surber samples (0.05 m^2; mesh size 200 µm) were collected randomly from pebble–cobble substratum at 14 dates spread over the study period. All samples were collected between 10:00 and 14:00 and preserved in the field in 70% ethanol. Note we found no significant variation in macroinvertebrate assemblages over the day in the study area (Cauvy-Fraunié et al. 2014a). In the laboratory, Surber samples were rinsed through a 200-µm sieve and sorted without use of magnification. Invertebrates were identified under a microscope at 10 × magnification range to morphospecies, genus or (sub) family, according to Fernández and Domínguez (2001).

Data analyses

Wavelets and indices to characterize flow variation

Stream water level time series exhibit fluctuations at different scales (or periods) that might change with time. To identify at which scales occurred those temporal fluctuations, we performed wavelet analyses on water level time series (Torrence and Compo 1998). The wavelet transform analysis is a time-dependent spectral analysis that decomposes a data series in time-frequency space. The wavelet transforms therefore express a time series in a three-dimensional space: time (x), scale/frequency (y), and power (z). Previous work has reviewed in detail the concepts of wavelet analysis for different applications (Torrence and Compo 1998). Below, we list the main steps of this analysis which is described in details in Cauvy-Fraunié et al. (2013).

The continuous wavelet transform $W_n(s)$ of a discrete time series x_n (n being the time position) at scale s is defined as the convolution of x_n with a scaled and translated version of the wavelet function $\psi(t)$:

$$W_n(s) = \sum_{n'=0}^{N-1} x_{n'}\, \psi * \left[\frac{(n'-n)\delta t}{s}\right] \tag{1}$$

where N is the number of points in the time series, $\psi*(t)$ is the complex conjugate of wavelet function (the Morlet wavelet in our case, see Cauvy-Fraunié et al. 2013) for justification and formula) at scale s and translated in time by n, δt is the time step for the analysis (Torrence and Compo 1998). The local wavelet power spectrum $|W_n(s)|^2$, defined as the squared absolute value of the wavelet transform, permits to visualize the magnitude of the variance in the series at a given wavelet scale and location in time. The scale-averaged wavelet power spectra $\overline{W_n^2}$, defined as the weighted sum of the wavelet power spectrum (over two scales s_1 to s_2), over the whole measurement period:

$$\overline{W_n^2} = \frac{\delta j \delta t}{C_\delta} \sum_{j=j_1}^{j_2} \frac{|W_n(s_j)|^2}{s_j} \tag{2}$$

where δj is the spacing between discrete scales, δt the time step of the time series, and C_δ the reconstruction factor (Torrence and Compo 1998), permits to examine fluctuations in power over a range of scales (a band).

At a given scale, the flow variation could be considered as significant when the scale-averaged wavelet power spectrum is higher than the 95% confidence level (see Torrence and Compo 1998 for the 95% confidence level calculation details). Following Cauvy-Fraunié et al. (2013), we determined three indices: intensity, frequency, and temporal clustering, to describe significant flow variation at a given scale, in our case at the diurnal time scale. Intensity was defined as the integration of the scale-averaged wavelet power over a delimited period corrected by its corresponding 95% confidence level. We then calculated the mean intensity by dividing the intensity by the number of days in that period. Frequency was calculated as the number of days with significant flow variation divided by the total number of days in the study period. Concerning, temporal clustering, we first defined two "hydrological states" corresponding to days with and without significant flow variation at a given scale. Temporal clustering (C) was calculated as one minus the number of hydrological state changes ($\mathrm{N_{HSC}}$) divided by the total number of days in the study period ($\mathrm{N_D}$) minus one.

$$C = 1 - \frac{\mathrm{N_{HSC}}}{\mathrm{N_D} - 1} \tag{3}$$

Mean intensity, frequency and temporal clustering will be referred as I, f, and C in the rest of the manuscript. If at a given scale, the flow variation is significant every day; then $f = 1$, and $C = 1$. If it is never significant; $f = 0$, and $C = 1$. If the flow variation is significant every second day, $f = 0.5$, and $C = 0$ (Cauvy-Fraunié et al. 2014b). Wavelet analyses and the calculation of the three flow variation indices were performed in MATLAB, version R2010a (The Mathworks Inc., Natick, MA, USA).

Calculation of the community dissimilarity indices

β-diversity is a measure of variation in species composition either between two or more local assemblages (Anderson et al. 2011). Changes in species composition can be partitioned into two components: dissimilarity due to nestedness and dissimilarity due to spatial turnover (Baselga 2010). Nestedness reflects the loss of species (i.e. the poorest assemblage is a strict subset of the richest assemblage), whereas spatial turnover reflects the replacement of some species (Baselga 2010). Among the numerous measures of beta diversity, Baselga (2010) proposed to use the Sørensen dissimilarity index, β_{sor} (based on presence-absence data), as a measure of the β-diversity and provided appropriate indices to partition β_{sor} into two additive components, disentangling the contribution of the nestedness, β_{nes}, and spatial turnover, β_{turn} (Simpson dissimilarity), to the β-diversity pattern. Using an analogous approach, (Baselga 2013) also provided a partition of the Bray-Curtis coefficient, the abundance-based extension of the Sorensen index (Anderson et al. 2011; Baselga 2013). Bray-Curtis dissimilarity, d_{BC}, can be partitioned into the *abundance gradient*, $d_{BC\text{-}nes}$, whereby some individuals are lost from one assemblage when compared to the other; and the *balanced variation in species abundances,* $d_{BC\text{-}turn}$, whereby the individuals of some species in one assemblage are substituted by the same number of individuals of different species in another site. Dissimilarity measures are used to compare community structure within a given spatial or temporal extent (Anderson et al. 2011). In our study, we determined the communities dissimilarity among the 14 sampling dates calculating the Sørensen dissimilarity index, β_{sor} (based on presence-absence data), and the Bray-Curtis dissimilarity index, d_{BC} (based on abundance data). Furthermore, for each pairwise dissimilarity index (β_{sor} and d_{BC}), we calculated the two components: turnover (β_{turn}) and nestedness (β_{nes}) partitioning Sørensen index and the balanced variation ($d_{BC\text{-}turn}$) and abundance gradient ($d_{BC\text{-}nes}$) partitioning Bray-

Curtis index. These analyses were carried out in R (R Development Core Team, 2013, version 3.0.2), using the R package *betapart*.

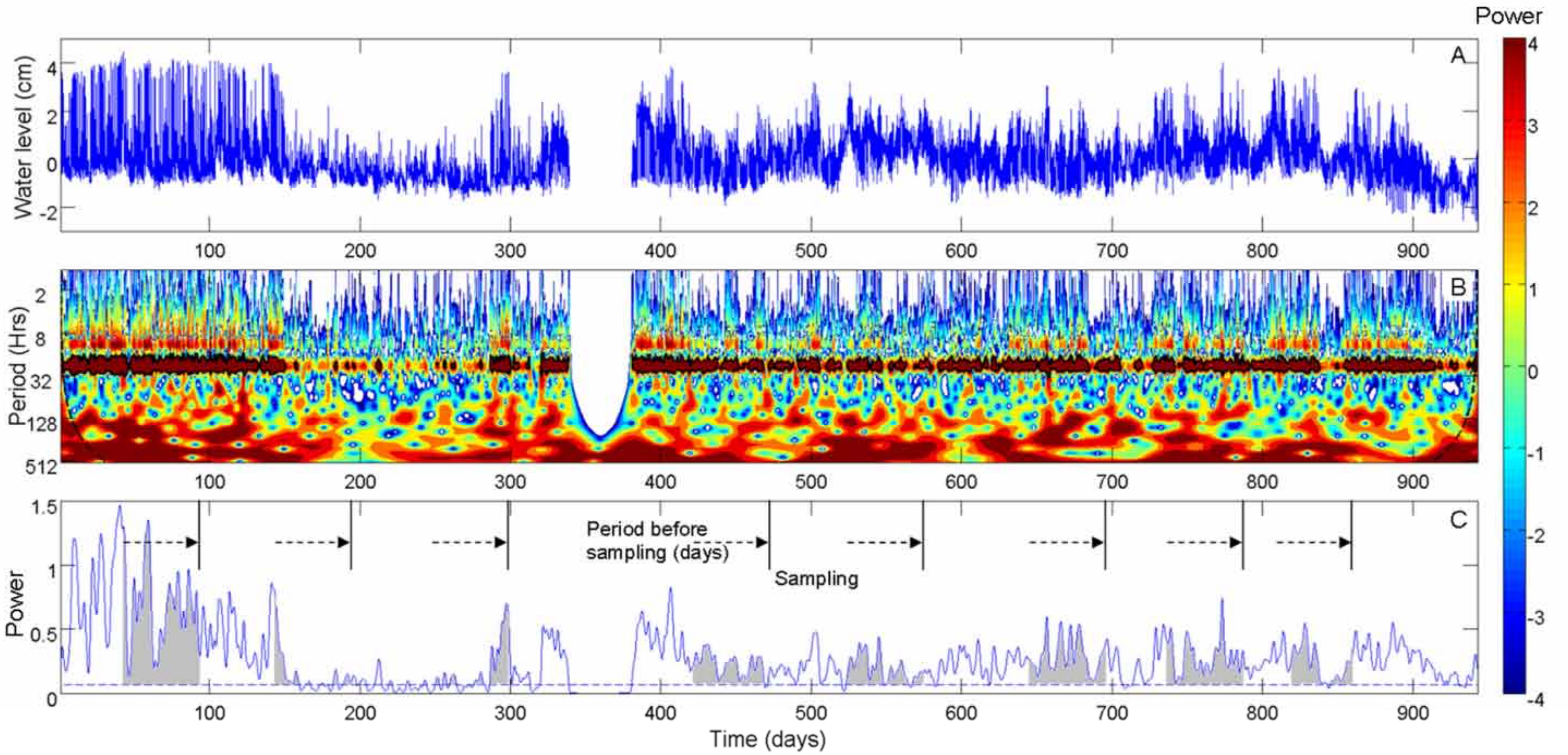
Temporal scaling effect on macroinvertebrates

As significant flow variations in our time series occurred only at the 24-h scale we focused on temporal variability effect on invertebrates of daily flow disturbance events. We first assessed how the three flow variation indices (I, f, C) differed across a range of temporal scales (2-50 days). We calculated I, f and C for times series of 2 to 50 days before day 50 (12 February 2009), 51, 52, …., 338 (27 November 2010) and day 430 (27 February 2011), 431, 432, …, 924 (22 July 2012). I, f, and C were thus calculated for a total of 800 dates throughout the entire study period (total of 39,200 values for each index and each stream site). Figure 1C illustrates this calculation procedure for days 75, 175, 280, 460, 570, 685, 780, 860. For each stream site and for the 800 dates, we plotted the variation of I, f and C against the length of the time series (from 2 to 50 days). We then plotted the probability distribution (i.e. $P(I)$, $P(f)$, and $P(C)$) of the 39,200 indices values across all time series and for each of the 49 time series.

Second, we tested the hypothesis that higher differences in flow variation between two dates (total of 14! = 105 pairs of sampling dates) would result in a higher dissimilarity in invertebrate communities. This analysis was performed using Sørensen community dissimilarity, β_{sor}, for the three flow variation indices (I, f, C), and the 49 time series (from 2 to 50 days) before invertebrate sampling dates. The relationships between ΔI, Δf, ΔC and the Sørensen dissimilarity index was fitted to linear models, whose statistical significance was assessed through their r^2, F and P values. As the relationships between β_{sor} and Δf and ΔC were generally non-significant (see Results), we only plotted turnover (β_{turn}) and nestedness (β_{nes}) components of Sørensen index against ΔI. Likewise, we also plotted balanced variation

($d_{BC\text{-}turn}$) and abundance gradient ($d_{BC\text{-}nes}$) partitioning Bray-Curtis index against ΔI. Here again the bivariate relationships were fitted to linear models for which we calculated *R*, *F* and *P* values. We further identified which invertebrate taxa partly explained community dissimilarity among sampling dates. All Figures and analyses were performed using Matlab (version R2010a) and using the package *betapart* in R (R Development Core Team, 2013, version 3.0.2).

Figure 1: Wavelet analyses outputs for water level time series of site 3 and illustration of the flow variation indices calculation for time series of 50 days before sampling. **A**: averaged normalized water-level time series. **B**: normalized local wavelet power spectrum. Black line delineates the areas where the power is considered significant at the 24-h scale (i.e. exceeds the 95% confidence level of a red-noise process). Dashed black line delineates the cone of influence that delimits the region not influenced by edge effects. Color bar shows the legend for the different colors: blue and red for low and high power, respectively. Note that, both period and power values were transformed by taking the binary logarithm. **C**: normalized scale-averaged wavelet power spectra at 24-h scale. Dashed blue line shows the corresponding 95% confidence level for the red-noise spectrum. When the scale-averaged wavelet power spectrum at the 24-h scale curve is above the 95% confidence level line, the diurnal flow variation is considered significant. The flow variation indices were calculated for periods of 2 days, 3 days, …. until 50 days before the sampling dates. The intensity was calculated as the area in-between the scale-averaged wavelet power spectrum curve and the 95% confidence level line (the area is colored in grey, as examples) divided by the number of days considered in the time series. Frequency was determined as the frequency of days with significant flow variation in the time series. Temporal clustering was calculated as the number of hydrological changes within the time series (see methods for details).


Power
4
3
2
1
0
-1
-2
-3
-4
A
Water level (cm)
4
2
0
-2
100
200
300
400
500
600
700
800
900
B
Period (Hrs)
2
8
32
128
512
C
Power
1.5
1
0.5
0
Period before sampling (days)
Sampling
Time (days)

Results

Temporal scaling effect on flow variation

In the three stream sites, temporal scaling affected the distribution of flow intensity index (I), i.e. I distributions differed depending on the length of the hydrological time series considered (Fig. 2 A-C and Appendix 1 A-C). This effect was particularly strong for stream site 1 where I distributions calculated with long time series (> approximately 15 days) differed from those calculated with short time series (Fig. 2 A and Appendix 1 A). Daily flow disturbance events were frequent and clustered in the three stream sites ($0.74 < f < 0.99$ and $0.89 < C < 0.99$), and their distributions were also modified by the length of the time series used for calculation (Fig. 2 D-I and Appendix 1 D-I). As a noticeable effect, $P(f=1)$ and $P(C=1)$ decreased with increasing length of the time series : at 2 days, $P(f=1) = 0.99$, 0.88, 0.65 and $P(C=1)= 0.99$, 0.90, 0.78; while at 50 days, $P(f=1) = 0.84$, 0.45, 0.16 and $P(C=1)= 0.84$, 0.45, 0.15 (for site 1, 3, 2, respectively – see Appendix 1 D-I). Also, $P(f=0)$ decreased with increasing length of the time series.

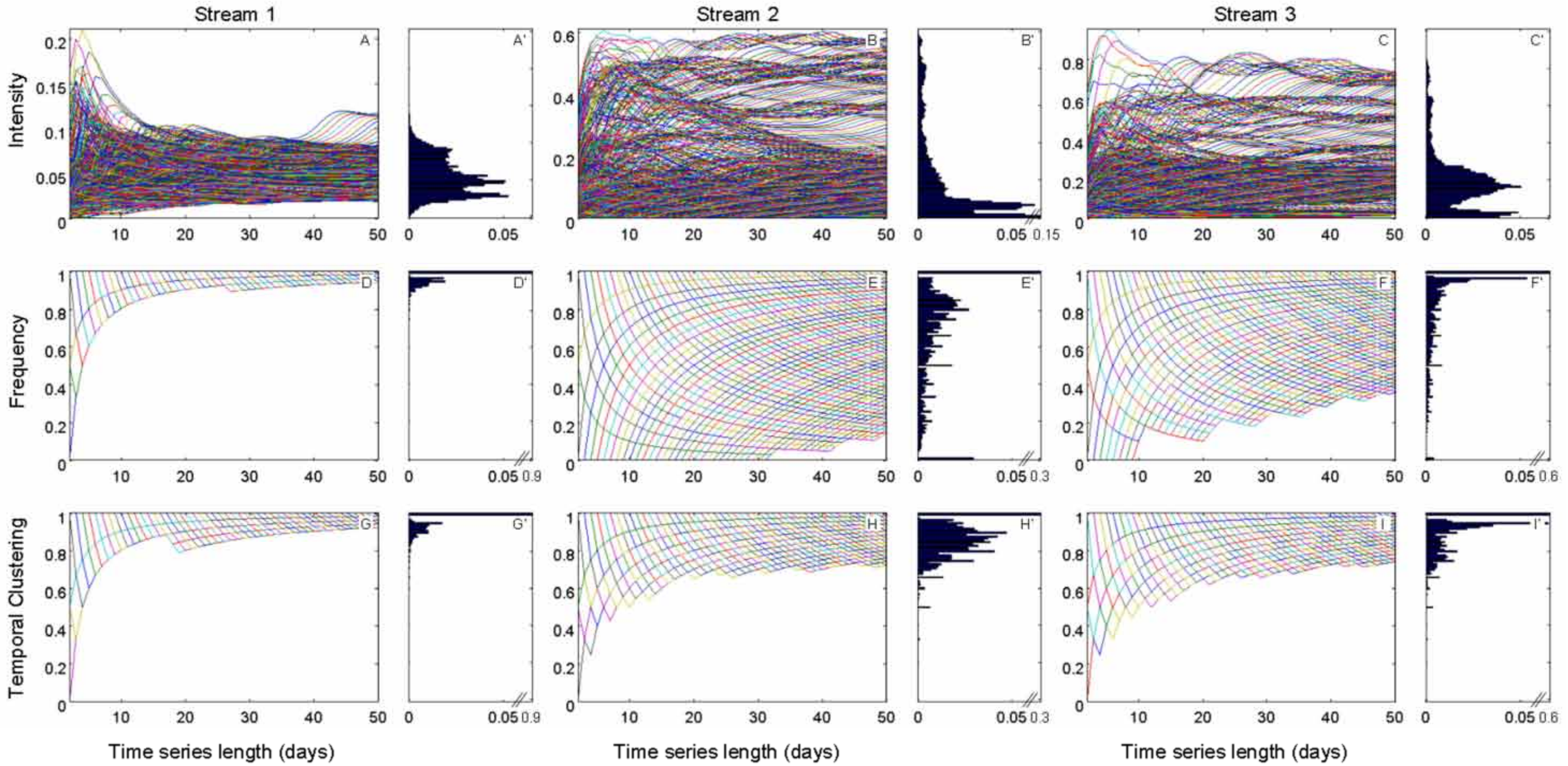


Figure 2: Plot of the flow variation indices: intensity (A, B, C), frequency (D, E, F), and temporal clustering (G, H, I) vs. length of the time series. Note that 800 curves were represented at each of those panels. It appears that panels D, E, F, G, H, and I have fewer curves because most are superposed. Histograms of the distribution probability of each flow variation index value across all periods are shown to the right of each plot. Probabilities were calculated for intensity (A’, B’, C’), frequency (D’, E’, F’), and temporal clustering (G’, H’, I’) for the three stream sites.

Effect of flow disturbance on macroinvertebrates communities

The three sites presented different dominant taxa (*Hyallela* and Orthocladiinae for site 1, *Hyallela* and *Andesiops* for site 2, *Andesiops* and Orthocladiinae for site 3). Despite these differences, benthic communities in the three sites showed similar response patterns to flow disturbance. At all stream sites, β_{sor} significantly increased with increasing ΔI independently of the length of the time series considered (Fig. 3 A-C). Overall, the relationships between β_{sor} and Δf and ΔC were non-significant except for site 2 where β_{sor} significantly increased with increasing Δf (Fig. 3 D-I, Table 1). For the three sites, β_{nes} showed similar values along the ΔI gradient (Fig. 4 A-C, Table 2) while β_{turn} increased with increasing ΔI for all stream sites (significant for site 2 and 3; Fig. 4 B-C, Table 2). For all sites, $d_{BC\text{-}nes}$ significantly increased with increasing ΔI, whereas $d_{BC\text{-}turn}$ remained unchanged (Fig. 4 D-F, Table 2).

Community dissimilarities among sampling dates were mainly caused by abundance gradient in the dominant taxa along the temporal flow intensity gradient. The abundance of *Hyallela*, *Andesiops*, and Orthocladiinae strongly declined the sampling days with highest *I* values (Fig. 5 A-C). At two sites (2 and 3), community dissimilarities among sampling dates were also significantly explained by taxa replacement along the temporal flow intensity gradient (Fig. 4 B-C). For example *Sphaeriidae* were replaced by *Nepticulidae* and *Prionocyphon sp2* (site 2) and Naididae sp1 were replaced by *Nectopsyche* and *Blepharicera sp1* at site 3 (Fig. 5 B-C).

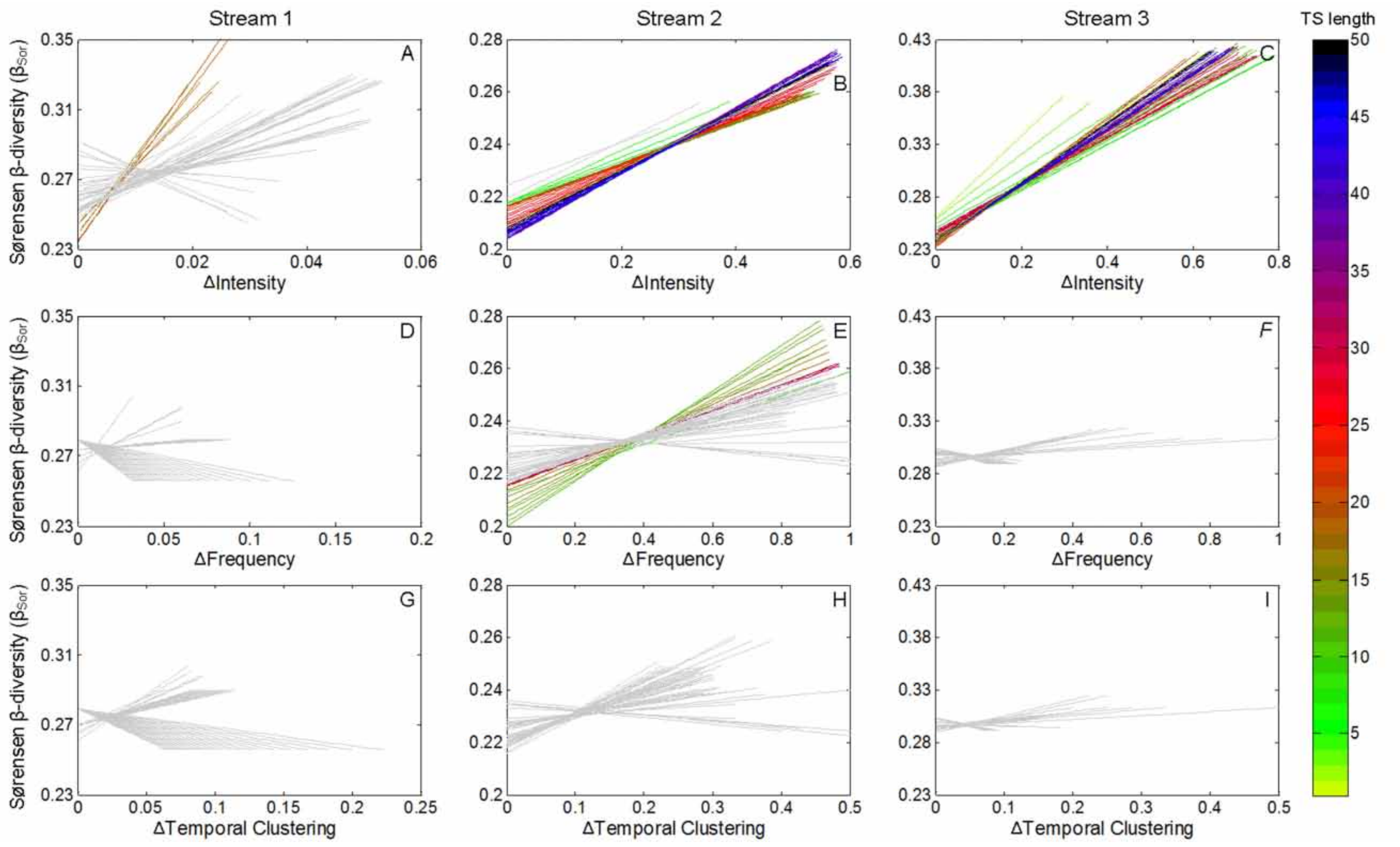


Figure 3: Predictions of the linear regression models of the Sørensen β-diversity (β_{sor}) vs. the difference in intensity (ΔI, A-C), frequency (Δf, D-F), and temporal clustering (ΔC, G-I) for the three study sites. Predictions of the linear regression models were calculated for time series length from 2 to 50 days before the 14 sampling dates. Colors correspond to the length of the time series. Grey regression lines correspond to non-significant relationships.

Table 1: Results of the linear regression models of the Sørensen β-diversity (β_{sor}) vs. the difference in intensity, frequency, and temporal clustering (ΔI, Δf, and ΔC). Regression models have been performed for the three study stream sites and for the 49 periods from 2 to 50 days. The line "% of significant periods" corresponds to the percentage of periods, for which the relationship between the Sørensen β-diversity vs. the difference in flow variation was significant. For each stream site, each flow variation indices, we also presented the range of r^2, F, and p-value found among the 49 periods.

	Stream sites	% of significant periods	r^2 (range)	F (range)	p (range)
Intensity	1	12	< 0.001 - 0.16	0.008 - 9.84	0.003 - 0.93
	2	96	0.01 - 0.15	0.98 - 13.3	< 0.001 - 0.33
	3	100	0.062 - 0.31	5.0 - 34.1	< 0.001 - 0.03
Frequency	1	0	0.001 - 0.07	0.04 - 3.98	0.05 - 0.84
	2	26	< 0.001 - 0.15	0.005 - 13.1	0.001 - 0.94
	3	0	< 0.001 - 0.02	< 0.001 - 1.1	0.29 - 0.99
Temporal Clustering	1	0	0.01 - 0.07	0.56 - 3.98	0.05 - 0.46
	2	0	0.001 - 0.04	0.06 - 3.19	0.08 - 0.80
	3	0	< 0.001 - 0.01	< 0.001 - 1.12	0.29 - 0.99

Table 2: Results of the linear regression models of the nestednes (β_{nes}, $d_{BC\text{-}nes}$) and turnover (β_{turn}, $d_{BC\text{-}turn}$) components of the Sørensen (β_{sor}) and Bray-Curtis (d_{BC}) dissimilarity indices vs. the difference in intensity (ΔI) among the 14 sampling dates. Regression models have been performed for the three study stream sites for a period of 15 days.

	Sørensen β-diversity *(β_{sor})*			Bray-Curtis β-diversity *(d_{BC})*		
	r^2	F	p-value	r^2	F	p-value
	Nestedness (β_{nes})			*Abundance gradient ($d_{BC\text{-}nes}$)*		
Stream site 1	0.001	0.008	0.930	0.518	68.815	< 0.001
Stream site 2	0.036	3.334	0.071	0.151	15.7681	< 0.001
Stream site 3	< 0.001	< 0.001	0.987	0.229	26.480	< 0.001
	Turnover (β_{turn})			*Balanced variation ($d_{BC\text{-}turn}$)*		
Stream site 1	0.033	2.190	0.144	< 0.001	< 0.001	0.983
Stream site 2	0.217	24.657	< 0.001	0.006	0.553	0.460
Stream site 3	0.183	19.954	< 0.001	0.009	0.833	0.364

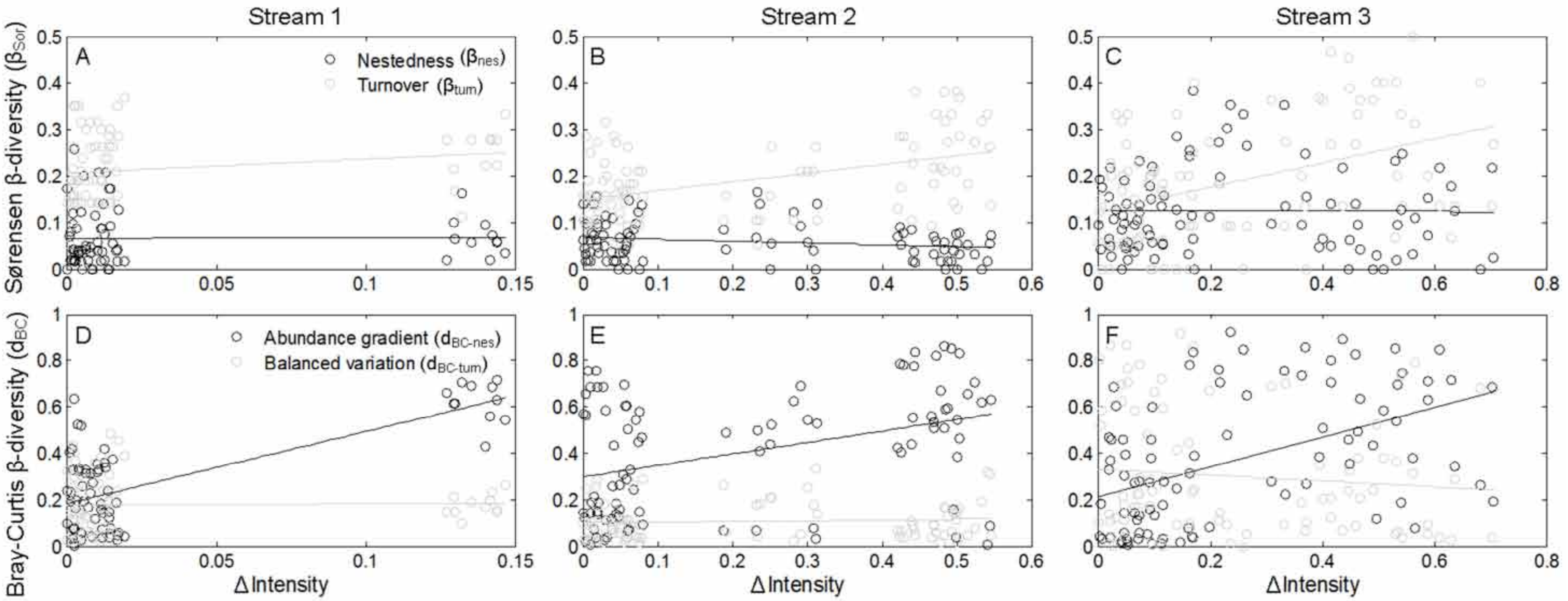


Figure 4: Scatter plot of the nestedness, β_{nes}/ abundance gradient, $d_{BC\text{-}nes}$ (black open dots) and turnover, β_{turn}/ balanced variation, $d_{BC\text{-}turn}$ (grey open dots) components of the Sørensen (β_{sor}) and Bray-Curtis (d_{BC}) dissimilarity indices vs. difference in intensity (ΔI) among the 14 sampling dates. Black and grey lines correspond to the predictions of the linear regression models for nestedness/ abundance gradient, and turnover/ balanced variation components, respectively. Analyses were performed for a period of 15 days for the three study stream sites.

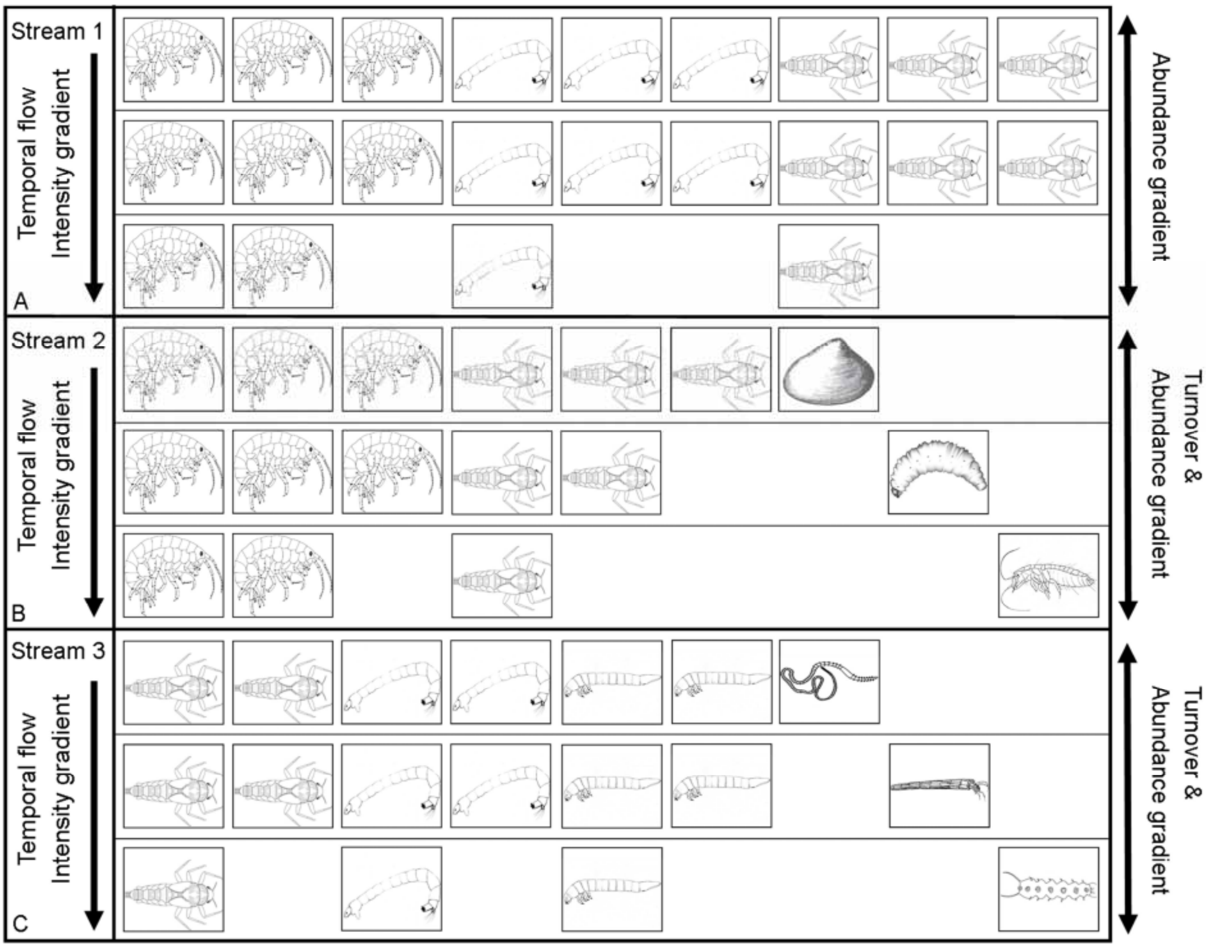


Figure 5: Illustration of the community dissimilarity found in the three study sites along the temporal flow intensity gradient. **A**: at site 1, community dissimilarity was caused by an abundance gradient of dominant taxa (e.g., *Hyallela*, Orthocladiinae, and *Andesiops*). **B and C**: at site 2 and 3, community dissimilarity was caused by both abundance gradient of dominant taxa (e.g., *Hyallela* and *Andesiops* at site 2, and *Andesiops*, Orthocladiinae, and *Neoelmis* at site 3) and taxon turnover (e.g., *Sphaeriidae* were replaced by *Nepticulidae* and *Prionocyphon sp2* at site 2 and Naididae sp1 were replaced by *Nectopsyche* and *Blepharicera sp1* at site 3).

Discussion

Temporal scaling of flow disturbance effects on freshwater ecosystems

Several studies have pointed out that the effects of hydrological variability on aquatic biota depend on the temporal scale considered (Naiman et al. 2008; Denny and Benedetti-Cecchi 2012). Indeed, previous studies shown that various physical (e.g., drag, nutrient transfer) and biological processes (e.g., competition, dispersion) control aquatic ecosystem structure and function at different temporal scales, from millisecond to decades (Biggs et al. 2005; Roberts et al. 2007). Nevertheless, empirical studies on the effects of disturbance events on aquatic communities at multiple time scales remain scarce, especially because long-term continuous biological data are required (Geheber and Piller 2012), but also because analytical tools to handle and analyze long-term flow and taxon density time series are rarely used by freshwater ecologists. In this context, our study confirms that wavelet analyses are a promising tool to describe and analyze temporal scaling effects of flow regime on biota (see also Stewart-Koster et al. 2014).

Our wavelet analyses showed that the duration of hydrological time series affected the values of flow disturbance metrics (I, f, and C) but not their relationships with biota metrics. This may be explained by the fact that flood events in equatorial glacier-fed streams occur at a relatively high frequency (every day) and moderate intensity, which may allow macroinvertebrate adaptation (Cauvy-Fraunié et al. 2014a). While previous studies have shown that daily glacial floods induce invertebrate downstream drift (Jacobsen et al. 2014b), it remains uncertain whether flow speed and variability significantly rearrange the stream bed (Cauvy-Fraunié et al. 2014a). Another explanation would be that the disturbance threshold, statistically defined by the wavelet analysis (see Cauvy-Fraunié et al. 2013), has limited ecological relevance. Complementary studies - either empirical or experimental - would allow better defining flow disturbance thresholds above which studied aquatic taxa are affected (see

Rosman et al. 2013 for an example of the type of experimental study that could be performed). Once these potential caveats have been examined, wavelets analyses could be a relevant tool for studies examining flow-biota relationship at multiple time scales, especially in aquatic systems experiencing high temporal variability (e.g., temporal streams, snow-fed streams). Moreover, wavelets analyses are not only applicable to stream flow time series but also to others abiotic parameters (e.g., temperature, chemical components), which compose the cocktail of multiple stressors that generally accompanies flow variation.

Effect of flow temporal variability on community composition

Understanding the composition of specific stream communities at a given point in time requires a history of the flow regime, and especially a detailed description of disturbance events (Fraterrigo and Rusak 2008). As extreme flow events may potentially reset the aquatic community (Lake 2000) observed taxon assemblages mainly depend on the time elapsed since the last important disturbance (Lake 2008). However, the response of aquatic organisms to flow disturbance also depends on the rate of change (i.e. abrupt or gradual; Imbert and Perry 2000), as well as on the predictability of the flow disturbance (Lytle and Poff 2004). Indeed, gradual and predictable disturbance events are supposed to be less damaging than abrupt and unpredictable events because they allow taxa to anticipate and actively move into flow refugia (Lake 2008). In our study system, even though flow disturbances were highly predictable, temporal variations in glacial flood intensity significantly affected macroinvertebrate community composition. Thus, although a flow disturbance might be strongly predictable, its intensity could be quite variable and largely unpredictable (Jacobsen et al. 2014a), preventing less adapted taxa to anticipate strong disturbance events (Lake 2008).

Disturbance frequency is another key variable affecting aquatic community structure (e.g. Lytle and Poff 2004). In the specific case of equatorial glacier-fed streams, we never observed more than 9 consecutive days without glacial flood and we found no effect of disturbance frequency on macroinvertebrate community composition. This suggests that flow disturbances were too frequent to allow taxa washed away by glacial floods to recolonize upstream sites between two events. Our findings agree with an experimental study by Mccabe and Gotelli (2000) who found no effect of the frequency of substrate scouring events on stream macroinvertebrates. High disturbance frequency also prevents competition exclusion from generalist species (Huston 1979) and thus protects specialized species (adapted to high disturbance frequency) from generalist species, usually more competitive (Lytle and Poff 2004).

Temporal flow variability generates beta-diversity

Although variation in species assemblages could be examined across both spatial and temporal scales, studies on spatial β-diversity largely outnumber those on community dissimilarity patterns through time (Korhonen et al. 2010). Such an issue is particularly relevant in the case of glacier-fed streams as they exhibit strong temporal flow variability at inter-annual, seasonal and diurnal time scales (Milner et al. 2009). For example, Milner et al. (2008) and Finn et al. (2010) identified an intra-annual variability in aquatic taxon assemblages related to glacier retreat patterns. Moreover, Robinson et al. (2001) found that variability in macroinvertebrate community composition in temperate glacier-fed streams occurred at a seasonal time scale, characterized by low macroinvertebrate density and taxon richness in summer when flow intensity is at its maximum and *vice versa*. In equatorial glacier-fed streams aquatic communities do not exhibit significant variation at the seasonal time scale, but there is a significant flow-related temporal variability in communities (Jacobsen et al. 2014a).

Our results support Jacobsen et al. (2014a), who found a significant effect of diurnal flow variation intensity on aquatic community composition using an independent data set. Indeed, our results show that daily glacial flood had no “resetting effect” on the aquatic community, but rather induced slight changes in community composition, characterized by a decrease in the density of dominant taxa and taxon turnover along the temporal flow intensity gradient. We explain this temporal turnover by taxon displacements along the glacial influence gradient, from glacier snout to downstream parts. Our results suggest that these displacements results from an interplay between flow disturbance intensity and frequency. While high flow events would induce downstream displacements (Jacobsen et al. 2014b), some taxa might move upstream during low flow periods (Finn et al. 2010; Jacobsen et al. 2014b). Indeed, our data revealed that high flow events in glacier-fed streams are generally highly clustered, thereby providing extended periods (30 days) with no significant disturbance events, as well as long periods (> 50 days) with low disturbance events. These periods of low flow disturbances may represent windows of opportunities for the upstream colonization of generalist species. While our study focused on glacier-fed streams, it would be worth examining the relevance of the interaction between temporal variability in flow intensity and frequency for β-diversity organization in other dynamic aquatic systems.

This study highlights the critical importance of considering 1) various temporal scales, 2) the past temporal variability in flow, and 3) the temporal β-diversity when examining flow-ecology relationships. Indeed, the consideration of each of those components provides a more complete view of the physical and ecological processes affecting community organization, and improves our understanding of underlying mechanisms. Our study strongly suggests that both spatial and temporal heterogeneity provided by glacier-fed streams generate beta-diversity in glacierized catchments. The previously underestimated role of temporal flow disturbances intensity and frequency on invertebrate β-diversity in glacierized catchments is of particular interest in the context of an increase in extreme flow event frequency (Sorg et al. 2012), whose impact of fauna organization would merit further attention. More broadly, a better consideration of temporal scaling effects of flow disturbance on aquatic fauna could improve our understanding of biodiversity response to increasingly altered flow regimes worldwide.

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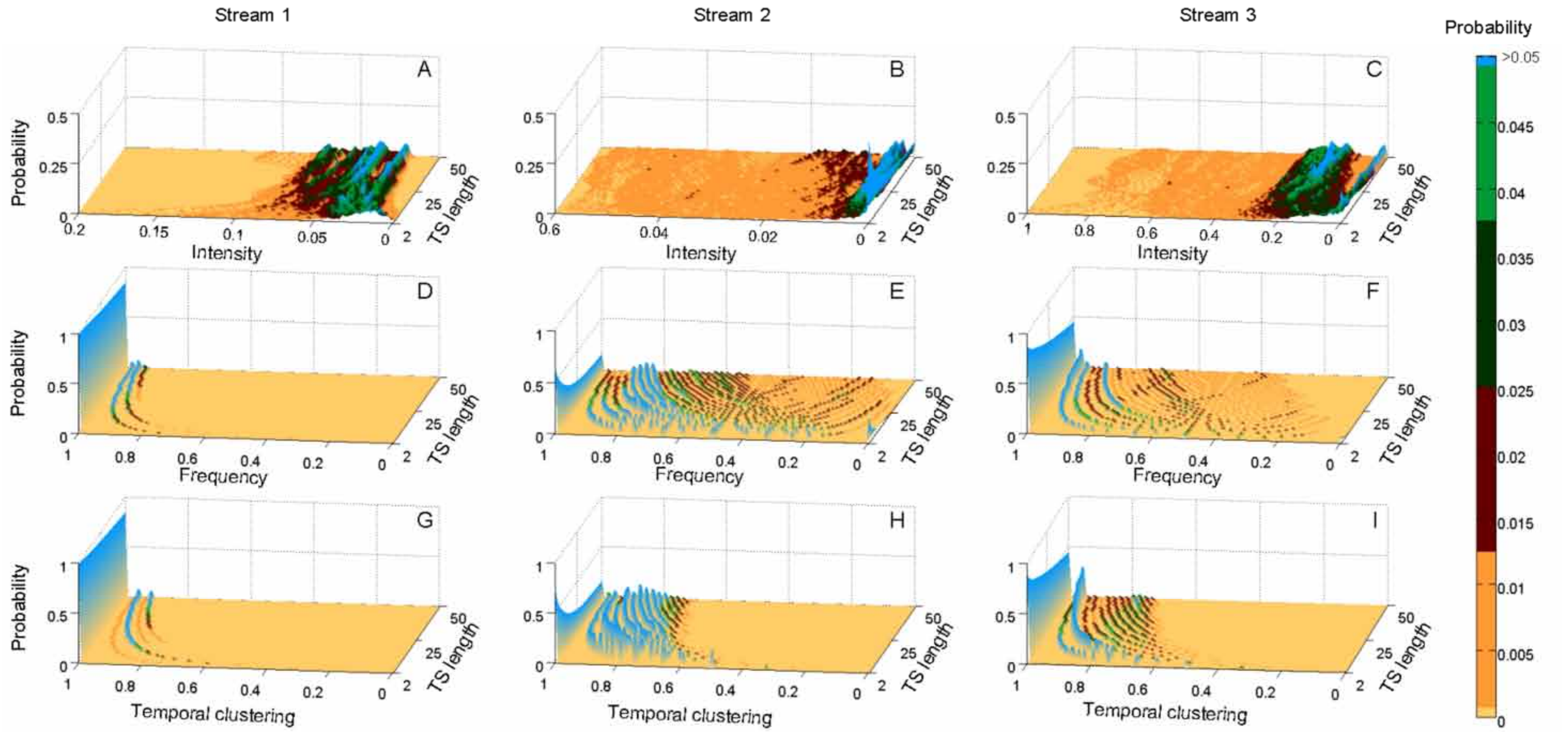
Appendix 1

Figure: Surface plot of the flow variability distribution probability variation with increasing time series length (TS length). Probabilities were calculated for intensity (A-C), frequency (D-F), and temporal clustering (G-I), and for the three study stream sites



CHAPTER 3

Glacier influence on invertebrate metacommunity structure and dynamics in an Andean stream network

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Running head: glacial influence and metacommunity structure

Keywords: climate change, glacier retreat, glacierized stream network, metacommunity structure and dynamics, macroinvertebrates, environmental filtering, dispersal limitation

Abstract

Alpine glacierized catchments are unique freshwater ecosystems, as they exhibit a singular environmental heterogeneity of habitats associated to specific species assemblages. One impact of climate change is the acceleration of glacial shrinkage, resulting in a reduction in glacial meltwater contribution to alpine streams flow with likely consequences on aquatic biodiversity. It is thus crucial to understand glacier runoff effects on aquatic communities so that glacial shrinkage influences on aquatic biodiversity can be anticipated. In this study, we propose to use metacommunity theory as a conceptual framework to better understand how glacial meltwater contribution to stream flow influences the spatial organization of aquatic species assemblages in glacierized catchments. We sampled benthic macroinvertebrates and characterized geographical, physico-chemical and food resource conditions in 51 stream sites in a glacierized catchment of the Ecuadorian Andes. Using partial redundancy analysis, we partitioned community variation to evaluate the relative strength of environmental conditions (e.g. glacial influence) vs. spatial processes (e.g., overland, watercourse, downstream directional dispersion) in organizing the aquatic metacommunity. Results revealed that both environmental filtering and dispersal processes dictated metacommunity structure. Among all environmental variables, glaciality best explained community variation among sites. In addition, by providing harsh environmental conditions, glacial meltwater limited macroinvertebrate waterborne dispersion within the stream network. Glacial meltwater thereby generated high environmental heterogeneity and prevented non-adapted species with low overland (aerial) dispersal capacity to colonize throughout the entire catchment. Thus, glacial meltwater promoted high β-diversity within the watershed. Therefore, under a scenario of reduction in glacial meltwater, we expect a reduction in both environmental filtering and dispersal limitation, inducing a taxonomic homogenization of the aquatic fauna in glacierized catchments (i.e. decrease in β-diversity), and consequently a reduction in regional diversity.

Introduction

Ongoing climate change is accelerating the shrinking of mountain glaciers (Rabatel et al. 2013, Sakakibara et al. 2013), resulting in an alteration of glacial meltwater contribution to stream flow within glacierized catchments (Huss et al. 2008). At the early stages of glacier retreat, the reduction in ice volume would yield a significant increase in annual glacial runoff (Baraer et al. 2012). However, as the amount of frozen water stored in the glaciers decreases, runoff increase would reach a critical threshold after which it would decrease until the complete disappearance of the glacier (Mark et al. 2005). This reduction is expected to have strong effects on aquatic biodiversity as glacial meltwater engenders a high heterogeneity of environmental conditions within glacierized catchment (Brown et al. 2003), which in turn generates variation in local communities among stream sites (i.e. β-diversity; Brown et al. 2007, Finn et al. 2013). Moreover glacial streams shelter specialist and endemic species (Milner et al. 2009), hence glacial meltwater strongly contributes to the regional aquatic biodiversity (Jacobsen et al. 2012). Thus, regional biodiversity is threatened by both the loss of glacier-fed streams and the decrease in environmental heterogeneity within the catchments caused by the alteration of glacial runoff (Brown et al. 2007, Jacobsen et al. 2012).

Ideally, understanding and modeling the fate of aquatic communities as glaciers rapidly melt requires the long-term establishment of monitoring stations of both abiotic and biotic variables (see Milner et al. (2008) for the longest invertebrate abundance time series along a glacial stream). As an alternative approach, the space-for-time substitution framework encompasses analyses in which contemporary spatial phenomena are used to predict future events (e.g., Ferrier and Guisan 2006, Elith and Leathwick 2009). This approach is especially relevant when studying turnover of species among communities because it can be quantified independently across space or through time (Blois et al. 2013). Space-for-time substitution framework can be coupled to metacommunity theory, which not only allows describing spatial patterns of community organization, but also helps understanding underlying physical and biological processes resulting in such patterns. A metacommunity is a set of local communities connected through the dispersal of multiple potentially interacting species (Leibold et al. 2004). Metacommunity theory recognizes two types of forces that can affect the structure of communities: local forces which include species interactions and local environmental conditions, and regional forces which include dispersal processes of organisms between local communities (Urban 2004, Holyoak et al. 2005). Leibold et al. (2004) have provided the basic background and theory of metacommunity structure (pattern of spatial species distribution) and dynamics (mechanisms that arise within metacommunities) and suggested four main models that balance local environmental factors and dispersal differently in structuring metacommunity. The neutral model assumes that patches are identical, that all species are functionally equivalent and that community dynamics are driven by stochastic processes. In the patch dynamics model, all habitats are equivalent, but species have different competition/colonization abilities that drive community dynamics. The species sorting model assumes that dispersal is moderate, allowing species to sort along environmental gradients according to niche theory (Hutchinson 1959). In the mass-effect model, high rates of dispersal can swamp or interact with local influences so that local community structure is largely driven by regional processes (Amarasekare 2004, Chase et al. 2005). Although it is unlikely that natural communities will conform solely to any one of these models, they help to understand mechanisms driving real metacommunity structure (Ellis et al. 2006).

Stream networks possess several features that differentiate them from the majority of metacommunity configurations (Brown et al. 2011). First, streams are dendritic ecological networks (Campbell Grant et al. 2007), i.e. systems with a hierarchical branching structure in which main stems connect multiple branches. The flux of organisms is predicted to be greater through main stems relative to headwaters as main stems integrate movement of organisms from and between branches (Fagan 2002). Moreover, the directionality of water flow engenders a stronger influence of upstream sites on downstream sites than vice versa due to directional fluxes of matter and energy (Brown et al. 2011). Thus, both stream geometry and flow directionality strongly affect the dispersion of organisms (Campbell Grant et al. 2007, Brown and Swan 2010). Moreover, depending on the organism, dispersal in stream networks can occur across watershed (i.e. overland dispersal, e.g. adult flying insects; Finn et al. 2006) and/or along the stream channel (i.e. watercourse, e.g., diatoms, insect larvae; Liu et al. 2013), either through active behavior (i.e. flight, swim, crawling, e.g. upstream movement by fish; Brown et al. 2011) or through passive transport (through animal vectors, by wind or flood, e.g., crustacean, snails, aquatic mites; Meutter et al. 2007, Shurin et al. 2009). In addition, stream networks are highly heterogeneous systems, presenting strong differences in in-stream environmental conditions among sites, especially in headwater catchments (Clarke et al. 2008), but probably even more in headwater glacierized catchments (see above). Therefore glacierized stream networks likely present particular and complex metacommunity dynamics (Brown and Swan 2010, Brown et al. 2011) yet very little information exist about this.

Here, we examined spatial patterns in benthic community organization in a tropical glacierized watershed providing a wide gradient of glacial influences to explain, and eventually predict, temporal change that would occur along a glacier melting process. Our study uses metacommunity theory to (1) identify mechanisms driving the spatial organization of aquatic metacommunities in particular the relative influence of local (i.e. environmental conditions) vs. regional processes (i.e. dispersion) on this organization, and (2) determine the contribution of glacial meltwater to the community variation among stream sites, either by generating high environmental heterogeneity, or by limiting invertebrate dispersion. We hypothesized that (1) among several environmental variables, glaciality (i.e. glacial influence) best explained community variation among sites, (2) glaciality explained community variation among sites better than spatial variables, and (3) glaciality affected invertebrate dispersion within the stream network. We also examined whether (1) the dispersal abilities of stream macroinvertebrates (i.e. flying, non-flying adults) and (2) the geographical location of stream communities within the framework (i.e. upstream vs. downstream sites) affected our predictions. Finally, we used our results to discuss potential future effects of glacial flow alteration (both increase and decrease) on the organization of benthic metacommunity.

Materials and methods

Study site

The study was conducted in 51 stream sites, located in an 115 km^2 watershed in the Ecological Reserve of Antisana, Ecuador (0° 33′ 09″S, 78° 14′ 58″W, mouth coordinates). The watershed was composed by stream catchments showing different glacier influence (Fig. 1). Among the 51 stream sites, 21 had no glacier influence and 30 were located along four glacier-fed streams and presented between 1 and 93% of glacier cover in the catchment (see Table 1; this percentage was calculated by dividing the glacier area by the total catchment basin area). The four main glacier-fed streams originated above 4800 m a.s.l; one from the glacier “15” (the furthest North on the map, Fig. 1), which covered an area of about 0.60 km^2 at the time of the study in 2010; the second from the glacier “14”, covering an area of about 0.45 km^2; the third from the “Los Crespo” glacier covering an area of about 1.82 km^2; and the fourth from the glacier “11” covering an area about 0.2 km^2 (see Rabatel et al. 2013) for glaciological data). Among the 51 stream sites, 25 were located on first-order streams and 26 on second and third-order streams. Fourteen first-order stream sites were fed by groundwater and/or rain fall while the 11 others were fed by glacial meltwater (see Table 1). All study sites were located between 3886 and 4835 m a.s.l. Glacially-influenced stream sites were located at distances of 15 m - 15.2 km from the glacier snouts (see Table 1).

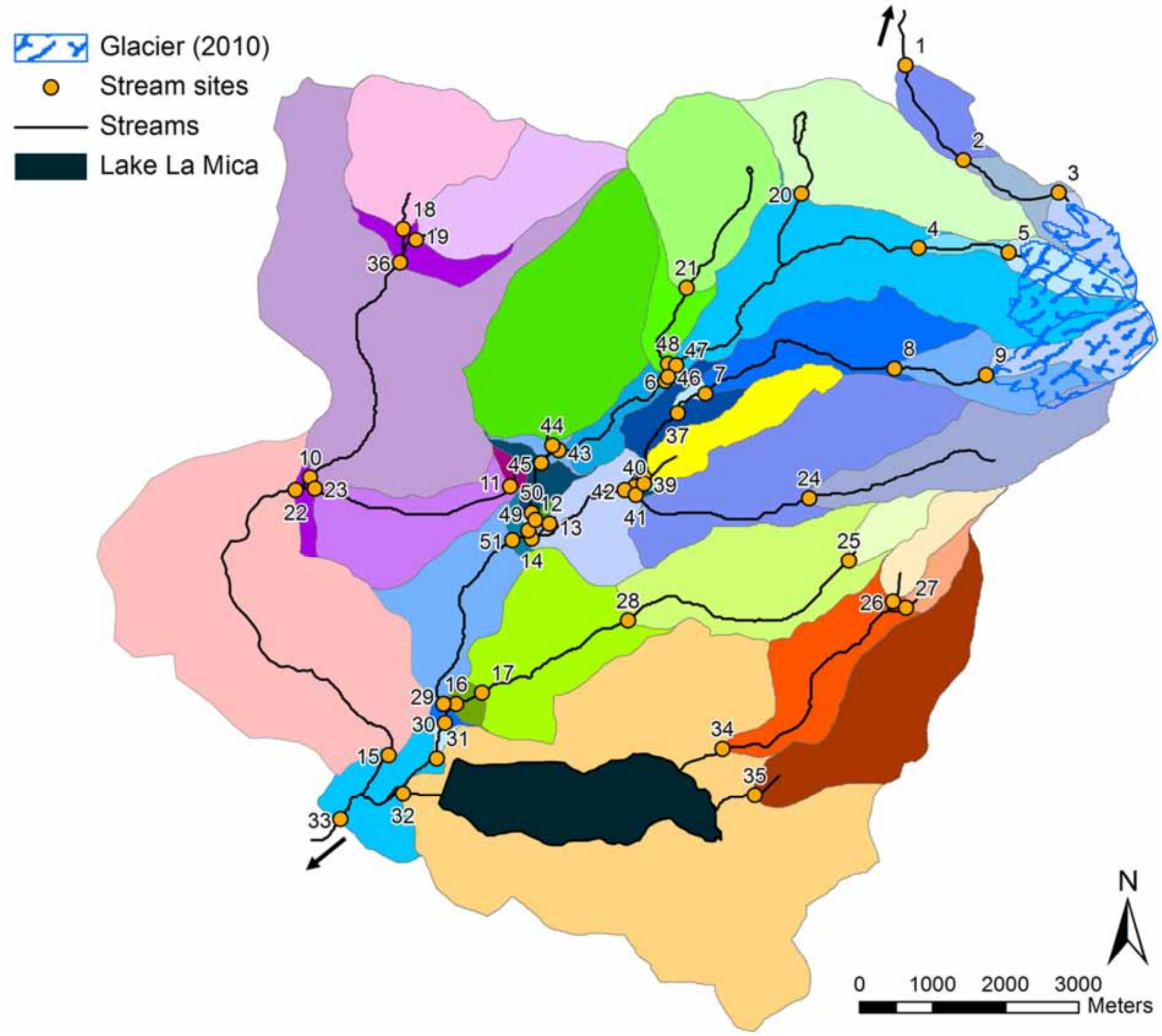


Figure 1: Map of the study area at the Antisana volcano, Ecuador. Study sites are represented by orange circles. Black arrows show the stream directionality. Catchment basins of all sites are represented by polygons (blue polygons for glacial streams). The catchments were delimited based on a 40m resolution DEM using SAGA GIS (2.0.8). The glacier outlines were calculated based on LANDSAT satellite images from 2010 (see Cauvy-Fraunié et al. 2013 for glacier outlines and catchment delimitation details). The map was made using ArcGis (10.0).

Macroinvertebrate sampling

At each site, macroinvertebrate sampling was performed once between May 2009 and January 2010. We assumed that differences in sampling dates did not significantly affect the results of our study as benthic community patterns and dynamics in the study area are mostly aseasonal (Jacobsen et al. 2014a). At each site, we randomly collected five quantitative Surber samples (0.05 m^2; mesh size 200 μm) from pebble–cobble substratum along a 20- to 30-m stretch. All samples were collected in the morning before daily glacial flood and preserved in the field in 70% ethanol. In the laboratory, Surber samples were rinsed through a 200-μm sieve and sorted without use of magnification. No subsampling was applied. Invertebrates were identified under a microscope at 10× magnification range to morphospecies, genus or (sub) family, according to Fernández and Domínguez (2001).

Environmental characterization

A detailed characterization of each stream site was performed the same day we collected macroinvertebrates. Stream width was measured at 5 transects located every 5 m along a 20- to 30-m stretch. Water stage was measured 10 times along the 5 transects (i.e. in total 50 times). We measured stream slope at each site with a transparent plastic tube that carried flowing water from the upstream to the downstream end of the reach. Slope was calculated as the difference between the water level inside the tube when raised until flow stopped and that of the surface of the stream water at the downstream end, divided by the distance between the upstream and downstream ends of the tube (~25 m). To quantify the physical stability of the stream, a score system (15-60, with 60 as the most unstable) based on the channel bottom component of the Pfankuch index (Pfankuch 1975) was applied once to each of the 20- to 30-m reaches where invertebrate samples were collected.

At each site, conductivity (at 25°C), water temperature, and pH were measured with portable meters, model Cond 315i and pH 315i, respectively (WTW, Weilheim, Germany). Water turbidity was measured with a Eutech TN-100 Turbidimeter (Eutech, Nijkerk, The Netherlands).

We estimated the food resources available to macroinvertebrates by sampling pebbles for quantification of epilithic algae and collecting the benthic detritus obtained in Surber samples (see below). At each site, we collected 9 small pebbles (~2 - 4 cm) at random (but we avoided pebbles with filamentous algae), placed 3 pebbles in each of 3 containers, and extracted chlorophyll *a* in 96% ethanol for 1 to 3 days in the dark until further processing in the laboratory. After settlement for a few hours, we transferred a sample to a spectrophotometer and measured absorption at 665 and 750 nm. We calculated the concentration of total chlorophyll *a* (including phaeopigments) according to the method published by Københavns Universitet (1989). Stone surface area was estimated with the formula proposed by Graham et al. (1988), using the length, width, and height of the stones. We quantified benthic detritus by collecting all material (inorganic and organic) present in the Surber samples after sorting out the animals. This material was dried at 80°C for ~24 h and weighed. We used mass loss upon combustion at 550°C as the ash-free dry mass of organic material > 200 μm in the sample.

Table 1: Physico-chemical attributes of the study stream sites measured once at the same date as invertebrate sampling (see location of the sites on Fig. 1). Upstream sites were represented in bold in the column Sites. GCC=glacier cover in the catchment. Stream sites with zero %GCC have no visible connection to the glacier. Cond = conductivity. Temp = Temperature. Pfan = Pfankuch index. Chl *a* = Chlorophyll *a*. Dens = Density. Taxa richn = Taxa richness. UTM coordinates refer to stream site coordinates in UTM-WGS84 zone 17S expressed in meters.

	UTM Coordinates					"Glaciality index" parameters				Instream parameters				Resource parameters		Invertebrates	
Sites	X (long.)	Y (lat.)	Altitude (m a.s.l)	Distance from glacier (km)	% GCC	Cond (μS cm^{-1})	Temp (°C)	Turbidity (NTU)	Pfan	Width (cm)	Water stage (cm)	Slope (%)	pH	Chl *a* (mg m^{-2})	Benthic detritus (g m^{-2})	Dens (ind m^{-2})	Taxa richn
1	814618	9949706	4335	3.72	22	6.6	7.2	290.0	43	63.1	10.4	0.3	6.4	0.8	7.3	856	17
2	815612	9948458	4521	1.85	39	15.0	5.8	325.0	39	59.1	5.8	0.4	6.9	1.2	0.7	1148	16
3	817040	9947921	4835	0.15	72	3.0	4.1	1000.0	41	66.8	5.2	0.5	8.0	0	0.4	176	2
4	815010	9947128	4521	1.57	65	8.2	4.2	511.0	32	132.8	10.4	0.4	7.0	2.0	1.2	1360	15
5	816356	9947098	4789	0.15	84	7.2	3.1	237.0	29	71.9	6.3	1.0	6.3	0.2	0.5	372	5
6	811651	9945306	4188	6.25	11	87.9	9.9	58.0	31	132.7	17.5	0.1	7.2	0.6	1.1	3040	20
7	812259	9945238	4210	5.05	27	11.8	7.4	414.0	36	158.4	18.7	0.4	7.0	0.4	2.4	1072	17
8	814760	9945508	4496	1.83	56	4.3	4.9	774.0	39	204.3	13.1	0.3	6.4	1.1	3.1	428	9
9	816437	9945235	4728	0.02	93	1.6	2.4	543.0	39	38.5	3.1	0	7.5	0.1	0.4	348	6
10	807111	9944074	3988	0	0	164.0	7.9	5.0	32	60.2	55.8	0.1	7.7	1.1	1.2	2136	19
11	809653	9944010	4092	0	0	241.0	11.8	1.2	49	531.0	19.1	0.1	8.0	6.9	4.0	8464	28
12	809920	9943440	4050	0	0	139.6	7.2	1.0	37	355.5	32.1	0.3	7.1	9.0	2.9	9600	16
13	809919	9943238	4050	0	0	154.0	7.9	1.8	34	55.5	17.5	0.4	8.1	7.3	1.8	6928	34
14	809888	9943190	4042	8.93	9	150.6	10.6	202.0	23	145.6	32.8	0.1	8.4	3.4	1.2	6040	33
15	807788	9940158	3917	0	0	235.0	11.6	9.3	32	181.4	18.7	0.1	8.9	4.3	1.3	6776	26
16	808727	9940728	3950	0	0	275.0	10.6	6.4	42	227.6	42.9	0.2	8.0	6.7	1.7	16808	27
17	809103	9941030	3975	0	0	276.0	10.3	6.8	50	223.0	65.8	0.2	8.0	6.7	1.9	5516	25
18	808072	9947364	4090	0	0	121.0	7.3	9.1	28	57.0	18.4	5.0	7.3	4.2	5.3	16536	33
19	808184	9947282	4090	0	0	146.5	8.5	4.2	27	68.6	8.5	8.8	7.3	7.2	3.1	5628	26
20	813487	9947876	4368	0	0	14.9	16.9	4.3	29	48.8	5.5	2.3	7.7	3.7	1.5	15416	24
21	811943	9946616	4262	0	0	98.6	8.2	5.9	35	80.4	6.8	3.9	8.7	3.8	5.5	16180	16
22	806750	9943866	3988	0	0	201.0	14.1	4.7	27	111.0	26.0	0.9	6.5	2.2	3.4	6656	28
23	806952	9943812	4006	0	0	230.0	13.4	4.6	30	212.0	14.7	0.7	7.7	2.3	3.1	7336	32

24	813521	9943670	4246	3.9	3	45.1	12.9	75.3	29	50.6	18.5	4.8	7.4	0.2	3.9	6584	34
25	814168	9942874	4268	0	0	94.1	16.9	5.2	46	227.0	4.3	6.8	7.5	2.0	2.9	17584	23
26	814744	9942256	4218	0	0	79.4	13.1	20.5	31	140.0	8.6	27.0	7.2	0.2	4.7	8304	23
27	814801	9942182	4226	0	0	100.4	10.1	7.3	30	101.0	13.1	15.4	6.6	0.2	3.7	5140	25
28	811104	9942040	4009	0	0	270.0	9.2	3.2	36	195.0	23.4	4.6	8.1	2.0	6.6	12288	37
29	808563	9940792	3950	12.18	7	149.9	11.8	66.6	30	259.0	27.2	2.4	8.5	4.1	0.9	4112	27
30	808548	9940528	3930	12.47	6	163.2	9.4	24.4	34	408.0	30.3	1.2	7.5	2.2	4.1	11876	36
31	808438	9940298	3922	12.75	6	180.6	10.7	21.0	28	344.0	13.7	1.8	7.3	14.0	2.4	11292	35
32	808325	9939596	3928	0	0	352.0	11.2	97.0	44	504.0	24.7	0.6	5.7	11.3	0.5	928	14
33	806893	9938980	3886	15.18	3	261.0	13.5	19.6	25	462.0	37.8	2.1	5.4	10.3	1.0	10380	26
34	812471	9940326	3944	0	0	183.2	14.8	30.0	32	148.3	9.2	3.7	7.9	3.5	2.6	8504	30
35	812784	9939636	3945	0	0	128.8	9.5	33.3	21	136.7	16.9	8.2	7.7	3.8	1.1	42256	27
36	808062	9947152	4077	0	0	124.4	8.6	8.5	39	96.4	19.7	4.3	7.2	9.4	3.1	13468	32
37	811692	9944864	4183	5.84	27	9.8	8.3	282.0	23	199.0	6.8	2.5	7.9	3.6	0.4	448	10
38	811078	9943872	4109	7.19	23	38.8	9.0	284.0	23	80.5	8.8	3.8	7.4	2.3	1.5	232	15
39	811098	9943836	4110	0	0	303.0	17.0	5.0	41	110.0	13.3	4.3	7.9	3.3	2.6	2220	18
40	811025	9943792	4105	7.3	18	184.4	16.2	111.0	23	79.3	20.6	6.3	8.0	1.6	3.7	904	21
41	811088	9943738	4108	6.67	1	157.4	11.7	7.0	38	80.2	24.5	3.1	7.7	2.7	4.0	2580	25
42	810941	9943760	4093	7.4	10	167.2	13.4	44.0	23	115.0	29.2	2.0	8.0	2.3	3.4	1452	26
43	809927	9944126	4093	8.58	11	35.9	10.8	92.0	26	74.6	19.1	3.3	7.1	2.1	7.1	10744	35
44	809890	9944154	4090	0	0	209.0	9.6	10.0	40	70.6	13.1	5.9	7.1	6.2	4.1	11188	22
45	809877	9944066	4085	8.67	7	165.3	9.8	32.0	25	76.0	20.1	3.0	7.2	8.1	1.8	3976	32
46	811710	9945398	4193	6.14	11	22.0	11.4	131.0	24	91.4	15.2	5.2	7.8	2.5	1.4	4924	27
47	811725	9945452	4195	6.08	17	20.0	11.8	133.0	25	65.6	10.3	5.6	7.7	2.4	2.3	3236	20
48	811707	9945446	4202	0	0	108.0	12.2	4.0	33	55.5	7.0	38.8	8.5	3.8	5.0	5812	25
49	809793	9943234	4045	9.72	7	142.0	9.9	17.0	30	98.2	31.5	2.5	7.4	3.5	1.5	5980	29
50	809783	9943444	4056	9.43	7	138.0	9.9	62.0	34	67.6	26.5	6.4	8.6	18.8	1.6	11132	28
51	809661	9943130	4039	9.18	8	102.2	10.8	60.0	37	181.4	43.6	5.4	7.5	2.3	6.8	5820	31

Overall modeling framework

To test each of our three hypotheses related to the spatial organization of benthic invertebrate assemblages (see Introduction), we built three comparative models (Fig. 2).

Model 1 compared the relative importance of *Glaciality* vs. two environmental variables (*Instream* and *Resources;* see below) in structuring benthic metacommunity.

Model 2 compared the relative importance of *Glaciality* vs. spatial variables to explain metacommunity structure. Because spatial processes in aquatic networks potentially occur through overland, watercourse and directional downstream dispersion, we built three sub-models with each of these three spatial variables. In addition, as both geographical and altitudinal distances might enhance community variation among sites (Barquín and Death 2006, Soininen et al. 2007, Moritz et al. 2013) we assessed the relative contribution of the three spatial variables (overland, watercourse and directional downstream) computed using either geographical or altitudinal distances.

Model 3 assessed the effect of spatial variables (watercourse and directional downstream) computed using *Glaciality* distances (i.e. difference in *Glaciality* among stream sites, see below).

We ran each of the three models using four taxa matrices (namely *All taxa*, *Flying taxa*, *Non-flying taxa*, and *Taxa Order I;* see below) to assess the influence of taxa dispersal ability and stream site location on our predictions.

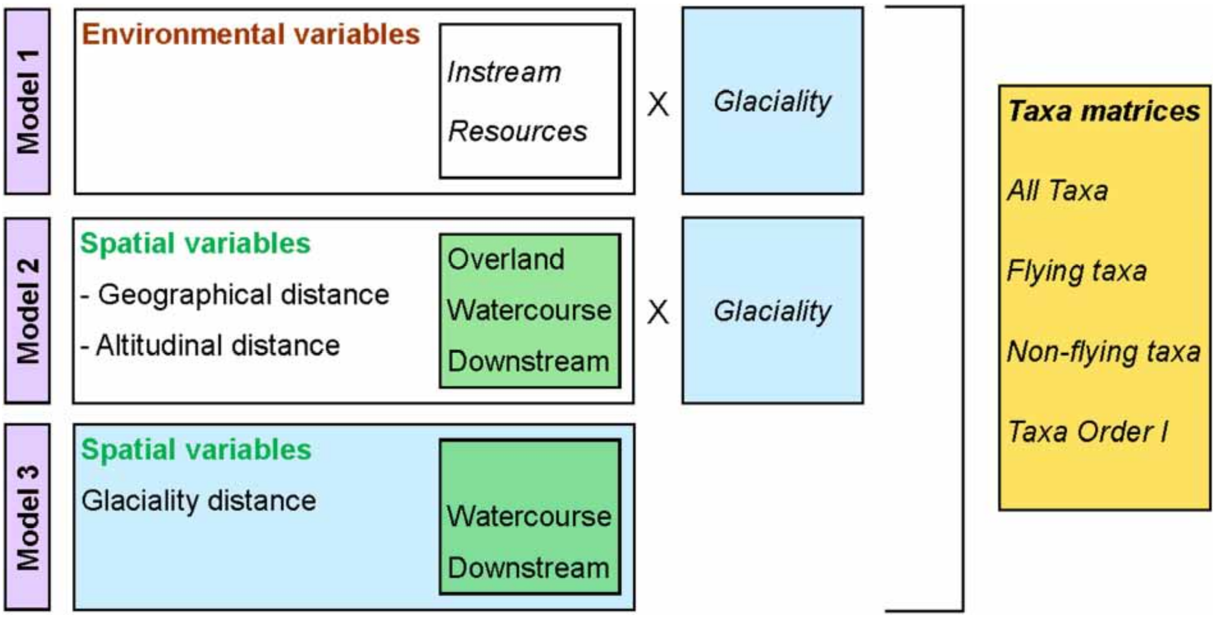


Figure 2: Illustration of the three models used to determine the factors structuring the metacommunity. Model 1: comparison of the performance of the two environmental variables *Instream* and *Resources* vs. the variable *Glaciality*. Model 2: comparison of the performance of three spatial eigenfunction-based variables based on overland, watercourse, downstream distances using either geographical or altitudinal distances vs. the variable *Glaciality*. Model 3: comparison of the performance of the two spatial eigenfunction-based variables based on watercourse and downstream glaciality distances. The three models were performed for *All taxa*, *Flying taxa*, *Non-flying taxa*, and *Taxa Order I* matrices.

Data preparation

Geographical distance

We calculated the following geographical distances: (1) the overland distance, the shortest straight line distance between sites was calculated in ArcGis (version 10.0) using the *Analysis/Proximity/Point distance* tool, and (2) the watercourse distance, the distance among sites following the stream channel was calculated after creating the stream network using the *Network Analyst* tools in ArcCatalog (version 10.0) and then computing the distance following the stream channel in ArcGis using both *Network Analyst/Make OD Cost Matrix* and *Add location* tools.

Altitudinal distance

We calculated the overland and watercourse altitudinal distance between all pairs of sites as the difference between the highest and the lowest point along the shortest overland straight line between sites, and the difference between the highest and the lowest point along the stream channel, respectively. For this purpose, we first created a digital elevation model (DEM) using a 40-m resolution contour line from the Ecuadorian Military Geography Institute (available at http://www.igm.gob.ec/site/index.php) in ArcGis. Then we created overland and watercourse features between all pairs of sites in ArcGis using the *Linear referencing/Create routes* tool, and we attributed the features with elevation information derived from the DEM using the *3DAnayst/Functional surface/Add surface information* tool.

Glaciality distance

We calculated the difference in glacial influence among sites using the glaciality index provided by Ilg and Castella (2006). For all study sites, we first scaled between 0 and 1 water temperature, conductivity, 1/turbidity (≈1/suspended sediment) and 1/Pfankuch. We then processed the four variables using a non-centred principal component analysis (NPCA) and used the ordination scores of the sites along the first axis as an index of glaciality. Moreover we transformed the first axis values to obtain only positive values, with the highest values corresponding to the most glacially-influenced sites. The principal component analysis was performed in R (R Development Core Team, 2013, version 3.0.2) using the package *vegan*. Note that contrary to Ilg and Castella (2006), we also applied this index to non glacial streams, which allowed us to assign a quantified environmental stress to those streams. This index allowed us to have a more precise index than the percentage of glacier cover in the catchment which is zero for all non glacial stream. We then assigned a glaciality value to all stream segments - a segment is either a segment between two sites if there is no node between the two sites (i.e. no stream confluence) or a segment between a site and a node. Finally we calculated the difference between the highest and the lowest glaciality among all pairs of sites following the stream channel.

Environmental matrices

We constructed three environmental matrices: (1) the *Glaciality* matrix composed by temperature, conductivity, 1/turbidity and 1/Pfankuch, (2) the *Instream* matrix, composed of stream width, mean water stage, slope, and pH, and (3) the *Resources* matrix, composed of the chlorophyll *a* and benthic detritus. All environmental variables were previously scaled between 0 and 1.

Taxon matrices

We built four taxon matrices: *All taxa*, *Flying taxa*, *Non-flying taxa*, and *Taxa Order I* matrix. *All taxa* consisted of an abundance matrix including all identified taxa, *Flying taxa* consisted of an abundance matrix of adult flying taxa, *Non-flying taxa* consisted of an abundance matrix of exclusively aquatic taxa, and *Taxa Order I* matrix consisted in an abundance matrix of only upstream sites (Order I). Due to the lack of data on the dispersal ability of Andean stream invertebrate taxa, we were not able to construct a precise classification of dispersal abilities (e.g. Poff et al. 2006) and therefore divided taxa into only two groups (i.e. *Flying taxa* and *Non-flying taxa*). The four abundance matrices were transformed using Hellinger transformation prior to statistical analysis which is appropriate for the analysis of community composition data (see Legendre and Gallagher 2001 for details) using the package *vegan* in R.

Data analysis

Computation of the spatial eigenvectors

We generated eigenfunction-based spatial variables (i.e. eigenvectors) from overland distance and watercourse distance matrices using Moran's Eigenvector Map (MEM) analysis (Dray et al. 2006), and from directional downstream distance matrice using Asymmetric Eigenvector Map (AEM) analysis (Blanchet et al. 2008b). More details on the methods are given in Appendix 1. In the exactly same way, we computed the spatial eigenvectors using either geographical, altitudinal, or glaciality distances. Note that we did not compute the eigenvectors from overland glaciality distances as it was not relevant; there is no difference in glaciality among sites throughout the air.

Community variation partitioning

We performed variation partitioning using redundancy analysis ordination to assess the relative performance of the different variables in our three models (Borcard et al. 1992); i.e. to separate the relative effect of the different explicative factors on the structure of species communities. Variation partitioning aims at quantifying how much of the variance in species community structure can be explained uniquely by each explanatory variable (pure contribution), as well as the shared variance explained by the explanatory variables. The significance of each independent fraction (i.e. unique fraction) was tested with 999 permutations (Blanchet et al. 2011, Borcard et al. 2011). Those analyses were performed using the package *vegan* in R.

When running variation partitioning analyses, we also tested whether the effects of geographical, altitudinal and glaciality distances were not confounded. We performed separately variation partitioning analyses on spatial eigenvectors based on overland, watercourse and directional downstream distances using geographical, altitudinal and glaciality distances. All those analyses were performed for the four taxon matrix: *All taxa*, *Flying taxa*, *Non-flying taxa*, and *Taxa Order I*.

Results

We identified a total of 85 taxa from the 51 stream sites. Local richness ranged from 2 (at site 3) to 37 taxa per site (at site 28, Fig. 1) and macroinvertebrate density ranged from 176 (at site 3) to 42,256 ind.m^{-2} (at site 35; see Table 1). Dominant taxa were Orthocladiinae, *Podonominae* sp1, and *Simulium* in first-order glacier-fed streams; Orthocladiinae, *Andesiops*, and *Alluaudomyia* in mixed streams; and Orthocladiinae, *Hyallela*, and *Andesiops* in groundwater streams.

Environmental variables vs. glaciality (model 1)

Figure 3 A shows the proportion of community variation explained by the three environmental variables *Glaciality*, *Instream*, and *Resources* (details on the fractions of explained variances are given in Appendix 2). In total, these variables explained between 26.1 and 35.4% of the community variation depending on the taxon matrix considered, among which *Glaciality* always had the biggest contribution to community variation. The total portion of community variation explained by all environmental variables, as well as the unique contribution of *Glaciality,* were bigger for upstream sites (35.5 and 20.6%, respectively) than when considering all sites together (26.2 and 15.7%, respectively). *Instream* variable had a significant (but low) unique contribution (around 4%) for *All taxa*, *Flying taxa* and *Non-Flying taxa*, while the *Resources* variable had no significant effect on community variation.

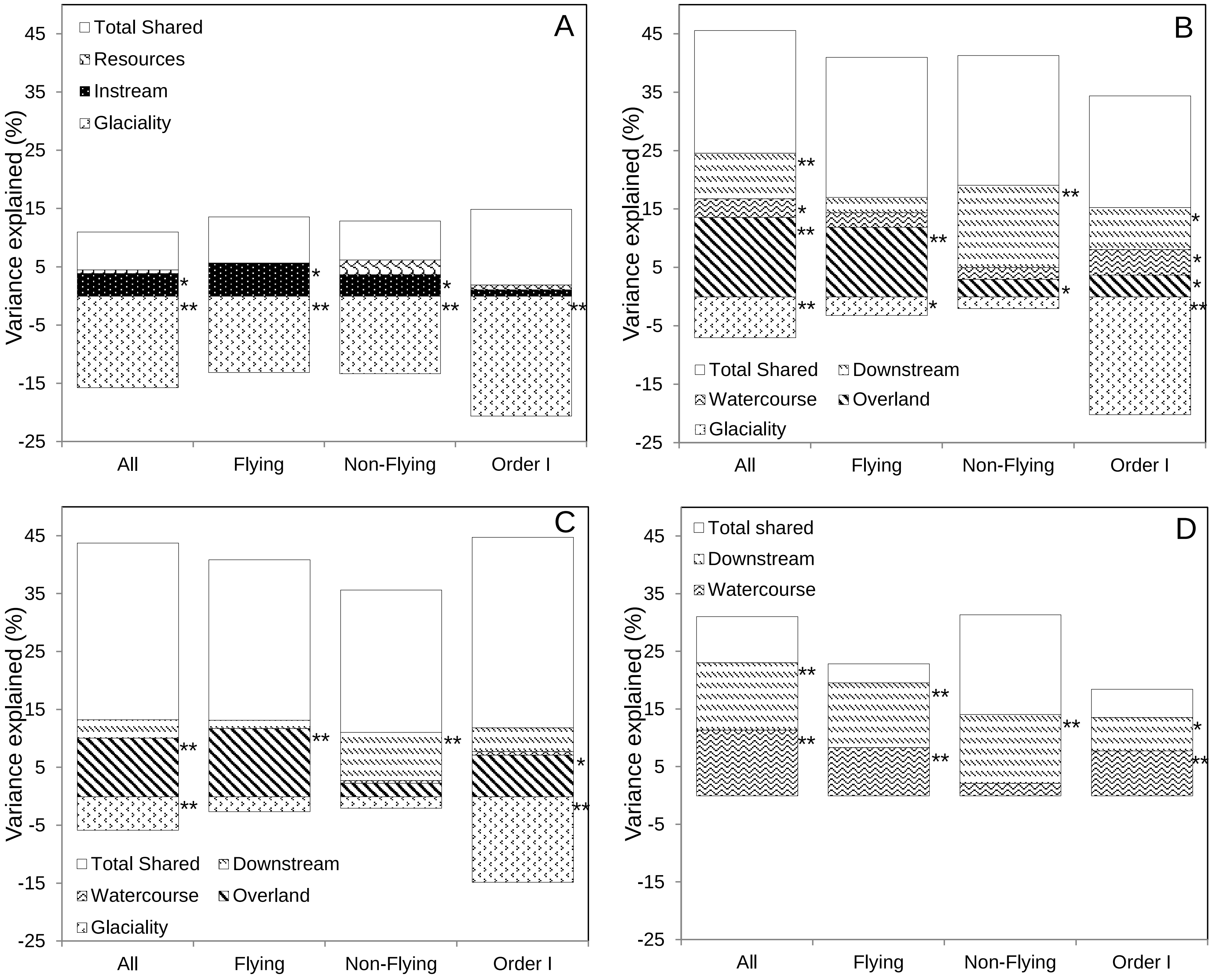

A
□ Total Shared
Resources
Instream
Glaciality
B
□ Total Shared
Downstream
Watercourse
Overland
Glaciality
C
□ Total Shared
Downstream
Watercourse
Overland
Glaciality
D
□ Total shared
Downstream
Watercourse
Variance explained (%)
45
35
25
15
5
-5
-15
-25
All
Flying
Non-Flying
Order I
*
**

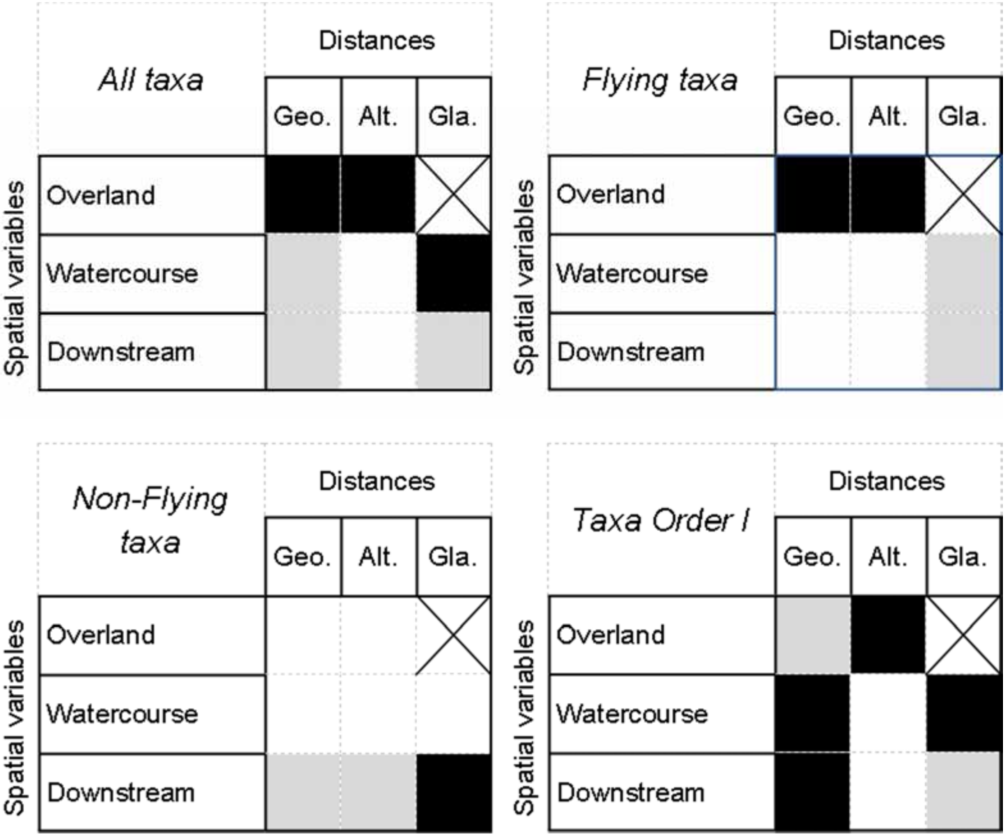
Figure 3: Results of variation partitioning analyses performed on (**A**) the two environmental variables *Instream* and *Resources* and the variable *Glaciality* (model 1), (**B**) the three spatial eigenfunction-based variables computed using overland, watercourse, downstream geographical distances and the variable *Glaciality* (model 2), (**C**) the three spatial eigenfunction-based variables computed using overland, watercourse, downstream altitudinal distances and the variable *Glaciality* (model 2), and (**D**) the two spatial eigenfunction-based variables based on watercourse and downstream glaciality distances (model 3). All analyses were performed for the four taxon matrices (*All taxa*, *Flying taxa*, *Non-flying taxa*, and *Taxa Order I*). Figure shows the amount of variation (%) in the structure community that is uniquely explained by each explanatory variable as well as the total shared variance (i.e. all the shared components between two, three and four explanatory variables). The level of significance is indicated next to the bars (** $P < 0.01$, * $P < 0.05$). Note that the percentage of variation explained by *Glaciality* was represented with negative value, in panel A-C, to better differentiate *Glaciality* from the others variables.

Spatial variables and glaciality (model 2 and 3)

Figure 3 B shows the proportion of community variation explained by *Glaciality* and the three spatial variables (overland, watercourse and downstream) computed with geographical distances. Spatial variables and *Glaciality* contributed almost half of community variation (residuals < 60%). However, the relative unique effect of spatial variables and *Glaciality* on community variation differed considerably among taxon matrices. Total pure contribution of spatial variables was larger than pure contribution of *Glaciality* for *All taxa* (27.2 against 7%), while it was the opposite for *Taxa Order I* (16.1 vs. 20.2%). For *All taxa,* overland distances best explained community variation (13.6%) while downstream distances did for *Taxa Order I* (7.2%). For *Flying taxa*, overland distances best explained community variation (11.9%; $P < 0.01$) while for *Non-Flying taxa*, downstream distances best explained community variation (14.1%). When computing the three spatial variables (overland, watercourse and downstream) using altitudinal distances (Fig. 3C), we found that overland distances best explained community variation of *All Taxa*, *Flying Taxa*, and *Taxa Order I* while downstream distances did so for *Non-Flying taxa*.

Figure 3 D shows the proportion of community variation explained by watercourse and downstream glaciality distances (model 3). Both distances explained between 18.5 and 31.5 % of the community variation depending on taxa matrix. Both watercourse and downstream distances significantly explained community variation of *All taxa*, F*lying taxa* and *Taxa Order I*, while only downstream distances did so for *Non-flying taxa.*

For each spatial variable (overland, watercourse, and downstream), the effects of geographical, altitudinal and glaciality distances on community variation were highly confounded (see Appendix 3). For example, the effect of geographical downstream distances on community variation of *Non-flying taxa* was highly confounded with the effects of both altitudinal and glaciality distances (see Appendix 3, Fig. 1C). Taking into account these confounding effects allowed us to determine which distance type had a unique significant effect on community variation (Fig. 4). Geographical and altitudinal overland distances as well as glaciality watercourse distances had significant unique contributions to community variation of *All taxa*. Geographical and altitudinal overland distances had a significant unique contribution to community variation of *Flying taxa*. Glaciality downstream distances had a significant unique contribution to community variation of *Non-flying taxa*. Geographical watercourse and downstream distances, as well as altitudinal overland and glaciality watercourse distances had a significant unique contribution to community variation of *Taxa Order I.*



All taxa	Distances		
Spatial variables	Geo.	Alt.	Gla.
Overland	■	■	☒
Watercourse	▨		■
Downstream	▨		▨

Flying taxa	Distances		
Spatial variables	Geo.	Alt.	Gla.
Overland	■	■	☒
Watercourse			▨
Downstream			▨

Non-Flying taxa	Distances		
Spatial variables	Geo.	Alt.	Gla.
Overland			☒
Watercourse			
Downstream	▨	▨	■

Taxa Order I	Distances		
Spatial variables	Geo.	Alt.	Gla.
Overland	▨	■	☒
Watercourse	■		■
Downstream	■		▨

Figure 4: Illustrative figure indicating, for each spatial variables (overland, watercourse, and downstream) which distance type had a significant effect on community variation of *All taxa*, *Flying taxa*, *Non-flying taxa*, and *Taxa Order I*. A black mark indicates that the corresponding distance had a unique significant effect on community variation, and that its effect was not confounded with others types of distance. A grey mark indicates that the corresponding distance had a unique significant effect on community variation, but that its effect was confounded at least one of the others type of distance.

Discussion

Mechanisms driving the metacommunity structure in a glacierized stream network

The main objective of this study was to identify the mechanisms driving the benthic invertebrate metacommunity structure in a glacierized stream network. First, we found that environmental variables had significant effects on community variation among sites, suggesting that environmental filtering at least partly dictate the metacommunity structure. Among all environmental variables, glaciality best predicted the spatial organization of the metacommunity. Moreover, although it was spatially structured and contained a directional component, glaciality contributed in a unique and significant way to the explanation of community variation. Therefore, glaciality was the primary environmental filter structuring the spatial organization of the aquatic invertebrate metacommunity. Second, our results show that the three spatial variables based on geographical distances contributed almost 30% of the community variation of the whole community (i.e. *All Taxa*). In line with other studies, we interpret the spatial effects in the studied metacommunity as an indicator of dispersal limitation (Jenkins et al. 2007, Shurin et al. 2009, Verleyen et al. 2009). Therefore, both dispersal processes and environmental filtering drove metacommunity structure in the equatorial glacierized stream network. However, clear differences were observed between hierarchical scales in the catchment (whole catchment vs. upstream sites). Indeed, glaciality better explained community variation than spatial variables for upstream sites whereas it was the contrary at the whole catchment scale. Our result is in line with Brown and Swan (2010) who suggested that the metacommunity of benthic invertebrates was structured according to a species sorting paradigm in headwater streams (i.e. by environmental filtering, due to its isolation from the regional species pool; Clarke et al. 2008), while main stem communities were structured according to a mass effects paradigm (i.e. environmental filtering and dispersal processes; Chase et al. 2005).

Geographical overland distances best explained community variation, especially for taxa with a flying stage. This indicates that most dispersion events occurred through overland aerial dispersal (e.g. adult flight), which has been already highlighted as an important process of macroinvertebrate community organization (Petersen et al. 1999, Bilton et al. 2001, Brown and Swan 2010). However, downstream distances also contributed in a unique and significant way to the community variation, especially for exclusively aquatic taxa. Note, however, that we could not identify whether geographical, altitudinal or glaciality distances limited the downstream dispersion. Nevertheless, this result indicates that dispersion also occurred through downstream drift, which was not surprising in our system as glacial flood occurred regularly (Cauvy-Fraunié et al. 2013) and generated a daily increase of the downstream water flux. This result is supported by Jacobsen et al. (2014b) that, in the same study area, demonstrated elevated invertebrate drift and downstream displacement of fauna during glacial floods.

In addition, we found that invertebrate dispersion was not only limited by the geographical distances but also by altitudinal distances among stream sites. In particular, overland dispersion of taxa with a flying stage was limited by difference in elevation among sites, potentially including hills between two sites. While altitude is often used as a proxy of other environmental variables (e.g., temperature, vegetation type; Altermatt et al. 2013) to explain community variation among sites, altitudinal distances are often neglected in freshwater metacommunity studies (e.g., Shurin et al. 2009, Brown et al. 2011). By contrast, our study pointed out that altitudinal distances could be an important component of invertebrate dispersal limitation in stream network (see also Barquín and Death 2006).

Likewise, glacial meltwater is considered in most glacial stream studies as a strong environmental filter (e.g., Brown et al. 2007, Finn et al. 2013) but, to our knowledge, it has never been recognized as a potential component of invertebrate dispersal limitation. Nevertheless, our results indicate that aquatic non-directional dispersion was limited by difference in glaciality among sites. Indeed, as not all invertebrates are adapted to the harsh conditions caused by glacier runoff (Milner et al. 2001, Brown et al. 2009b) displacement through glacially influenced stream reaches was probably restricted to adapted taxa. Therefore, glacial runoff restricts the colonization throughout the catchment of species not adapted to that type of environmental conditions.

While glaciality appeared to be a key driver of benthic metacommunity structure, part of the spatial structure in the metacommunity remained, however, unexplained. This might be due to unmeasured environmental variables such as oxygen availability (Jacobsen 2008, Verberk et al. 2011) and discharge or current velocity (Lods-Crozet et al. 2001, Jiang et al. 2013), all known to affect macroinvertebrates distribution. Although we found epilithic algae and benthic detritus had no significant effect on community variation, other food resources like macrophytes, bryophytes, and filamentous algae might contribute to the spatial variability in communities (Milner et al. 2001, Mykrä et al. 2011). The unexplained variance could also be due to unstudied species interaction (Brown et al. 2011) and fish predation (Effenberger et al. 2011).

Predicting metacommunity structure under different glacial runoff scenarios

Glacierized catchments exhibit a wide range of streams with contributions from different water sources, from meltwater- to groundwater-dominated streams, thereby creating different environmental conditions (Brown et al. 2009b). Therefore, any increase in glacial runoff during the first phases of glacier melting should increase the difference in glaciality among sites (i.e. increase the environmental heterogeneity within the catchment), probably enhancing community variation among sites (Hannah et al. 2007, Jacobsen and Dangles 2012). Indeed, our results showed that glacier runoff not only acts as an environmental filter, but also limits invertebrate dispersal, thereby restricting both species establishment and waterborne dispersion. Hence, an increase in glacial meltwater contribution to stream network should limit even more the colonization of generalist species non-adapted to the harsh glacial conditions. Consequently, we expect that any increase in glacial runoff would enhance β-diversity within glacierized stream network.

As opposed to this, we expect that any reduction in glacier runoff, as during the second phase of glacial shrinkage, should lead to environmental homogenization within the catchment and consequently induce changes in the metacommunity structure. Indeed, complete loss of glaciers in a catchment should promote establishment of species not adapted to glacial meltwater. In addition, although invertebrate dispersion would still be limited by geographical distances and differences in elevation in a catchment without glacial runoff, watercourse dispersal would not be limited anymore by difference in glaciality. This should facilitate dispersion of generalist species not adapted to glacial streams into new sites. Therefore under a scenario of reduction in glacial meltwater, loss of most environmental filtering and reduction of dispersal limitation should decrease β-diversity and consequently regional diversity (Brown et al. 2007, Jacobsen et al. 2012). Moreover, in addition to being threatened by changes in environmental conditions (Brown et al. 2009a, Milner et al. 2009) specialized species adapted to glacial meltwater are also threatened by the migration of more generalist species. Likewise, species in groundwater headwater streams, known to be specialist species (Clarke et al. 2008) might also be threatened by the upward migration of potentially more competitive species (Cochrane 2011) as they will no longer be isolated by "inhospitable" stream conditions (Richardson and Danehy 2007), in our case glacial streams. Finally, under climate change conditions, all taxa might be threatened by upward migration of more competitive species (Finn et al. 2010, Cochrane 2011, Dieker et al. 2013). Species survival would thereby strongly depend on species' ability to shift to suitable habitats (Pearson 2006). However, as macroinvertebrate dispersion seems to be strongly limited by elevation, some species might not be able to reach upper suitable habitats before the colonization of more competitive species. Therefore, under the ongoing climate change, reduction in glacier runoff might induce both extinction of specialized species and a homogenization of the aquatic fauna in glacierized catchments (i.e. decrease in β-diversity), resulting in an irreversible reduction in regional diversity (Brown et al. 2007, Jacobsen et al. 2012).

In this study, we proposed a new framework to understand the potential effect of climate change on aquatic biodiversity in a glacierized catchment. Most previous studies on the effect of glacial meltwater on macroinvertebrate communities investigated macroinvertebrate responses to glacial influence at the local community scale (Ilg and Castella 2006, Milner et al. 2006, Brown et al. 2007, Milner et al. 2009, Brown et al. 2010, Jacobsen and Dangles 2012, Jacobsen et al. 2012). To our knowledge, our study is the first to investigate the macroinvertebrate metacommunity structure and dynamics in a glacierized stream network. Although we are aware that long-term macroinvertebrate samplings are needed in order to be able to verify the effect of glacial meltwater alteration on aquatic metacommunity in glacierized catchment, this study demonstrated the necessity of working at the whole catchment scale and understanding many mechanisms driving the metacommunity structure in order to be able to predict the effect of glacier retreat on aquatic biodiversity.

Acknowledgments

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Appendices

Appendix 1

Details on methods: Computation of eigenfunction-based spatial variables

The computation of Moran's Eigenvector Map (MEM) requires a connectivity matrix (i.e. the list of links among sites), and a matrix of weights to be applied to these links. The connectivity matrix is a binary matrix defining which pairs of sites are connected (1) and which are not (0). The weighting matrix provides the intensity of the connexions; the commonly used weighting function is: weight = $1 - (d/d_{max})^3$, where d is the distance between connected sites and d_{max} the largest distance in the stream network. The final spatial weighting matrix results from the Hadamard (i.e. term- by term) product of these two matrices (Borcard et al. 2011). In our case, we constructed the connectivity matrix on the basis of the distance; i.e. we selected a distance threshold and connected all sites that are within that distance. We created 10 connectivity matrices with different thresholds: from the smallest distance connecting all sites (i.e. all sites are at least connected to one site) to the maximum distance found in the stream network (i.e. all sites are connected to the others 50 sites; Fig. 4 A-P). We constructed 10 spatial weighting matrices based on those 10 different connectivity matrices, but using the same weighting function. From each of the 10 spatial weighting matrices, we computed MEM eigenvectors and kept only the eigenvectors with positive eigenvalues (i.e. corresponding to positive spatial correlation; Dray et al. 2006, Borcard et al. 2011). We then tested the contribution of each eigenvectors matrix (10 matrices) to the community variation. For, this, we computed the corrected Akaike Information Criterion (AICc) for each eigenvectors matrix, and retained the spatial weighting matrix yielding the lowest AICc. For example, the MEM eigenvectors, based on overland geographical distance, yielding to the lowest AICc for *All Taxa* matrix was computed for a distance threshold of 3222 m (Appendix 2, Fig. 4 A). Finally, we computed the MEM eigenvectors based on the spatial weighting matrix selected and kept only the eigenvectors with positive eigenvalues. All analyses were performed in R using the package *spacemakeR*, and *vegan*.

The computation of Asymmetric Eigenvector Map (AEM) requires information about the direction of the physical process, plus the same information as MEM (i.e. connectivity and weight). First the stream network was divided into edges (i.e. segments between two sites or between one site and one node). Then we constructed a rectangular sites-by-edges matrix E, including both the information of connection among sites and flow direction; $E_{ij} = 1$ when the site i is influenced by the edges j; otherwise and $E_{ij}= 0$ (see Blanchet et al. 2008b, Blanchet et al. 2011 for sites-by-edges matrix examples). Then we assigned weight to the edge matrix based on the watercourse distance transformed by the same weighting function as the one used for the MEM eigenvectors. Those analyses were performed using the package *AEM* in R.

Note that, when computing the watercourse *connectivity matrices* and the *sites-by-edges* matrices, we intentionally did not connect sites 1, 2, and 3 to any other one because the corresponding stream flowed to the north side of the volcano whereas the others streams flowed to the south side (connection among the streams did not occur before more than 350 km). Moreover we did not connect sites 26, 27, 34, and 35 to the others sites due to the presence of a lake (Fig. 1).

Then, for each distance matrix (e.g. overland geographical distance), we performed a global test using all spatial eigenvectors with positive eigenvalues in a redundancy analysis. When global tests were significant, we proceeded with a forward selection procedure to reduce the number of spatial eigenvectors to make the model more parsimonious (see Blanchet et al. 2008a for details). Those preliminary analyses were performed in R using the package *packfor* and *vegan*.

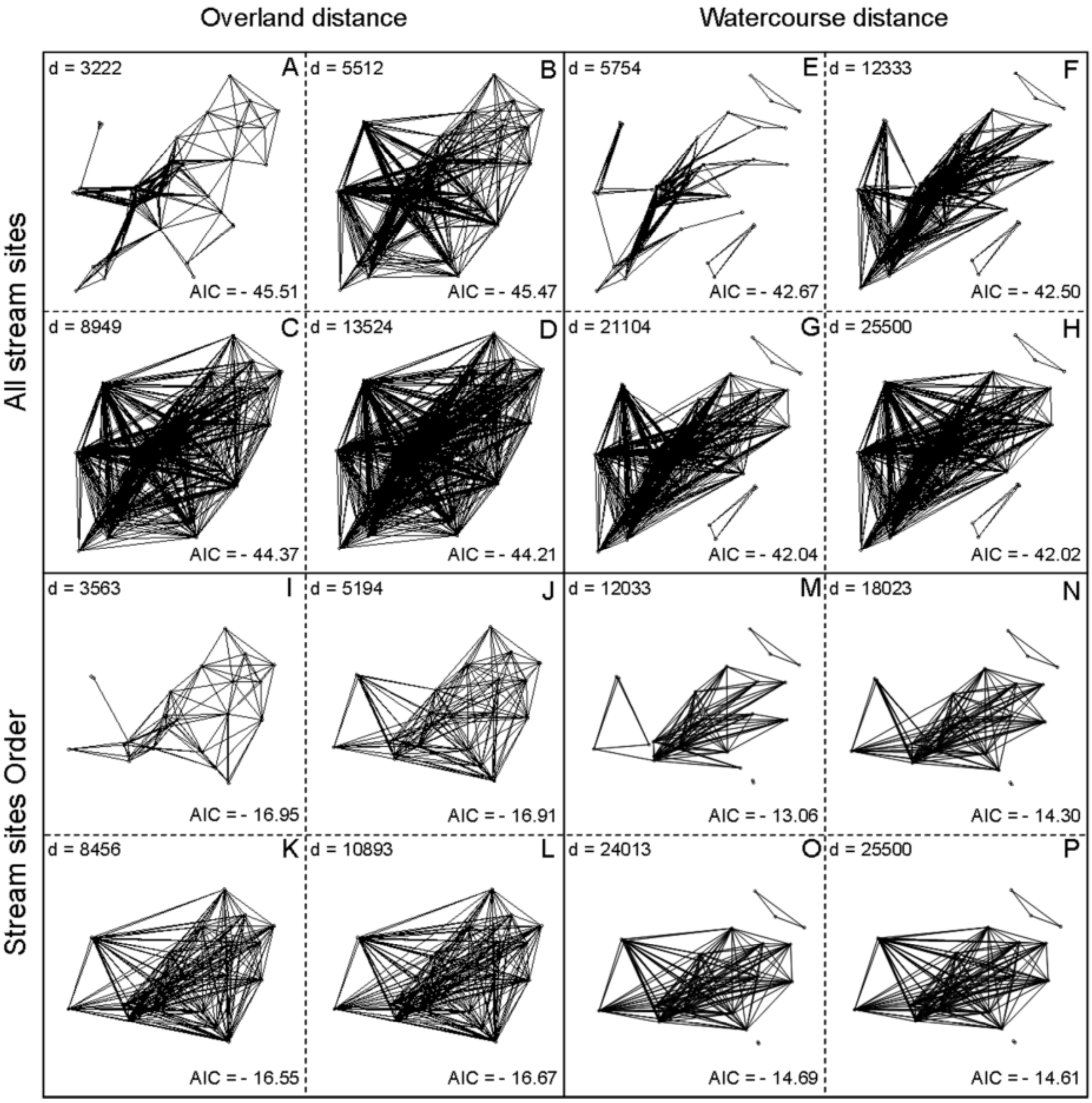
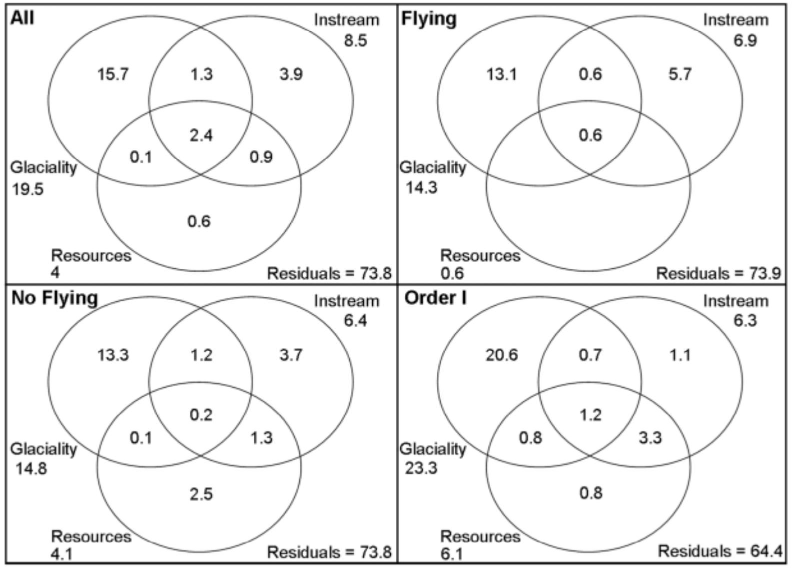


Figure: Examples of connectivity matrices created based on different distance thresholds: from the smallest distance connecting all sites (i.e. all sites are at least connected to one site; A, E, I, and M) to the maximum distance found in the stream network (i.e. all sites are connected to the others 50 sites). Connectivity matrices were represented for overland (A-D and I-L) and watercourse (E-H and M-P) geographical distance for all study sites (A-H) and for upstream sites (I-P). Thresholds distance (d) and corresponding AIC_c were represented for each connectivity matrix. Note that in the connectivity matrices based on watercourse distance, six study sites were not connected to the other ones (see methods for justification; E-H and M-P).

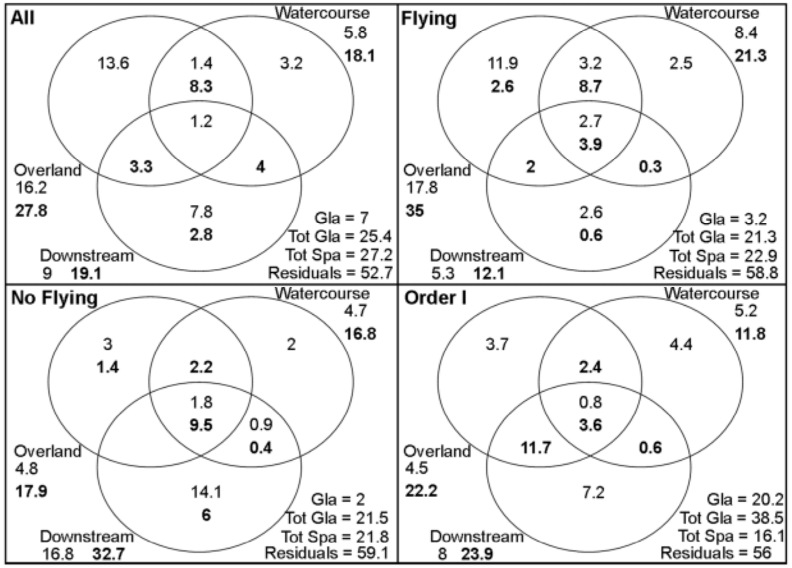
Appendix 2

Figure: Details of each component (unique and shared) of the variation partitioning analyses performed for *All taxa*, *Flying taxa*, *Non-flying taxa*, and *Taxa Order I* on (1) the three environmental variables (*Glaciality*, *Instream* and *Resources*); (2) the three spatial variables computed using overland, watercourse, downstream geographical distances and *Glaciality*; (3) the three spatial variables computed using overland, watercourse, downstream altitudinal distances and *Glaciality*; and (4) the two spatial variables computed using watercourse, downstream glaciality distances. Upper numbers inside the circles represented the amount of variation that is uniquely explained by each explanatory variable and the shared part of variance explained between all pairwise variables. For geographical and altitudinal distances, lower bold numbers inside the circles represented the shared part of variance explained between each spatial variable and the variable *Glaciality*. Number outside the circle corresponded to the total amount of community variation explained by each explanatory variable excluding the portion shared with *Glaciality*. For geographical and altitudinal distances, lower bold number outside the circles corresponded to the total amount of community variation explained by each explanatory variable including the portion shared with *Glaciality*. Residuals correspond to the percentage of the community variance unexplained by the model. For geographical and altitudinal distances panels, Gla corresponds to the unique portion explained by *Glaciality*, Tot Gla corresponds to the total fraction explained by *Glaciality* (including the spatially structured part). Tot Spa corresponds to the total fraction explained by the three spatial variables excluding the parts shared with *Glaciality*. The empty fractions correspond to explanatory variables that explain less of the community variation than would be expected by chance.

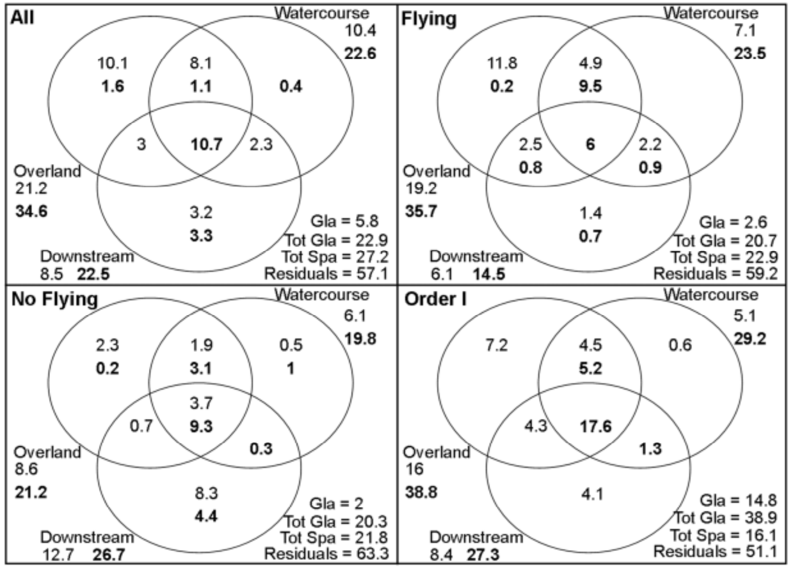
ENVIRONMENTAL VARIABLES



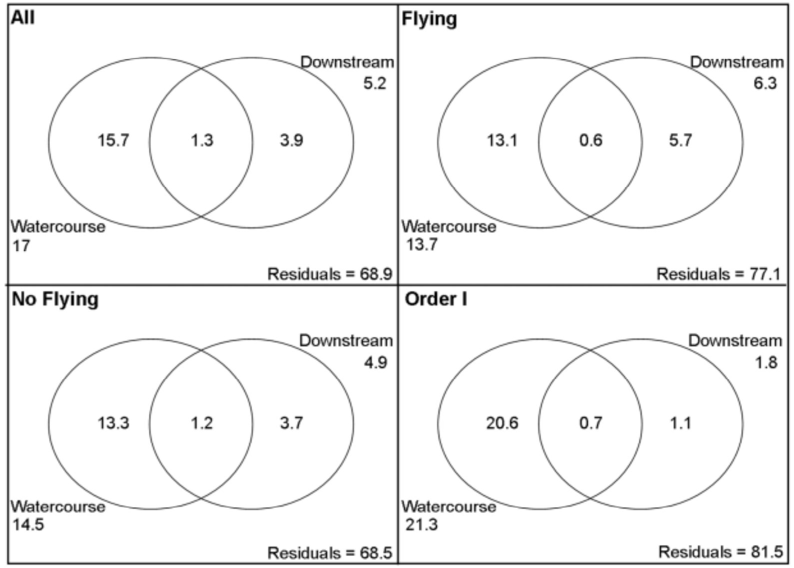
GEOGRAPHICAL DISTANCES



ALTITUDINAL DISTANCES

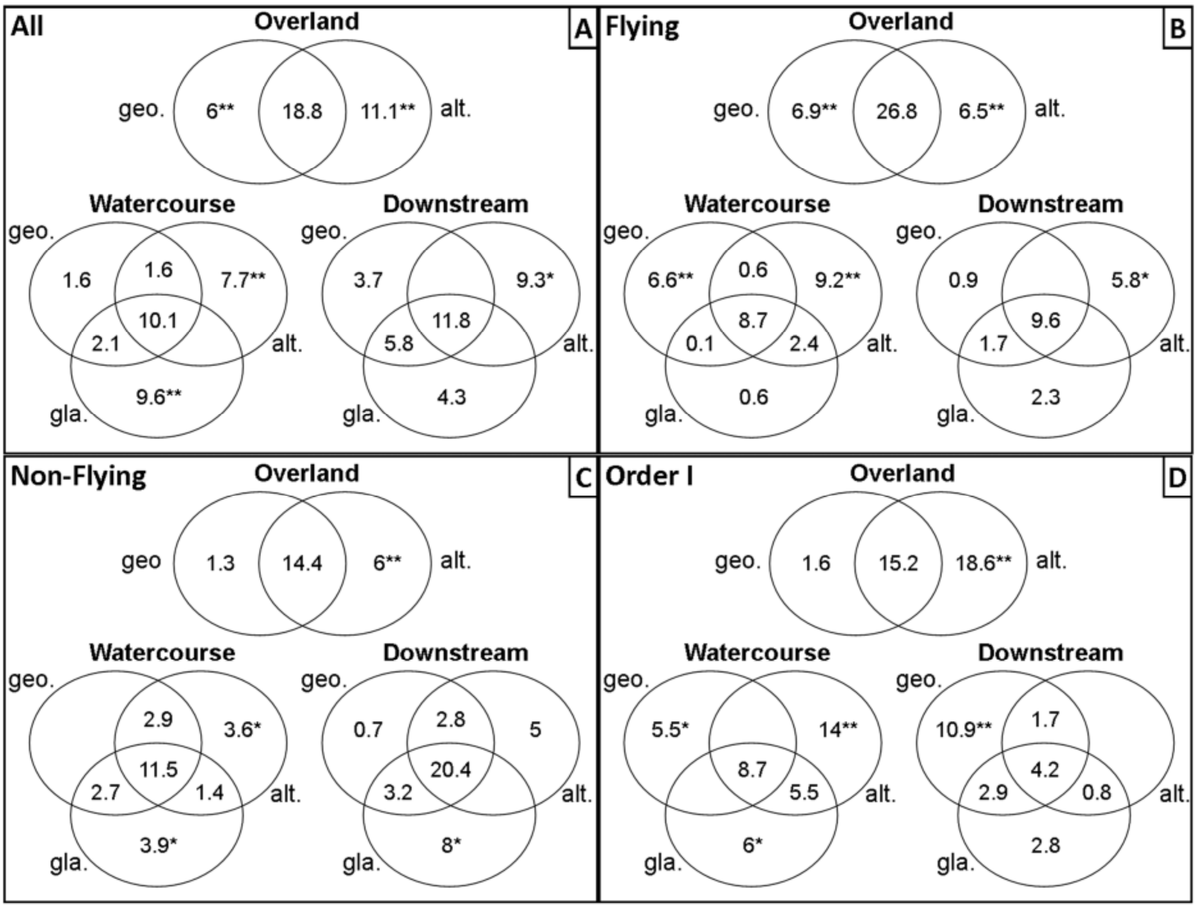


GLACIALITY DISTANCES



Appendix 3

Figure: Results of variation partitioning analyses performed on the spatial eigenfunction-based variables computed using overland geographical (geo.) and altitudinal (alt.) distance at the top. Results of variation partitioning analyses performed on the spatial eigenfunction-based variables computed using watercourse geographical (geo.), altitudinal (alt.), and glaciality (gla.) distance on the bottom left. Results of variation partitioning analyses performed on the spatial eigenfunction-based variables computed using downstream geographical (geo.), altitudinal (alt.), and glaciality (gla.) distance on the bottom right. Analyses were performed for the four taxon matrices *All taxa* (**A**), *Flying taxa* (**B**), *Non-flying taxa* (**C**), and *Taxa Order I* (**D**). The figure shows the amount of variation (%) in the structure community that is uniquely explained by each spatial variable as well as the shared portion. The level of significance was indicated next to the numbers (** P < 0.01, * P < 0.05).The empty fractions correspond to explanatory variables that explain less of the community variation than would be expected by chance.



DISCUSSION

In the context of global warming, it is of critical importance to recognize the effect of glacial meltwater contribution to alpine stream flow on aquatic communities to predict the effect of glacier retreat on freshwater biodiversity in glacierized catchments. To our knowledge, this thesis is the first dedicated to glacier-fed streams in the tropics. This work is part of a series of hydro-ecological studies that have been performed in the Antisana since 2008. Our research group led by Dean Jacobsen (*University of Copenhagen*) and Olivier Dangles (*Institute for research and Development*) is composed by Ecuadorian, Danish, Canadian, and French students (Fig. 1). In this discussion, we include some results of other studies performed in the Antisana by different members of our group. We first synthesize our main findings, underline the difference with studies in temperate zones, and expose our assumptions about macroinvertebrates community response to glacier retreat. Then, we discuss some conceptual and methodological issues that would merit further investigations. Finally, we suggest future perspectives for research to improve our general knowledge and understanding on glacier-fed freshwater ecosystems.

1. Thesis synthesis

The study of glacier-fed freshwater ecosystems could be divided into two parts: the study of undiluted glacier-fed streams, i.e. before any confluence with non-glacial stream, and the study of glacierized catchments displaying a range of streams with contributions from different water sources, from meltwater to groundwater-dominated streams.

Figure 1: Illustration of some studies performed by our research group at the Antisana. **A-C** drift study (Cueva 2013). **A.** Andres Morabowen measuring conductivity by night. **B.** Dean Jacobsen fishing. **C.** Olivier Dangles retrieving the drift net. **D.** Gabriel Mosquera, Rodrigo Espinosa, Patricio Andino, and Vincent Fugère selecting invertebrates for the species interaction study (Fugère et al. 2012). **E.** Philip Brask Madsen performing its experiment of invertebrate movement activity (unpublished data). **F-G.** Experimental flow manipulation (unpublished data) with Sophie Cauvy-Fraunié and Andres Morabowen removing a dam (**G**).

1.1. Glacier-fed stream ecosystems

Studies by our group revealed that equatorial glacier-fed streams exhibit a similar macroinvertebrates spatial pattern as in temperate zones, i.e. low density and taxa richness close the glacier margin that increased with increasing distance from the glacier (Jacobsen et al. 2010, Jacobsen et al. 2014b). However, we found strong differences in the temporal pattern of community composition of equatorial glacier-fed streams as a result of their distinct flow regimes. While in both temperate and equatorial zones, glacier-fed streams exhibit temporal variability in flow at the inter-annual and diurnal time scale (during the ablation season), equatorial glacier-fed streams display no seasonal flow variation as temperate streams do (see Fig. 5 in Introduction, Chap.2 Part1 - Cauvy-Fraunié et al. 2013). Consequently, contrary to most studies in temperate zones (e.g., Robinson et al. 2001, Schütz et al. 2001, Burgherr et al. 2002), we found no seasonal pattern in macroinvertebrates assemblage (see Chap.2 Part3 and Jacobsen et al. 2014a). However, we found a significant temporal variability in community composition linked to the temporal variability in intensity of the diurnal flow variation (see Chap.2 Part3 and Jacobsen et al. 2014a). Our results also indicate that the diurnal increase in hydraulic stress during daily glacial floods had a small effect on macroinvertebrate organization at a reach scale (Chap.1 - Cauvy-Fraunié et al. 2014a). This result was supported by a complementary study performed at the same stream sites (Cueva 2013), where the author found no change in drift density and taxa richness between low and high flow conditions. Our studies suggest that glacial floods induce a longitudinal displacement of taxa along the glacial influence gradient from glacier snout do downstream part (see Chap.2 Part 3 and Jacobsen et al. 2014b) rather than a spatial reorganization of communities through taxa seeking flow refugia (Chap.1 - Cauvy-Fraunié et al. 2014a, Cueva 2013, Jacobsen et al. 2014b). In addition, our studies indicate that taxon inhabiting equatorial glacier-fed streams are probably highly resistant to the short-term flow variation (Chap.1 - Cauvy-Fraunié et al. 2014a, Chap.2 Part2 -

Cauvy-Fraunié et al. 2014, Chap.2 Part3) and more importantly, that the extremely high frequency of daily glacial floods (Chap.2 Part1 - Cauvy-Fraunié et al. 2013), limits the colonization of taxa non adapted to diurnal flow variation in glacier-fed streams, thereby preventing competition exclusion from generalist taxa (Chap.2 Part3).

1.2. Glacierized catchment ecosystems

In accordance to previous studies (e.g., Brown et al. 2007, Finn et al. 2013), we found that the spatial variability in glacial influence of streams located in glacierized catchments generate spatial β-diversity (Chap.2 Part2 - Cauvy-Fraunié et al. 2014b, Chap.3). However, in contrast to the general assumption that local richness increases with decreasing glacial meltwater contribution to stream flow (e.g., Brown et al. 2010, Khamis et al. 2014) we found a hump shaped relationship between local taxon richness and glacial influence (see also Jacobsen et al. 2012), with some taxa occurring only at intermediate level of glacial influence. This result implies that although glacial meltwater induce low α-diversity at the glacier-fed stream scale, its contribution to alpine streams at the catchment scale may enhance local diversity.

In addition, our study on benthic metacommunity structure (Chap.3) shows that glacial influence was the main environmental filter dictating macroinvertebrates spatial distribution. However, we found that the metacommunity structure was not only dictated by local processes, but also by regional processes such as dispersion. Indeed we found that part of community variation among sites was explained by dispersal limitation due to geographical distance, difference in elevation and difference in glacial influence among sites. Thus, glacier runoff not only acted as an environmental filter but also limited invertebrate aquatic dispersion, thereby restraining both establishment and dispersion of taxa not adapted to the harsh conditions of glacier-fed streams. Consequently, glacier runoff prevented non-adapted taxa to colonize throughout the stream network (Chap.3).

To summarize, glacial meltwater 1) shelters specialized taxa close to the glacier snout (Brown et al. 2007), 2) isolates taxa (often specialized; Clarke et al. 2008) in headwater streams (Chap.3, Finn et al. 2013), 3) generates local (α) diversity when mixing with groundwater streams (Chap.2 Part2, and 4) engenders high spatial β-diversity within glacierized catchment by generating high environmental heterogeneity and limiting aquatic dispersion (Chap.3); thereby enhances regional (γ) diversity (Jacobsen et al. 2012).

2. Aquatic communities response to climate change

Based on our results, we present some assumptions about future effects of glacier retreat on aquatic biodiversity in glacierized catchments. Here, we only consider the variation in glacier runoff (see Fig. 5 in Introduction) and not others factors associated to climate change such as increase in air and water temperatures or change in precipitation regime. Under the ongoing glacial shrinkage, we first expect an increase in glacial meltwater runoff, followed by a decrease until the complete disappearance of the glacier (Baraer et al. 2012).

2.1. Scenario of increase in glacier runoff

Under a scenario of increase in glacier runoff, we first assume an increase in both environmental harshness and diurnal flow variation intensity in glacier-fed streams, thereby increasing glacial influence gradient within the glacierized catchment. Consequently, within glacier-fed streams (before any confluence), we expect a decrease in local taxon richness as well as a downward shift of macroinvertebrate communities (Fig. 2; Chap.2 Part2, Jacobsen et al. 2014b). However, at a given stream site we expect an increase in temporal β-diversity (Chap.2 Part2) as flow variability is expected to increase (see Baraer et al. 2012). At the catchment scale, we anticipate an increase in spatial β-diversity linked to an increase in environmental heterogeneity (Chap.3) as well as a downstream shift of the position of the maximum local taxon richness (Chap.2. Part2). In addition, we envisage a limitation in water-borne invertebrate dispersal in glacier-fed streams thereby increasing the isolation of taxa in headwater streams (both glacial and groundwater streams, Chap.3). This could eventually lead to genetic drift (Finn et al. 2013, Jacobsen et al. 2014b).

2.2. Scenario of decrease in glacier runoff

Under a scenario of extreme decrease in glacier runoff, we first assume a decrease in both environmental harshness and diurnal flow variation intensity of glacier-fed streams, thereby decreasing glacial influence gradient and consequently also the spatio-temporal environmental heterogeneity within the catchment. Under such conditions, we expect an increase in α-diversity in glacier-fed streams (Brown *et al.*, 2007). However, as we evidenced a hump-shaped relationship between glacial influence and α-diversity (Chap.2 Part2 - Cauvy-Fraunié *et al.*, 2014b, see also Jacobsen *et al.*, 2012), we assume that α-diversity would peak at intermediate level of glacier runoff alteration and decrease until the complete disappearance of the glacier due to competition exclusion at low level of glacial influence. In addition, we expect a decrease in environmental filtering and aquatic dispersal limitation (Chap.3), thereby allowing generalist taxa to colonize throughout the catchment. As a result, we expect some extinction of specialized species adapted to harsh environmental conditions of glacial meltwater due to both change in their habitats and the migration of more generalist species (Fig. 2; Chap.1 - Cauvy-Fraunié et al. 2014a, Chap.2 Part3, Chap.3, Brown et al. 2007). Likewise, we expect some extinction of specialized species in groundwater headwater streams threatened by the upward migration of potentially more competitive species as they will no longer be isolated by “inhospitable” stream conditions, i.e. glacial meltwater. In addition, we envisage a decrease in maximum local richness (Jacobsen et al. 2012), in spatial β-diversity among stream sites (Finn et al. 2013), and in temporal β-diversity caused by a reduction in spatio-temporal environmental heterogeneity. Therefore, we expect an overall taxonomic homogenization of the aquatic fauna, yielding to an irreversible decrease in regional diversity (Chap.3, Jacobsen et al. 2012).

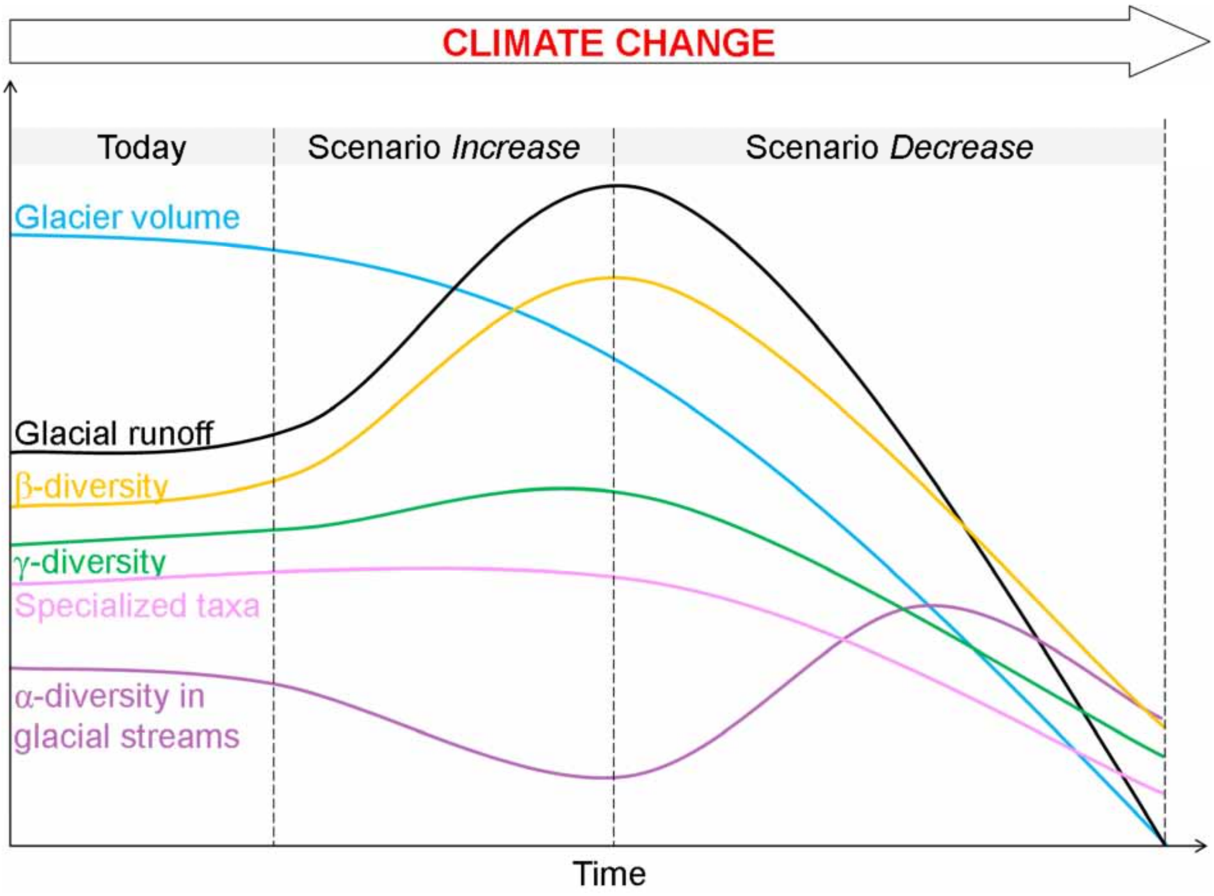


Figure 2: Conceptual diagram illustrating the expected temporal changes in α-diversity in glacier-fed stream, in spatial β-diversity, γ-diversity, and number of specialized taxa (in both glacial streams and headwater groundwater streams) within the glacierized catchment according to glacial runoff fluctuation during glacial shrinkage.

3. Contribution of this work

Here we highlight some findings of our work that may have implications beyond the glacier-fed stream ecology literature.

3.1. Aquatic dispersal limitation

In stream network community analyses, the main aquatic dispersal barriers considered are usually physical barriers that alter stream connectivity, such as water falls, partial drought of temporary streams during dry season, beaver dams, hydropower dams, and roads (e.g., Morita et al. 2009, Nislow et al. 2011, Bogan et al. 2013, Lokteff et al. 2013). However, our study evidenced that aquatic dispersion could also be limited by instream environmental conditions (Chap. 3). To our knowledge, such aquatic dispersal limitation has been poorly studied (but see Layer et al. 2011) and would merit further consideration, especially in watershed exhibiting streams with very distinct environmental conditions, such as watershed in geothermal area exhibiting cold and hot streams, or watershed in mining area exhibiting polluted and unpolluted stream segments.

3.2. Debate on the intermediate disturbance hypothesis

Currently, there is a debate around the validity of the Intermediate Disturbance Hypothesis (IDH, Fox 2012, Sheil and Burslem 2013). The IDH, introduced by Connell (1978) states that a peak in diversity should occur at intermediate intensities and frequencies of disturbance. The IDH postulates that disturbance prevents competitively dominant species from excluding other species from the community, and that there is a trade-off between species' ability to compete and their ability to tolerate disturbance. According to Fox (2012), the IDH has been refuted on both empirical and theoretical grounds. For example, Mackey and Currie (2001) showed that among compilation of published diversity-disturbance relationships, hump shaped relationships were not a majority. In our specific case, we found a hump shaped relationship between local taxa richness and glacial influence intensity. However, as we did not study precisely the mechanisms driving local communities, our study neither allowed us to approve nor to refute the IDH. Nevertheless, our results suggest that diversity-disturbance relationships depend on the disturbance gradient considered. Indeed, within glacier-fed streams, we found a negative relationship (Jacobsen et al. 2014a, see also Jacobsen et al. 2010), while using a larger glacial influence gradient at the catchment scale, we found a hump shaped relationship (Chap.2 Part2 - Cauvy-Fraunié et al. 2014). In addition, as revealed by Miller et al. (2011), we found that diversity-disturbance relationships also depend on the aspect of the disturbance considered (e.g., intensity, frequency Chap.2 Part2 - Cauvy-Fraunié et al. 2014).

3.3. Temporal β-diversity and wavelet analyses

Our study also pointed out the importance of studying the temporal β-diversity in hydroecology (especially in systems with high temporal variability) as well as the importance of considering various temporal scales in order to be able to identify the mechanisms involved in community structure (see Chap.2 Part 2 for details). Although poorly used by stream ecologists, wavelet analyses seem to be a promising tool to describe the temporal variability of stream flow regime especially for considering variability at multiple temporal scales (see also Stewart-Koster et al. 2014). Therefore, wavelets analyses could be especially relevant in studies about streams regulation effect on below dam biodiversity, and impact of climate change and water abstraction on desert streams communities, two topical issues (Bogan and Lytle 2011, Robinson et al. 2012). In addition, wavelets analyses could also be applied to others abiotic parameters (e.g., temperature, chemical components), which compose the cocktail of multiple stressors that generally accompanies flow variation. A further development of the wavelet analysis tool would thus allow studying in greater depth the impact of global warming and water pollution on aquatic ecosystems (e.g., industrial and urban wastewater, agricultural chemicals); i.e. the main threats to freshwater biodiversity (Moss 2008, Geist et al. 2011). Finally, wavelet analyses could also be efficient in others hydro-systems such as for the study of the effect of temporal variability in wave regime on intertidal organisms (see Denny et al. 2003).

4. Future perspectives for research in glacier-fed stream ecology

In this part, we propose further studies (both empirical and experimental) that could be conducted to improve our understanding on glacier-fed freshwater ecosystems and to predict the effect of climate change on aquatic communities. The first step would be to enhance our knowledge about the mechanisms driving the aquatic community structure. Then, we suggest performing stream manipulation to simulate changes in environmental conditions. Next, we highly recommend increasing interdisciplinary studies. A better knowledge on ecosystem function and endemism would also be essential for supporting biodiversity conservation. Finally, we recommend increasing monitoring at bigger temporal and spatial scales.

4.1. Mechanisms driving the metacommunity structure

4.1.1. Dispersal filtering and primary succession

In most previous studies, community patterns along glacier-fed streams were related to the variability in instream environmental conditions (e.g., Ilg and Castella 2006, Füreder 2007, Brown et al. 2010). Another approach would be to consider that the community pattern followed different stage of succession, and is therefore related to the stream age (Milner et al. 2008, Eisendle-Flöckner et al. 2013). Indeed, glacial recession creates deglaciated landscape and prolongs the upstream part of glacier-fed streams, nutrient-poor and lacking of biotic community (but see Anesio and Laybourn-Parry 2012). Thus, after deglaciation, we could expect a process of primary succession as it has been described in terrestrial ecology (Chapin et al. 1994), i.e. colonization of pioneer species at the early stage of succession, followed by later colonizers. In this context, species dispersal abilities could represent an important driver of the longitudinal distribution of aquatic organisms (Milner et al. 2008).

In addition, in our study about the metacommunity structure and dynamics (Chap.3), we also found that dispersal processes were important in structuring macroinvertebrates metacommunity. However, a better knowledge on dispersal abilities and strength of benthic species (e.g., female dispersal, adult flight, drifting propensity, swimming strength, crawling strength; Poff et al. 2006) would be needed to better understand the mechanisms driving metacommunity structure in glacierized catchments (Cottenie 2005, Heino et al. 2011). For example poorly-dispersing organisms may show stronger spatial structuring and weaker environmental control of community structure than stronger dispersers (Thompson and Townsend 2006, Meutter et al. 2007, Astorga et al. 2012). Moreover, adult flight of some taxa tends to be concentrated along riverine corridors (Petersen et al. 1999, Petersen et al. 2004, Macneale et al. 2005) implying that watercourse variables might reflect aerial dispersal for some taxa. Thus, to better identify dispersal processes, we should executed complementary studies such as those performed by Finn and Poff (2008), i.e. collecting flying insects along a perpendicular transect from alpine streams, or using genetic markers or stable isotopes (Briers et al. 2004, Finn et al. 2006).

4.1.2. Biotic filtering and species interactions

Although we mentioned competition processes in this thesis, we did not specifically examined species interactions even though it might be an essential process structuring local communities (Hart 1992, Allan and Castillo 1995, Leibold et al. 2004). In particular, species interaction, such as inhibition and facilitation, are potentially a crucial component of primary succession (Connell and Slatyer 1977, Grime 1977). Milner et al. (2008) evidenced that facilitation influenced aquatic successional patterns in a glacier-fed stream although it was not a major mechanism of community assembly. In addition, the stress gradient hypothesis (SGH), a major concept in plant community ecology (Callaway 2007, Lortie 2010), states that environmental stress modulates species interactions, causing a shift from negative interactions to net positive interactions with increasing stress (Bertness and Callaway 1994). For example, Anthelme et al. (2012) evidenced an increase in positive interaction among plants with increasing altitude (used as a proxy of abiotic stress) at the Antisana volcano (see also Anthelme et al. 2014). Fugère et al. (2012) tested this hypothesis with aquatic detritivorous invertebrates along a gradient of resource quality stress. Although the basic pattern proposed by the SGH was globally not approved to animals systems, species interactions switched from negative to neutral with decreasing resource quality. Using a similar experimental design as Fugère et al. (2012), i.e. a litter decomposition experiment with aquatic detritivorous invertebrates using variable litter quality, it would be possible to examine species interaction along a stress gradient of glacial influence. Additionally, gut content analysis would allow identifying predation among invertebrates and explaining eventual recurrent co-occurrence of certain species (Clitherow et al. 2013).

4.1.3. Environmental filtering

Little is known about species traits of macroinvertebrates in equatorial glacier-fed streams although it would provide valuable help for understanding local community composition. Similar laboratory experiments as those performed by Lancaster et al. (2006), i.e. manipulations of discharge in a flume would allow determining flow intensity thresholds above which macroinvertebrates are removed. In addition, it would permit to identify eventual macroinvertebrates displacements among habitats within stream reach during diurnal flow events.

After identifying the range in abiotic parameters (e.g., temperature, conductivity, turbidity) of species occurrence, it would be essential to identify for each abiotic parameter the optimum values of each species (i.e. where performance is maximized, Angilletta 2009) as well as the maximum of tolerance. This information would be necessary for understanding the actual spatial species distribution and predicting the future species distribution under global warming. For example, in the case of increase in water temperature, a given species might either migrate upstream to reach stream sites with similar water temperature as its previous site or remain at the same site. However, oxygen partial pressure decreases with altitude, affecting thus oxygen supply (Jacobsen 2008, Verberk et al. 2011). Therefore, more information on species physiology would allow determining 1) whether a given species would support an increase in water temperature and whether this increase would affect organisms performance, thereby decreasing its capacity to outcompete with others species (Warnock and Rasmussen 2014), including new species migrating upwards (Cochrane 2011), and 2) whether the species would support the abiotic conditions at upper sites. Studies using transplant experiments of invertebrate taxa and *in situ* experiments of movement activity are currently performed by our group and should allow improving prediction of future taxa spatial distribution at the Antisana watershed.

4.2. The Antisana: a natural laboratory

4.2.1. Towards an ecology of places

Several ecological and evolutionary concepts have been developed based on empirical studies of particulars organisms at specific places. One of the most famous examples is the Galápagos Islands that inspired Darwin's theory of evolution (Billick and Price 2010). Thus, ecologists and evolutionary biologists have long recognized the importance of particular kinds of place for analyzing problems, advancing theories or characterizing ecosystems by studying the interactions between organisms and the environment. Consequently, several field stations have been established for long-term studies; e.g., 30 years study of Darwin's ground finches at the Daphne Major island (Ecuador), 36 years study of mammalian carnivory in the Aleutian islands (Alaska), 29 years study of the dynamics of tropical forest on Barro Colorado island (Panama; Billick and Price 2010).

Likewise, certain natural systems exhibit such special conformation that they could be used as natural laboratories to identify relationship between organisms and environmental conditions along large gradients. For example, various studies used geothermal systems as natural laboratories to assess variability in community structure along a natural gradient of temperature (e.g., Friberg et al. 2009, Woodward et al. 2010, Demars et al. 2011). Similarly, the Antisana watershed could be considered as a natural laboratory as it displayed a perfect stream network for studying the effect of glacial influence on aquatic communities. First, the watershed contains one glacier-fed stream that does not meet any streams before 7.2 km from its glacier snout, corresponding to a difference of elevation of more than 600 m a.s.l. This stream allows studying longitudinal distribution of community composition along a progressive but low decrease in glacial influence (Jacobsen et al. 2010). In addition, three glacier-fed streams are abruptly diluted by consecutive groundwater and/or rainfall tributaries and allow thus studying the spatial variability in community composition along an abrupt and strong decrease in glacial influence (see Fig. 18. in Introduction; Chap.2 Part2 - Cauvy-Fraunié et al. 2014). It is thus important that Ecuadorian authorities (e.g., Ministerio del Medio Ambiente, SENESCYT: *Secretaría de Educación Superior, Cienca, Tecnología e Innovación*) could make the Antisana reserve a scientific station such as the Yasuní research station (http://www.yasuni.ec) to improve the overall understanding of glacier-fed freshwater ecosystems, especially in a context of climate change.

4.2.2. Experimental manipulation in natural ecosystems

One way to assess the effect of changes in instream environmental conditions on freshwater communities is to performed experimental manipulation in natural ecosystems. Experimental manipulations were performed in lakes to examine primary producers (e.g., zooplankton, phytoplankton, planktonic bacteria) response to nutrient enrichment according to the food web structure (Carpenter et al. 2001, Carpenter et al. 2011), and in streams to examine the effect of fish chemical cues on the size at emergence of mayflies (Peckarsky et al. 2002). Recently, O'Gorman et al. (2014) used manipulative warming experiments in a geothermal area as a sentinel system of climate change, and thus examined aquatic community response to different level of warming. Similarly, to study the effect of glacial meltwater alteration on aquatic species assemblage, we performed a BACI (Before-After-Control-Impact) experiment by manipulating the discharge of a glacier-fed stream (unpublished data). Although experimental manipulations are often confronted to logistical and technical challenges due to the harsh conditions in the Antisana, such kind of approaches need to be further developed to gain more knowledge on physical and ecological mechanisms that drive observed patterns and trends.

4.3. Interdisciplinary research approaches

This thesis shows the importance of interdisciplinary studies to link biological and physical processes and understand systems structure and functioning. Our study showed that it is definitively useful to merge disciplines such as ecology and glaciology for understanding the functioning of river-fed systems. This approach would also be powerful to develop models to predict the effect of climate change on glacier-fed freshwater ecosystems. We thus propose to couple climatic, glaciological, hydrological, environmental, and species distribution models to forecast freshwater ecosystem structure under variable scenarios of climate change. In the following, we present various types of models that could be combined to achieve this (Fig. 3).

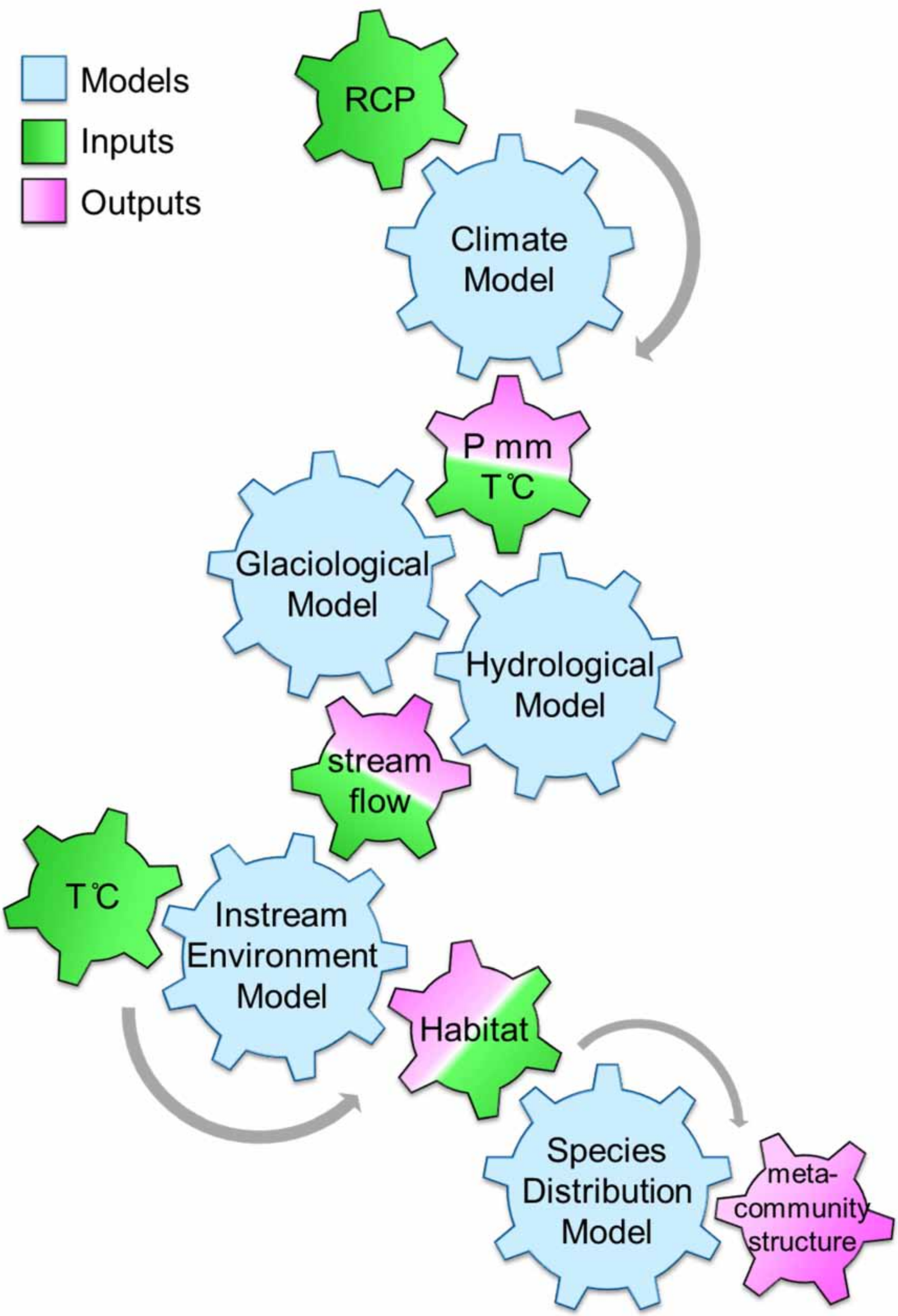


Figure 3: Schematic illustration of a combination of climatic, glaciological, hydrological, environmental, and species distribution models (in blue) to forecast future aquatic metacommunity structure under various scenarios of greenhouse gases and aerosols emission (RCPs). Inputs of each model are represented in green, outputs in pink. Several times, inputs of one model correspond to the output of the previous models. T ˚ C: air temperature. P mm: Precipitation (mm).

4.3.1. Climate models

Climate models simulate the response of the climate system (complex system consisting of atmosphere, hydrosphere, cryosphere, lithosphere and biosphere, and the interactions between them) to a scenario of future emission or concentration of greenhouse gases, aerosols (Representative Concentration Pathways, RCPs, IPCC, 2013). To simulate climate change at high resolution, previous studies (e.g., Huss et al. 2008, Buytaert et al. 2009, Radić et al. 2014) used either Regional Climate Models (RCMs), or the projections of Global Circulation Models (GCMs) downscaled using dynamical or statistical approaches (Fowler et al. 2007, Salathé et al. 2007). Those models forecast the climate, including air temperature and precipitation pattern, according to the RCP considered.

4.3.2. Glaciological models

Most rigorous glaciological models that assess changes in glacier geometry are combined models of surface mass balance reflecting the climatic forcing and ice flow dynamics (Huss et al. 2010). The climatic forcing acting on the glacier can be described using mass balance models of different complexity that relate meteorological variables to accumulation and ablation rates at the glacier surface (e.g. Pellicciotti et al. 2005). Ice flow dynamics can be assessed using a wide array of modelling approaches, from simple flowline models to complex 3-D ice flow models. However, these models require considerable field data input and computational resources (Jouvet et al. 2008). Alternative approaches that assess changes in ice-covered area, glacier length and ice thickness are also available, e.g., Δh-parameterization relating the elevation of the glacier surface h to the surface elevation change Δh occurring over a given time interval (Huss et al. 2008, Huss et al. 2010), used of the empirical relation of volume-area to estimate future change (Stahl et al. 2008). Those models allow forecasting the loss in ice volume base on the local climatic conditions forecasted.

4.3.3. Hydrological models

A vast number of hydrological models have been developed; they are usually based on a combination of linear and non-linear functions. Model structures are *metric* (based on empirical data), *parametric* (i.e. conceptual, used storage element as the main building component), or *mechanistic* (based on the conservation of mass, momentum and energy). In *parametric* models, storage elements are filled through fluxes such as rainfall, infiltration or percolation, and emptied through evapotranspiration, runoff, drainage, etc. Modelling approaches also range from *lumped* (catchment treated as a single unit) to *distributed* (catchment decomposed into a large number of elements or grid squares; Beven 2011). In glacierized catchments, alpine stream flows have been simulated using conceptual semi-distributed (Schaefli et al. 2005, Stahl et al. 2008), and distributed hydrological models (Klok et al. 2001, Verbunt et al. 2003, Huss et al. 2008). In most studies modelling glacierized catchment, a glacier sub-model was integrated into the hydrological model. Those models allow forecasting alpine stream flow of both glacier-fed streams and groundwater/rainfall streams.

4.3.4. Instream Environmental models

To simulate the spatiotemporal environmental heterogeneity of glacierized catchments, it is first necessary to identify the temporal variability in flow and environmental conditions of each stream type. To achieve this, one way would be to perform continuous measurements of flow and physico-chemical parameters (e.g., temperature, conductivity) during at least one year. Thus, using wavelet analyses, we could identify at which temporal scale occur most important signals (e.g. diurnal increase in temperature; Galiana-Merino et al. 2014) and reconstruct simplified time series for each type of stream (Krishna and YR Satyaji 2011, Pandhiani and Shabri 2013). Then, by coupling a hydrological model, that determine the discharge of each type of stream, and an environmental model that assess the environmental conditions of each type of stream, we could simulate the spatiotemporal environmental heterogeneity under climate change. Note, however, that we need to consider changes in environmental conditions during flow routing, e.g., increase in temperature with decreasing altitude, increase in conductivity with duration of flow routing (bed rock weathering; Nelson et al. 2011) and the effect of air temperature on water temperature (Erickson and Stefan 2000).

Therefore, to be able to perform an idealistic forecast, we first need not only to have a good comprehension of the functioning of the actual catchment, i.e. water source, flowpaths and residence times, but also to incorporate various statistical sub-models that assess change in instream environmental conditions within each stream, what requires considerable field data. In this context, Thermal Infra-Red (TIR) imagery could be a useful tool for both identifying the spatio-temporal dynamics of water sources and flowpaths; e.g., groundwater detection, identification of meltwater flowpaths during high flood event (see Fig. 4 for exemples of TIR images; Pfister et al. 2012, Röper et al. 2013) and examining the spatio-temporal variability in surface water temperature within stream. In addition, capturing TIR images from a drone would allow improving detection of water sources and flowpaths (e.g. in inaccessible zones), and building thermal orthophotos at high resolution screaming a whole catchment (see also Tonolla et al. 2012, Wawrzyniak et al. 2013).

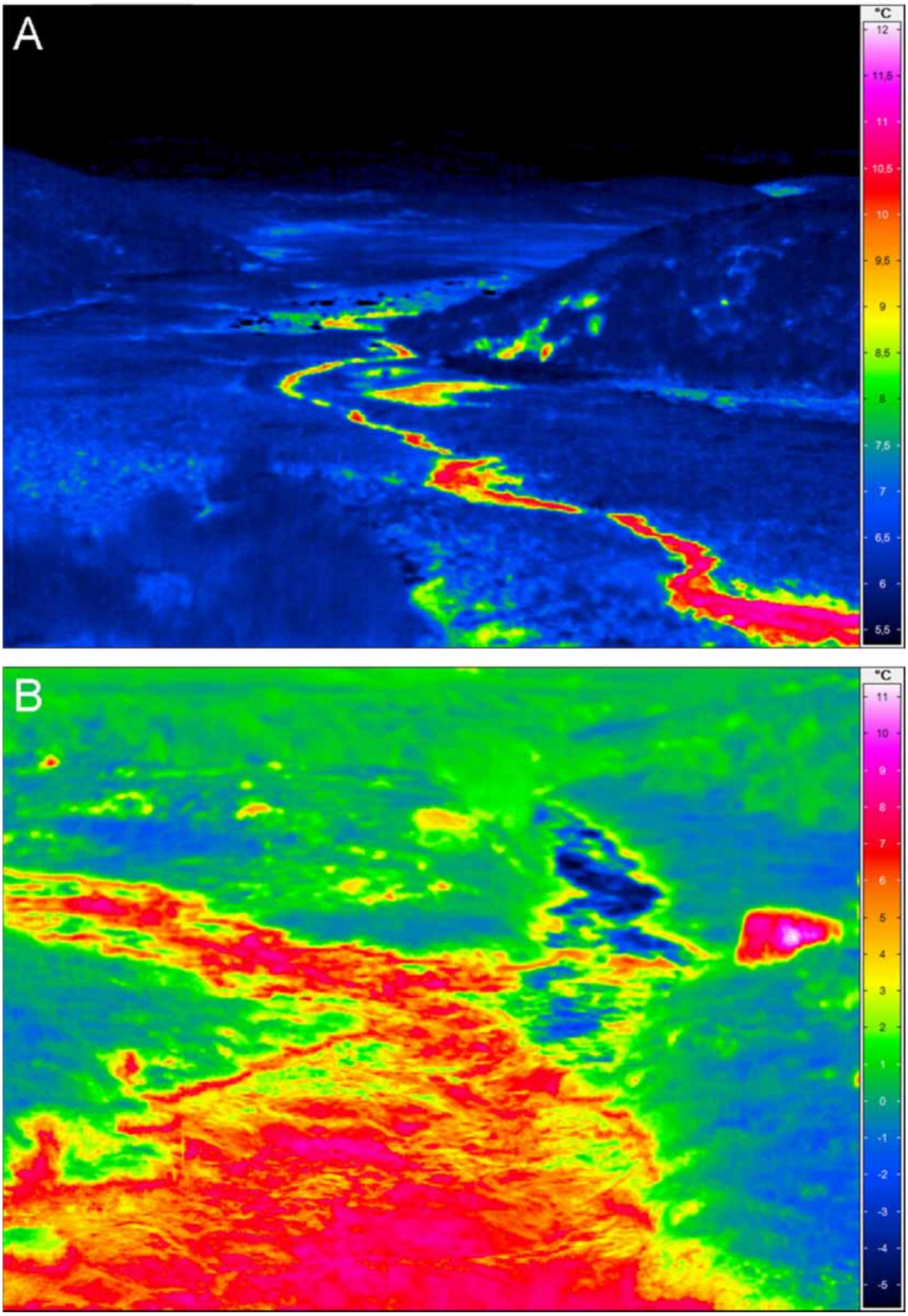


Figure 4: Thermal Infra-Red images taken by night of streams at the Antisana volcano. **A**. Red stream is a stream with both glacial and groundwater influence, the green spot on the bottom of the picture is a groundwater emergence. **B.** Confluence of a glacier-fed stream on the left and a groundwater stream on the right.

4.3.5. Species distribution models

Species distribution models (SDMs) are models relating species distribution data to environmental predictor variables (Guisan and Zimmermann 2000), that allow forecasting the spatial distribution of a species. SDMs could be significantly improved by incorporating processes governing species distribution and community composition (Elith and Leathwick 2009) such as physiological thresholds (Martínez et al. 2014), species interaction and evolutionary change (Guisan and Thuiller 2005, Hoffmann and Kellermann 2006, Buckley et al. 2010) and dispersal processes (Midgley et al. 2006, Schurr et al. 2007, Prasad et al. 2010). For predicting spatial patterns of species assemblages, two modelling approaches prevail: macroecological modelling (Gotelli et al. 2009) and stacked species distribution modelling (Ferrier and Guisan 2006). Recently, a new framework has been developed that unify the two approaches in a single framework - SESAM - and allow predicting spatial pattern of species assemblages based on dispersal, abiotic habitat (i.e. environmental) and biotic filtering (Guisan and Rahbek 2011). Therefore, a large spatial data set of the local aquatic community composition and environmental conditions, combined with knowledge on the mechanisms driving metacommunity structure (Part 4.1.) would permit to forecast the future metacommunity structure according to changes in environmental conditions forecasted.

4.4. Biodiversity conservation and ecosystem services

4.4.1. Endemism

In this thesis, we examined the community structure of aquatic macroinvertebrates; however, macroinvertebrates were not identified to species, but mostly to sub-family. A more precise taxonomic identification seems urgently needed to better characterize the community structure but also to identify rare and potentially endemic species. Previous studies have already showed that the tropical Andes shelter high amount of endemic species (Myers et al.

2000, Herzog et al. 2011). Moreover, isolation of Ecuadorian highlands (*Páramos* above 4000 m a.s.l.) promotes endemism (Vanschoenwinkel et al. 2011). For exemple, Moret (2005) found high *microendemism* of Carabids in Ecuadorian *Páramos*. To improve our taxonomic identification, we could also perform DNA barcoding, a process of identifying species based on short fragments of DNA (Fujita et al. 2012, Puillandre et al. 2012, Zhang et al. 2013).

4.4.2. Ecosystem function

Our work examined ecosystem structure but did not treat ecosystem function. Moreover, we only focused on aquatic macroinvertebrates. Complementary studies would be necessary to quantify the response of the rest of organisms inhabiting streams in glacierized catchments (e.g., fungi, algae, fish sampling; Eisendle-Flöckner et al. 2013), and assess food web structure (e.g., gut content and isotope analysis; Zah et al. 2001, Füreder et al. 2003, Clitherow et al. 2013, Cross et al. 2013). Those studies would allow both improving our description of the ecosystem structure and assessing the biological function of those specific freshwater ecosystems, including productivity, decomposition, and trophic interactions. Note that trophic interactions could also be included in species distribution models (see part 4.3.5) to improve forecasts. In addition, the study of ecosystem function could be even more important as it allows identifying ecosystem services, such as water purification.

4.4.3. Conservation of the Antisana reserve

At the Antisana, aquatic species are not only threatened by climate change, but also by water abstraction, species invasion, water pollution, and habitat degradation (Geist 2011). Indeed, although Antisana volcano is an ecological reserve since 1993, anthropogenic impacts are far from nil, even above 4000 m a.s.l.. First, rainbow trout (*Onchorhynchus mykiss*) has been introduced decades ago and is still present until at least 4100 m a.s.l. (Cueva 2013).

Second, the presence of cows and sheep has potentially negative effect on both terrestrial (grazing) and aquatic habitats (fecal contamination). The FONAG (*Fondo para la protección del Agua*) is actually examining the impact of terrestrial plant restoration on water quality after removing cows from a catchment next to our study catchment. Note, however, that since parts of the Antisana were purchased by governmental institutions in 2013, most herds have been removed from the highest parts (above 3900 m). Third, water abstraction closed to the lake *La Mica* strongly alters downstream flow regime (Fig. 5 A-B). Moreover, since 2013, a new water canal transports water from a glacier-fed stream on the south side of the Antisana volcano, above 4200 m a.s.l, to the lake *La Mica* (3900 m a.s.l.; Fig. 5 C). Finally, the lake *La Mica* has visible effect on the environmental conditions of downstream sites (Fig. 5 D).

Therefore, it is essential to inform governmental institutions and other stakeholders of the Antisana reserve about the importance of freshwater ecosystems, so that appropriate conservation policies could be adopted. Nevertheless, ecosystem services provided by aquatic invertebrates (e.g. food resource for fish) might have more weight on the future conservation decisions than the presence of endemic freshwater species as conservation policies generally favor terrestrial birds and mammals compared to freshwater invertebrates (Dudgeon et al. 2006, Strayer and Dudgeon 2010).

Figure 5: **A.** Stream before the water abstraction (built in 1999). **B.** Stream after the water abstraction. **C.** New water abstraction (2013). **D.** Stream flowing from the lake *La Mica*

4.5. *Monitoring at larger temporal and spatial sales*

In line with the outcomes of the GLAC-HYDRECO-NET[1] workshop, we highly recommend to extend the study of glacier-fed freshwater ecosystems at larger temporal and spatial scales.

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[1] European Science Foundation Exploratory Workshop GLAC-HYDRECO-NET: Glacier-Fed Rivers, Hydroecology and Climate Change; Current Knowledge and Future Network of Monitoring Sites, convened by Alexander Milner (*University of Birmingham, UK*), Dean Jacobsen (*University of Copenhagen, Denmark*) and David Hannah (*University of Birmingham, UK*) at the University of Birmingham, UK in July 2013.

4.5.1. Long-term monitoring at the Antisana

One of the best methodologies to assess the effect of glacial shrinkage on freshwater ecosystems would be to perform glacial and hydrological measurements and aquatic organism samplings over the longest period possible. For this reason, our team installed a fix station at the Antisana, along the glacier-fed stream originated from the glacier “Los Crespos”, at three stream sites already punctually monitored from 2008 to 2010 (see Jacobsen et al. 2014a). At those three sites, our group will measure continuously water temperature, conductivity, and water level and sample at least once a year benthic algae, detritus and macroinvertebrates.

4.5.2. Along the Equatorial line

After all, this thesis was conducted in one single equatorial glacierized catchment, which thus constitutes only one specific case in the tropic. Others studies should be performed to verify the observed trend in tropical glacier-fed streams. Many other glaciers occur in the tropical Andes; but outside the Andes, tropical glaciers remain only at four places: at Mount Kilimanjaro, Mount Kenya, and at the Rwenzori mountains in East Africa and at the Puncak Jaya Mountain in Indonesia. Note that, as the Antisana, those mountains are located close to the Ecuador line (< 4° from the Ecuador line). A comparative study among those tropical glaciers would permit to both test our findings in other regions and to examine the biogeographical pattern of species occurring in equatorial glacier-fed streams. However, many glaciers of those mountains are expected to disappear within the next 10 years (Klein and Kincaid 2006, Thompson et al. 2009, Cullen et al. 2012). We, thus, have to hurry if we want to study those ecosystems. Rapid glacial shrinkage would be an opportunity to observe the effect of glacier-fed stream loss on specialized species adapted to the conditions of glacial streams, i.e. examine whether they will be extinct or resist to new environmental conditions and the coexistence of more generalist species.

4.5.3. Across South America

Along a latitudinal gradient, glacier-fed streams exhibit variable temporal flow regimes and variable environmental conditions linked to the distinct cycles of glacier melting and climatic conditions (Cuffey and Paterson 2010). Consequently, glacier-fed freshwater ecosystem structure and function vary with latitude (Jacobsen and Dangles 2012). For this reason, I have the project of building a partnership with researchers from all countries from Venezuela to Chile (including Colombia, Ecuador, Peru, and Bolivia) to study freshwater ecosystem in glacier-fed streams from South Chile to Venezuela along a regular latitudinal gradient (e.g. every 5°). The aims of this project would be to assess the effect of glacial influence on freshwater ecosystems structure along a latitudinal gradient and examine the biogeographical pattern of aquatic species in glacier-fed streams (Fig. 6).

Figure 6: Research vehicle for the study of glacier-fed freshwater ecosystems across South America

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GENERAL APPENDICES

Temporal variability in discharge and benthic macroinvertebrate assemblages in a tropical glacier-fed stream

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Abstract: High flows are major disturbances in streams and cause benthic communities to vary temporally. Meltwater runoff in glacier-fed streams at temperate–arctic latitudes primarily follows a strong seasonal pattern. In contrast, such streams at the equator show less seasonal, but more-pronounced diel variability in discharge that tracks a year-round diurnal melting–nocturnal freezing cycle of glaciers. Consequently, qualitative and quantitative differences in temporal variability of macrobenthos communities should be expected between high-latitude and tropical glacier-fed streams. We explored temporal variability in density, taxon richness, and community composition of benthic macroinvertebrates and analyzed community responses to flow events at 3 sites along a glacier-fed stream in equatorial Ecuador (0.05, 1.6, and 4.3 km from the glacier front). We obtained continuous flow recordings and sampled fauna at approximately quarterly intervals over 30 mo. Temporal variability in the fauna was aseasonal. However, the overall magnitude of the coefficient of variability (CV) at the 3 sites was not lower than the CV at temperate latitudes. The explanatory power of flow did not differ among discharge parameters 3, 6, 9, 21, and 45 d before sampling. The effect of flow (slopes of regressions of faunal metrics vs flow) did not differ among sites, but the amount of variation explained by flow was significant only at the 2 downstream sites. Little synchrony was found in variability among sites, possibly because of differences among sites in physical characteristics (e.g., refugia space), which moderated the effect of disturbances, and taxonomic composition of communities. Our study is the first to show a close link between hydrological and biological fluctuations in an equatorial glacier-fed stream, a prerequisite for subsequent predictions of consequences of tropical glacier melting on diversity, composition, and stability of stream communities.

Key words: Ecuador, Andes, dynamics, flow, macrobenthos, fauna, communities, diversity-stability hypothesis

High-flow events are one of the most prevalent forms of natural disturbance in riverine systems (Lake 2000, Bunn and Arthington 2002). They have the potential to remove macroinvertebrates (Death 2008) and reduce food resources by carrying away benthic detritus and scouring benthic algae (Peterson and Stevenson 1992, Biggs et al. 1999), and thereby maintain nonequilibrium communities (e.g., Resh et al. 1988, Townsend 1989). Flow regime in glacier-fed streams is controlled primarily by glacial melting, which varies on a diel and seasonal basis. At temperate latitudes, discharge peaks during summer glacial melting and is almost nil during winter (Milner and Petts 1994, Smith et al. 2001, Brown et al. 2003). Therefore, the composition of biological communities in temperate glacier-fed streams varies greatly over the year, with density and diversity reaching maxima during seasons of low flow (e.g., Füreder et al. 2001, Lods-Crozet et al. 2001, Robinson et al. 2001). Glaciers at the equator have different dy-

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namics because melting occurs throughout the year (Favier et al. 2008). Thus, the main variability in discharge takes place on a diel basis because of diurnal melting and nocturnal freezing. Therefore, temporal variability in equatorial glacier-fed stream communities is expected to differ quantitatively and qualitatively from that in temperate glacial streams.

Glacier-fed streams typically originate as physically unstable, cold, and nutrient-poor habitats (Milner et al. 2001). With increasing distance from the glacier, the stream environment becomes less influenced by the glacial source, and stream temperature, channel stability, and ionic strength of the water usually increase (Milner et al. 2001, Jacobsen et al. 2010). Therefore, benthic macroinvertebrate communities in glacier-fed streams show a characteristic increase in species diversity and turnover along the stream (Jacobsen et al. 2012).

This longitudinal increase in species richness is a result of decreasing environmental harshness (Jacobsen and Dangles 2012) in terms of the abiotic environment and resource availability. In general, extreme or severe environmental conditions (e.g., very cold, hot, dry, saline, acidic, or O_2-depleted) are assumed to limit species richness compared to more benign conditions (Connell 1975, Currie et al. 2004). According to the diversity–stability hypothesis (MacArthur 1955, Elton 1958), high species richness is expected to stabilize fluctuations in community density, biomass, and diversity (for reviews see, e.g., Cottingham et al. 2001, Cardinale et al. 2006, Jiang and Pu 2009). Thus, this hypothesis suggests an indirect link between environmental harshness and community stability, through species richness. Depending on how harshness and community stability are defined, the expectation is that as harshness increases, species richness and community stability decrease.

One aspect of environmental harshness could be temporal environmental variability or disturbance, which may have a direct effect on temporal variability of communities, regardless of whether these are poor or rich in taxa. Glacier-fed streams seem to be particularly harsh environments because of a high degree of environmental variability (Hieber et al. 2002, Ilg and Castella 2006). Factors that may affect a community's response to a given disturbance are habitat properties, such as refuge space where organisms may escape the impact of disturbances (Townsend and Hildrew 1994, Townsend et al. 1997).

Interconnected sites along glacier-fed streams potentially share the same taxon pool. They are ideal systems in which to explore relationships between temporal variability in discharge and benthic macroinvertebrate assemblages because they are subject to the same frequency of disturbances in the form of discharge variability, but differences in taxon richness are produced by a natural and steep gradient in environmental harshness. Equatorial glacier-fed streams are particularly interesting because they are not constrained by seasonal short windows of favorable conditions that occur in temperate glacier-fed streams (Uehlinger et al. 2002). We obtained continuous records of discharge and did approximately quarterly sampling of benthos over 30 mo at 3 sites at varying altitudes and distances along a glacier-fed stream in equatorial Ecuador.

Differences in environmental characteristics and macroinvertebrate communities between sites along the stream have been explored previously (Jacobsen et al. 2010, Kuhn et al. 2011). Here, our purpose was to obtain insight into the temporal variability in benthic macroinvertebrate communities in a tropical glacier-fed stream. Our results should contribute to our understanding of the possible consequences of melting of tropical glaciers on aquatic communities. Our objectives were to: 1) document the spatiotemporal variability (CV) in the benthic macrofauna of a tropical glacier-fed stream and to discuss this variability in a broader context in a review of literature from glacier-fed streams in temperate regions, and 2) analyze the linkage between flow events (discharge) and the response of the fauna (density, taxon richness, and community composition) at different sites along the stream that differ with respect to habitat characteristics, taxon richness, and community composition. The hypotheses that we wanted to test were that: 1) temporal variability in the macroinvertebrate communities would be aseasonal, 2) broad-scale patterns in variability (coefficient of variability [CV]) would reveal lower values for our equatorial stream compared to temperate streams and that CVs would increase with glacial influence and duration of study, 3) the fauna at different sites along the stream would vary in a synchronous way, and 4) faunal variability and the amount of that variability explained by variations in runoff would decrease with increasing taxon richness and distance from the glacier.

METHODS

Study area

Our study stream, the Río Antisana, is a headwater of the River Napo, a main tributary of the upper Amazon River. It originates from the Crespo glacier on Mount Antisana in the eastern cordillera of the Andes of Ecuador (lat 0°28′S, long 78°09′W). The Crespo glacier covers an area of ~1.8 km^2 and originates at the summit of the mountain (5760 m asl). The ablation zone extends from ~5150 m to the glacier snout at 4730 m asl and is retreating 10 to 20 m of stream distance/y. Air temperature, humidity, and radiation do not vary systematically during the year, but precipitation, cloud cover, and wind speed are more seasonally variable (Cadier et al. 2007). The annual precipitation (mostly snow and hail) is ~800 mm (Maisincho et al. 2007), but hydrology is dominated by glacial meltwater (see below). Mean annual air temperature varies from ~3.7°C at the lowest site to 1.3°C at the upper site (Cáceres et al. 2005). The vegetation of the lower part of the study area is páramo, a moorland type of vegetation with scattered bushes characteristic of the northern Andes. Above ~4600 m asl vegetation is present only in the form of sporadic tufts of grasses and cushion plants. For more information on the study area, refer to Jacobsen et al. (2010) and Kuhn et al. (2011).

We selected 3 sites along a stretch of the stream that had no visible tributaries and, therefore, was ideal for studying the effect of the same hydrological regime on different communities. Site A (0.5–5 m wide) at 4730 m asl was ~50 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 seemed to freeze and cease 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 4490 m asl and 1.62 km from the glacier, and site C (1–2 m wide) was 4225 m asl and 4.30 km from the glacier. Sites B and C were in a confined, but eroding flood valley. Glacial cover was ~100, 67, and 42% of the catchment area of sites A, B, and C, respectively (Maisincho et al. 2007).

Environmental setting

We obtained data on the hydrological regime by continuously recording discharge during 2008–2010 at a gauging station at site B, which provided us with daily minimum, maximum, and mean discharge (Institut de Recherche pour le Développement [IRD], Instituto Nacional de Hidrología y Meteorología [INAMHI], Empresa Municipal de Alcantarillado y Agua Potable de Quito [EMAAP-Q]). We did not have discharge data from all 3 sites, so we used the discharge at site B indexed to maximum recorded discharge prior to each sampling as a standardized and comparable measure of intensity and predictability of disturbance at all sites (sensu Poff 1992). To ensure that discharge varied similarly at all 3 sites, we recorded water level continuously and simultaneously at all sites during April 2009 (Hobo loggers; Onset Computer Corporation, Bourne, Massachusetts).

We tested the presumed gradient in harshness along the stream by measuring a number of environmental variables that we suspected might influence macroinvertebrates. We measured temperature regime and O_2 saturation (precision: 0.1°C and 1% O_2) from data loggers (Oxylog, OxyGuard®, Birkerød, Denmark) placed in the stream and set to record every 30 min for 5 to 8 wk during January–March 2008 and for 2 to 5 wk during December 2011–February 2012. The O_2 probes hung freely from metal tubes inserted between boulders along the banks, and we placed them as close to the stream bed as possible where the current was swift. The equipment was initially calibrated in situ based on altitude (e.g., 100% O_2 saturation at sea level, 59.2% at 4200 m asl and 55.4% at 4700 m asl), and the O_2 saturation and water temperature verified with an YSI® 58 O_2 meter (Yellow Springs Instruments, Yellow Springs, Ohio) while introducing and retrieving the loggers.

Conductivity (at 25°C) and pH were measured with portable meters, model Cond 315i and pH 315i, respectively (WTW, Weilheim, Germany), on every visit to the study sites (10–12 measurements). Water turbidity was measured 5 to 6 times at each site with a Eutech TN-100 Turbidimeter (Eutech, Nijkerk, The Netherlands) and current velocity 2 to 3 times at each site by dilution gauging (White 1978). We added a known amount of dissolved salt (volume and conductivity) at the upstream end of the 15- to 25-m stream reach, and we measured the conductivity every 5 or 10 s at the downstream end of the reach. Mean current velocity was calculated as the time needed for ½ of the salt to pass the stream reach divided by the length of the reach. We measured stream slope at each site with a transparent plastic tube that carried flowing water from the upstream to the downstream end of the reach. Slope was calculated as the difference between the water level inside the tube when raised until flow stopped and that of the surface of the stream water at the downstream end, divided by the distance between the upstream and downstream ends of the tube (~25 m).

We estimated the food resources available to macroinvertebrates by sampling pebbles for quantification of epilithic algae and collecting the benthic detritus obtained in Surber samples (see below). At each site, we collected 9 small pebbles (~2–4 cm) at random (but we avoided pebbles with filamentous algae), placed 3 pebbles in each of 3 containers, and extracted chlorophyll *a* in 96% ethanol for 1 to 3 d in the dark until further processing in the laboratory where we gave the containers a 10-min ultrasonic bath to increase extraction efficiency. After settlement for a few hours, we transferred a sample to a spectrophotometer and measured absorption at 665 and 750 nm. We calculated the concentration of total chlorophyll *a* (including phaeopigments) according to the method published by Københavns Universitet (1989). Stone surface area was estimated with the formula

$$A = 1.15(LW + LH + WH) \qquad \text{(Eq. 1)}$$

proposed by Graham et al. (1988), where L is length, W is width, and H is height of the stones.

We quantified benthic detritus by collecting all material (inorganic and organic) present in the Surber samples after sorting out the animals. This material was dried at

80°C for ~24 h and weighed. We used mass loss upon combustion at 550°C as the ash-free dry mass (AFDM) of organic material >200 μm in the sample.

To obtain comparable estimates of environmental variability and disturbance level of the stream sites, we applied 4 measures: 1) the CV in water depth obtained from the loggers, 2) the average of the CVs for all nonflow variables (temperature, O_2, conductivity, pH, turbidity, benthic chlorophyll *a*, and detritus), 3) the skewness of the dilution-gauging curve used to measure current velocity (y = conductivity, x = time), where a large skewness is a measure of hydraulically dead space, which we considered as a measure of low-stress refugia for macroinvertebrates (low-flow areas are important refugia during high-flow events; Lancaster and Hildrew 1993, Rempel et al. 1999), and 4) a scoring system (15–60, with 60 as the most unstable) based on the channel-bottom component of the Pfankuch Index (Pfankuch 1975) evaluating properties, such as rock angularity, brightness, particle packing, stability of substratum, scouring and deposition, and clinging vegetation. The Pfankuch Index has been widely used to quantify channel bed stability in glacial streams (e.g., Castella et al. 2001).

Macrobenthos sampling

We sampled macroinvertebrates between April 2008 and September 2010 at intervals of 2 to 5 mo. At each site, we collected 5 quantitative Surber samples (500 cm^2; mesh size = 200 μm) randomly from pebble–cobble substratum in riffle/run habitats. All samples were collected during the day and preserved in the field in 70% ethanol. In the laboratory, the samples were rinsed through a 200-μm sieve and sorted without use of magnification. We applied subsampling to samples with large numbers of chironomids.

Complete species analysis of the Ecuadorian stream fauna was not possible because only a few groups can be identified to a taxonomic level lower than family. Invertebrates other than Chironomidae were identified mostly to family with keys published by Roldán (1996), Merritt and Cummins (1996), and Fernández and Domínguez (2001) and were separated into morphospecies. We sorted larval chironomids with the aid of a stereomicroscope at 10× magnification, dehydrated them in 96 and 99% ethanol, and mounted them in Euparal. Larvae were identified to subfamily with the aid of a compound microscope at maximum 400× magnification with keys in the current taxonomic literature (Wiederholm 1983, Ruiz-Moreno et al. 2000, Epler 2001). Larvae of Orthocladiinae were not identified further.

Data analysis

We analyzed 2 univariate faunal metrics based on the Surber samples: density (number of individuals in samples) and local taxon richness (number of taxa in samples). We generated autocorrelation function (ACF) plots in Minitab® (version 15.1.20.0; Minitab, State College, Pennsylvania) to test for temporal independence, periodicity, and seasonality in these faunal metrics and in monthly discharge measures.

We used CV as a measure of variability of faunal metrics. We compared our results with data from temperate systems to place our equatorial stream data in a broader context. However, we had to take into account 2 confounding factors that might influence temporal variability, variability of glacial influence among sites and the duration of study. In temperate systems, we expected studies including both summer and winter sampling to show higher variability than studies in which sampling occurred only in summer or only in winter. Therefore, we represented CVs of density and taxon richness in contour plots as a function of study duration (mo) and of the Glacial Index proposed by Jacobsen and Dangles (2012). This index is a simple and comparable measure of glacial influence at stream sites and is highly correlated with taxonomic richness in glacier-fed streams. It is related to the extent (area) of the feeding glacier and inversely related to the distance from the glacier. A value of 0 means no influence and 1 means maximum glacial influence. We made contour plots with a quadratic distance interpolation method in Minitab.

We used nonmetric multidimensional scaling (NMDS) ordination based on Bray–Curtis similarity (on $\log[x + 1]$-transformed data to down-weight the influence of very abundant taxa) to examine spatial patterns and temporal variability in community composition among sites. The NMDS goodness-of-fit was estimated with a stress function, which ranges from 0 to 1 with values close to 0 indicating a good fit. The composition of macroinvertebrate communities among sites was compared with analysis of similarities (ANOSIM). ANOSIM tests the null hypothesis that within-site similarity is equal to between-site similarity. ANOSIM generates a statistical parameter R, which indicates the degree of separation between groups. A score of 1 indicates complete separation, and a score of 0 indicates no separation. We used Monte Carlo randomizations (10,000) of the group labels to generate null distributions to test the hypothesis that within-group similarities are higher than would be expected by chance. These analyses were done on the data for specific dates (pooling the 5 Surber samples) in Primer (version 5.2.4, PRIMER-E, Plymouth, UK).

To test for periodicity in community composition, we compared Bray–Curtis similarities between temporal neighbor samples with those of all other possible combinations. To test for seasonality, we compared samples collected at about the same date in different years (maximum 1-mo difference) with those of all other possible combinations. These tests were done as t-tests in Excel (version 2003; Microsoft Corporation, Redmond, Washington).

We used 1-way analyses of variance (ANOVAs) followed by Tukey post hoc comparisons of means to test for differences in faunal metrics ($\log[x + 1]$-transformed data with replication) among the 3 sites, among sampling dates, and to test for differences between environmental factors ($\log[x + 1]$-transformed data without replicates). We used F-tests to test for differences in variances in faunal metrics between sites. All of these tests were done in Excel.

To obtain a measure of community-wide synchrony in the variability of taxon densities within each site, we applied the statistic provided by Loreau and de Mazancourt (2008), which permits comparison of communities with different number of taxa. The statistic is standardized between 0 (perfect asynchrony) and 1 (perfect synchrony).

From the measurements of environmental variables, we extracted minimum, maximum, and mean values, and CV (in %). Because the study included only 3 sites, these values were easily distinguished without use of multivariate analyses on environmental variables. We made an initial exploration of the effect of flow events on the benthos by relating faunal density, taxon richness, and NMDS axis-1 coordinates to mean, maximum, and mean maximum discharge extracted from the last 3, 6, 9, 21, and 45 d before sampling. We used individual and simple regression analyses because our interest here was not to optimize (often ecologically meaningless) modeling of relationships between faunal metrics and discharge, relationships were clearly either linear or exponential, and correlation coefficients between the above mentioned discharge measures were generally high ($r_p > 0.85$). We tested for differences between regression slopes of faunal metrics at 3 sites vs discharge measures with analysis of covariance (ANCOVA) using the freeware PAST (version 2.03; Hammer et al. 2001).

RESULTS

Environmental setting

The 3-y discharge records at site B showed significant periodic correlation with a lag of 1 mo ($p < 0.05$) and a tendency toward seasonality at lags of 6 and 12 mo (minimum values generally occurred in June–August and maximum values during January–March; Fig. 1A). Short-term (day-to-day) variability was considerable (Fig. 1A), and within-day variability in discharge (max – min) ranged from 1 to 359 L/s. Daily minimum discharge (usually reached during early morning hours) was 5 to 93 L/s (median = 16 L/s); mean flow was 7 to 193 L/s (median = 47 L/s), and the afternoon maximum flow was 8 to 411 L/s (median = 114 L/s) (Fig 1B). Precipitation had negligible effect on short-term variability in stream discharge because neither minimum, maximum, nor mean discharge was significantly correlated with daily precipitation records from the same day or the previous day. Measurements of daily maximum water depth obtained during April 2009 at site B were highly correlated with independent records of daily maximum discharge at that site (Fig. 1C). Water-level loggers at the 3 sites showed very similar patterns during April 2009 (Fig. 1D), so we assume a parallel hydrological regime at all 3 sites during the entire study period. However, in mid-April the depth curve at site 1 was displaced relative to the depth curve at the other 2 sites (Fig. 1D).

Mean temperature and O_2 saturation differed significantly among all 3 sites, whereas conductivity and benthic chlorophyll *a* differed significantly between 2 of the 3 sites (Table 1), and these 4 variables increased downstream. The Pfankuch Index was much higher (less physical stability) at site A (58) than at sites B (24) and C (21). In contrast, pH, turbidity, and detritus did not differ among sites (Table 1).

Overall faunal distribution

The total numbers of taxa found at each site during the entire study were 19, 29, and 48 at sites A, B, and C, respectively. Both measures of mean taxon richness (mean per sampling date and mean per Surber sample) increased significantly with increasing distance from the glacier (Table 2). Mean density did not differ among sites ($F_{2,24} = 0.40$, $p = 0.67$).

Overall community composition differed significantly among the 3 sites (Global $R = 0.909$, $p < 0.001$; Fig. 2, Table 3), and community composition differed for each pairwise comparison (all $p < 0.001$). Mean Bray–Curtis similarity was 46 ± 3% (SD) between sites A and B, 38 ± 10% between sites B and C, and 19 ± 7% between sites A and C.

The community at site A was completely dominated by chironomids (96.7% of all individuals), in particular Podonominae type 3 (77.4%) (Table 3). The abundance of this species decreased along the stream, and at site B, the fauna was dominated by Orthocladiinae and Podonominae type 1, two Diamesinae species, the caddisfly *Cailloma*, and *Simulium* blackflies. At site C, Orthocladiinae was still dominant, together with the midge *Alluaudomyia*, *Simulium*, the mayfly *Andesiops*, and the elmid beetle *Neoelmis*.

Seasonality and periodicity

Temporal variability in density and richness seemed to follow to some degree the periodic fluctuations in discharge (Fig. 3A, B). Nevertheless, these 2 faunal metrics were temporally independent at all sampling lags and showed neither a periodic nor a seasonal cycle at any of the 3 study sites ($p > 0.05$). Temporal variability in the community composition (Fig. 2), defined as mean Bray–Curtis dissimilarity among dates, did not follow a seasonal pattern at any site ($p > 0.05$) but did show a significant periodic pattern at sites B and C ($t_{43} = 2.787$, $p = 0.008$;

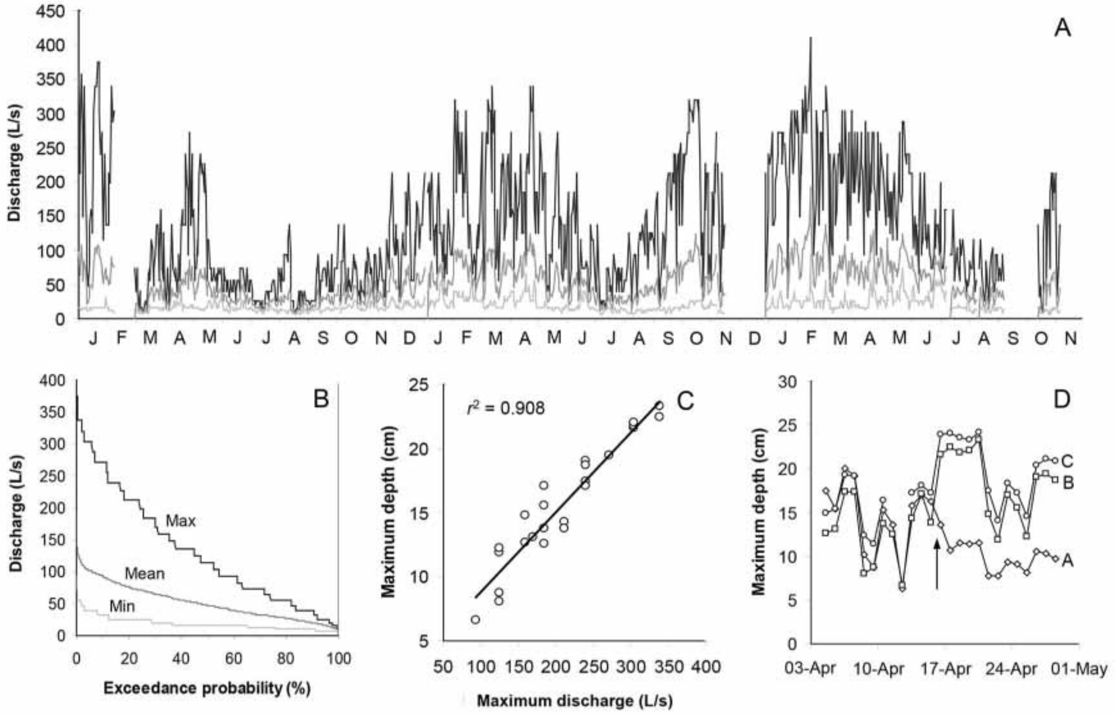

Figure 1. A.—Daily maximum, mean, and minimum discharge at site B (4490 m asl and 1.60 km from the Crespo glacier) during 2008–2010. B.—Exceedance probability in % of daily maximum, mean, and minimum discharge at site B. C.—Linear regression between independent records of maximum discharge (from gauge) and maximum depth (from Hobo® pressure logger) at site B during April 2009. D.—Daily maximum depth recordings from Hobo pressure loggers placed at each of the 3 study sites during April 2009. The vertical arrow indicates when recordings at site A were displaced with respect to the other 2 sites.

t_{43} = 2.890, p = 0.006, respectively). So, these data largely support our hypothesis that temporal variability in the macroinvertebrate communities would be aseasonal.

Broad-scale patterns in variability (CVs)

Analysis of the literature data showed that CV in density was almost always higher than CV in richness, and these 2 measures were not significantly related (r_p = 0.326, p = 0.091; Fig. 4A). The CV in density was related to neither the Glacial Index (r_p = 0.21, $p > 0.05$) nor the duration of the study (r_p = 0.12, $p > 0.05$; Fig. 4B). In contrast, CV in taxon richness increased significantly with the Glacial Index (r_p = 0.61, $p < 0.001$) but was unrelated to the duration of the sampling period (r_p = 0.24, $p > 0.05$) (Fig. 4C). In terms of CVs, our equatorial sites did not differ from the rest of the data. This result refutes our hypotheses that the overall magnitude of variability would be low compared to temperate latitudes and that it would increase with glacial influence and duration of study.

Synchrony in variability

The effect of sampling date on the variability in density (site A: $F_{8,36}$ = 4.36, p = 0.001; site B: $F_{9,40}$ = 13.67, $p < 0.001$; site C: $F_{9,40}$ = 6.23, $p < 0.001$) and mean taxon richness per Surber sample (site A: $F_{8,36}$ = 3.48, p = 0.004; site B: $F_{9,40}$ = 4.10, p = 0.001; site C: $F_{9,40}$ = 4.32, $p < 0.001$) was significant at all 3 sites, and the variability did not differ significantly among sites (F-tests, $p > 0.05$). However, synchrony between sites was far from perfect, and the variability in density and richness of pairwise correlations between sites were all nonsignificant ($p > 0.05$). Our hypothesis that sites at different distances along the stream should vary synchronously was not supported.

Mean CV in population (taxon) densities within communities tended to increase in a downstream direction (198, 211, and 225%), whereas synchrony in variability in population densities decreased downstream (0.791, 0.614, and 0.230 at sites A, B, and C, respectively).

Responses to flow

Only slight differences were found in the ability of the 3 discharge parameters and the length of period to explain variation in faunal metrics (Fig. 5A–C). Therefore, we chose maximum discharge the 3 d before sampling for further analyses (Fig. 6A–C). Density was negatively related to discharge, which explained 9.9 (p = 0.430), 81.0 ($p < 0.001$), and 73.0% (p = 0.001) of the variability at sites A, B and C, respectively. The pattern was similar for

Table 1. Mean, maximum, minimum, and coefficient of variation (CV) of environmental variables for the 3 stream sites. *n* = the number of single measurements that were performed at each site, respectively. For each variable, bold indicates significant differences among sites. Means with the same letter are not significantly different. Max = maximum, min = minimum, AFDM = ash-free dry mass.

Variable	Summary statistic	Site A	Site B	Site C	*p*
Slope (%)		1.4	8.7	9.0	
Mean current velocity (m/s)		0.22	0.38	0.21	
Pfankuch Index		58	24	21	
Skewness (hydrological dead space)		1.97	1.78	2.26	
Mean CV of all variables below except water depth		82	65	50	
Water depth (cm) (*n* = logging)	Mean	5	6	8	na
	Max	20	23	24	
	Min	0	0	0	
	CV	78	78	64	
Temperature (°C) (*n* = logging)	Mean	1.0^{a}	3.2^{b}	5.3^{c}	**<0.001**
	Max	15.0	9.8	19.4	
	Min	0.0	0.0	0.0	
	CV	209	57	66	
O_2 (%) (*n* = logging)	Mean	52^{a}	55^{b}	58^{c}	**<0.001**
	Max	64	59	69	
	Min	45	43	48	
	CV	6	2	4	
Conductivity (μS/cm) (*n* = 13, 17, 18)	Mean	8^{a}	11^{ab}	13^{b}	**0.008**
	Max	22	22	25	
	Min	2	3	5	
	CV	83	58	46	
pH (*n* = 11, 12, 13)	Mean	7.5	6.8	7.0	0.109
	Max	8.6	7.9	8.2	
	Min	6.0	6.1	6.3	
	CV	12	9	10	
Turbidity (NTU) (*n* = 4, 4, 5)	Mean	661	453	444	0.464
	Max	956	774	841	
	Min	285	298	264	
	CV	46	49	52	
Benthic chlorophyll *a* (μg/cm^2) (*n* = 9, 10, 10)	Mean	1.0^{a}	2.9^{b}	3.6^{b}	**<0.001**
	Max	3.2	7.0	11.5	
	Min	0.2	1.1	0.2	
	CV	84	153	105	
Benthic detritus (g AFDM/m^2) (*n* = 9, 10, 10)	Mean	13.6	14	17.6	0.337
	Max	48.2	62.6	42.2	
	Min	0.1	3.4	3.4	
	CV	131	130	64	

richness. Flow accounted for 23.3 (p = 0.180), 51.9 (p = 0.022), and 51.3% (p = 0.022) of the variability in taxon richness and 9.5 (p = 0.440), 80.8 ($p < 0.001$), and 21.4% (p = 0.184) of the variability in community composition at sites A, B, and C, respectively. However, regression slopes for density ($F_{2,22}$ = 3.241, p = 0.060), taxon richness ($F_{2,22}$ = 1.595, p = 0.228), and NMDS axis-1 coordinates ($F_{2,22}$ = 0.716, p = 0.501) did not differ among the 3 sites. Thus, the rate at which the fauna changed with flow was the same but the amount of the variation explained was different among sites. Therefore, our hypotheses that fauna variability and the amount explained by variation in runoff

Table 2. Mean, maximum, minimum, and coefficient of variation (CV) of density (individuals/Surber sample) and taxon richness (number of taxa/Surber sample). Means with the same letter are not significantly different ($p > 0.05$).

Variable	Site A	Site B	Site C
Density			
Mean	80.0^{a}	81.1^{a}	98.5^{a}
Max	277.8	279.6	200.6
Min	17.4	12.6	15.9
CV (%)	101.5	103.9	68.6
Taxon richness			
Mean	4.4^{a}	6.9^{b}	9.8^{c}
Max	5.6	9.2	12.2
Min	2.4	4.2	5.2
CV (%)	26.8	22.0	24.2

would decrease with increasing distance from the glacier were refuted.

DISCUSSION

Environmental setting and overall faunal distribution

The clear longitudinal patterns of mean faunal metrics reported here correspond well with results of our earlier studies on the same stream (Jacobsen et al. 2010, Kuhn et al. 2011) and with results from glacier-fed streams in general (Jacobsen and Dangles 2012). We assume that these patterns are caused by a steep gradient in environmental harshness along the stream (Jacobsen and Dangles 2012). Site A probably was more physically disturbed than the other sites by abrupt changes in stream channel morphology caused by substratum movement, the highly unstable moraine surroundings, and the diel freeze–thaw cycle of the stream (Jacobsen et al. 2010). Freezing is an important form of disturbance that can affect macroinvertebrate communities in Arctic streams (Irons et al. 1993, Parker and Huryn 2011). This effect was seen in a considerably higher Pfankuch Index (particularly a loose and easily moved substratum with no packing and consisting of only 0–20% stable materials) at site A than at sites B and C. In addition, average conditions of low mean temperature, conductivity, and benthic algal food availability, and higher mean CV in environmental variables should contribute to the harshness of site A and, thus, to the difference in taxon richness and community composition between sites A and B.

Sites B and C appeared to be quite comparable with respect to Pfankuch Index (24 and 21, respectively) and all measured environmental factors, and these 2 sites differed significantly only with respect to water temperature and % O_2 (Table 1). The increase in richness and change in community from site B to C seems to be a matter of temperature or O_2 levels (Jacobsen 2008a).

Seasonality and periodicity

As expected for a supposedly aseasonal environment at the equator, we did not find significant seasonal or periodic patterns in the variability of faunal metrics, even though the discharge of the stream did, in fact, show signs of seasonality and periodicity. This result indicates that faunal variability in the study stream is driven more by stochastic short-term flow variability than by seasonality per se. However, shorter sampling intervals could have revealed temporal dependency and, thus, a higher degree of periodicity. In 2 nearby rhithral streams that were sampled monthly/bimonthly during 1 y, temporal variability in density (CV = 39 and 95%) was about the same as in the glacier-fed stream and showed no seasonal cycle in density and richness (Jacobsen 2008b). Thus, the temporal variability in fauna in our glacier-fed stream seems to be comparable to that in other alpine streams at the equator with rain runoff as the main hydrological source.

In Bolivia, Molina et al. (2008) found CVs in density and richness of macroinvertebrates that were 20 to 25 and 70 to 90%, respectively, from quarterly samplings during 1 y at 3 sites (0.46–3.63 km) along a stream originating from a glacier on Mount Mururata. However, only their highest site was primarily glacier-fed. The lower sites had major contributions of rainwater runoff from tributaries. This runoff contribution probably explains why the highest site on the Mururata stream was largely aseasonal, whereas the 2 lower sites showed clear seasonality with high density and richness during the pronounced dry season of the outer tropics of Bolivia.

Broad-scale patterns of variability

In spite of the different seasonal flow dynamics in temperate and tropical glacier-fed streams (seasonal vs diel),

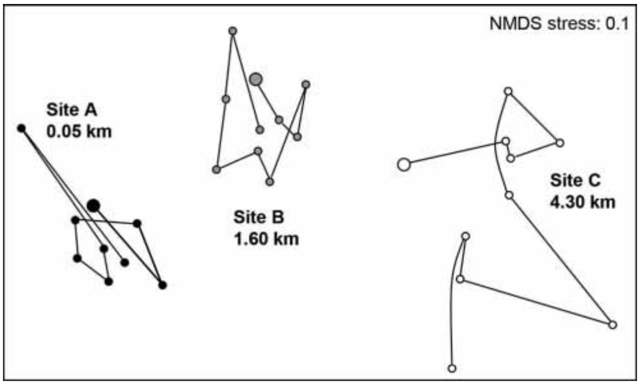

Figure 2. Nonmetric multidimensional scaling (NMDS) ordination plot based on Bray–Curtis similarities ($\log[x + 1]$-transformed) of community data from the 10 sampling dates at the 3 sites. Stress is low (0.1), indicating a relatively good 2-dimensional representation of the placements of sites. The large data points denote the 1st sample from each site. Distances are from the glacier snout.

Table 3. Taxa making up >1% of total richness at each of the 3 study sites. The mean proportion of the total (%), the coefficient of variation (CV) in density (%), and the Pearson correlation coefficient between density and mean maximum flow are shown. Bold indicates significant correlation ($p < 0.05$).

	Site A			Site B			Site C		
Taxon	% total	CV (%)	r	% total	CV (%)	r	% total	CV (%)	r
Andesiops sp.							7.3	122.4	−0.26
Neoelmis sp. 1 (L)							6.9	71.2	−0.13
Neoelmis sp. 1 (A)							1.1	106.8	0.02
Atopsyche sp. 1							2.0	149.1	−0.46
Cailloma sp. 1				6.5	96.8	−0.56	1.3	81.0	−0.59
Chelifera sp.							1.4	121.6	−0.58
Limnophora sp. 1				1.6	123.3	−0.27			
Simulium sp. 1				5.6	83.9	−0.65	10.9	104.2	**−0.72**
Alluaudomyia sp.1							20.3	218.8	−0.25
Podonominae sp. 1	13.9	68.5	−0.02	22.4	89.5	**−0.72**	1.2	145.4	−0.42
Podonominae sp. 3	77.4	124.6	−0.44	3.9	91.5	**−0.73**			
Podonominae sp. 4	5.4	92.5	−0.34						
Diamesinae sp. 1				8.8	251.4	−0.32			
Diamesinae sp. 2				4.5	232.5	−0.32			
Orthocladiinae	1.3	74.8	−0.30	45.5	134.1	−0.62	39.1	123.7	−0.65

the overall magnitude of variability (CV) in faunal metrics in the equatorial Antisana stream sites did not differ from the magnitude of variability in European temperate sites (Fig. 4A). Most studies of temperate sites cover only summer, but a few include winter. Brown et al. (2006) sampled 3 sites with low glacial inflow in the French Pyrenees in July and August in 2 consecutive years, and their data showed, in order of decreasing glacial influence, CVs in density of 184 (61 if 1 sample with extraordinarily high density is omitted), 58, and 47% and in richness of 12, 15, and 13%. Burgherr and Ward (2001) sampled from June to November at 10 sites along the Roseg River in Switzerland. They reported mean CVs in density of 139% at proglacial sites, 60% on the braided floodplain, and 90% along the lower constrained reach. CVs in taxon richness were 31, 31, and 20% along the same reaches, respectively. Lods-Crozet et al. (2001) sampled the Swiss Mutt stream in June, August, and September and found that CVs in density and richness at the glacier snout of 89 and 101%, respectively, decreased to 42 and 13% 3.6 km further downstream. On the other hand, Robinson et al. (2001) sampled monthly during a full year at 7 sites close to glaciers in Switzerland where they found CVs in density of 53 to 132% and richness of 33 to 59%. Monthly sampling during 2 y at 2 stream sites at 1200 and 3350 m from a glacier in Austria gave CVs in density of 100 and 215% and in richness of 38 and 28%, respectively (Schütz et al. 2001).

Our hypotheses were that temporal variability would be highest in studies covering seasons with very different runoff regimes and at sites close to (large) glaciers. We expected CVs to peak in the upper right-hand corner of the plots in Fig. 4B, C. However, the data from the studies mentioned above revealed that overall, neither the CV in density nor richness was significantly related to the duration of the study (Fig. 4B, C). Apparently, like in tropical glacier-fed streams, short-term variations in temperate glacier-fed stream faunas may be as pronounced as seasonal differences. In contrast, the CV in taxon richness, but not density, did indeed increase significantly with the Glacial Index (Fig. 4C). Thus, our expectation regarding the importance of glacial influence was only partially supported, perhaps because of zoogeographic differences among sites and local environmental conditions not captured through the Glacial Index.

Synchrony in variability

Our expectation of synchrony among sites in variability in density and taxon richness also was not met, probably because of differences in physical-habitat characteristics and composition of the fauna among sites (Fig. 2). For example, Orthocladiinae spp. composed 45 and 39% of the fauna, and the linear regression with flow explained 45 and 50% of the temporal variability in density of Orthocladiinae at sites B and C, respectively, whereas this group made up only 1% of the fauna at site A (Table 3). We found a similar pattern for *Simulium*. In contrast, Podonominae spp. contributed 97, 26, and 1% of the fauna at sites A, B, and C, respectively, but was significantly related to discharge only at site B ($r^2 = 0.60$) and not at sites A ($r^2 = 0.13$) and C ($r^2 = 0.15$). The response of benthic organisms to hydraulic stress is taxon-

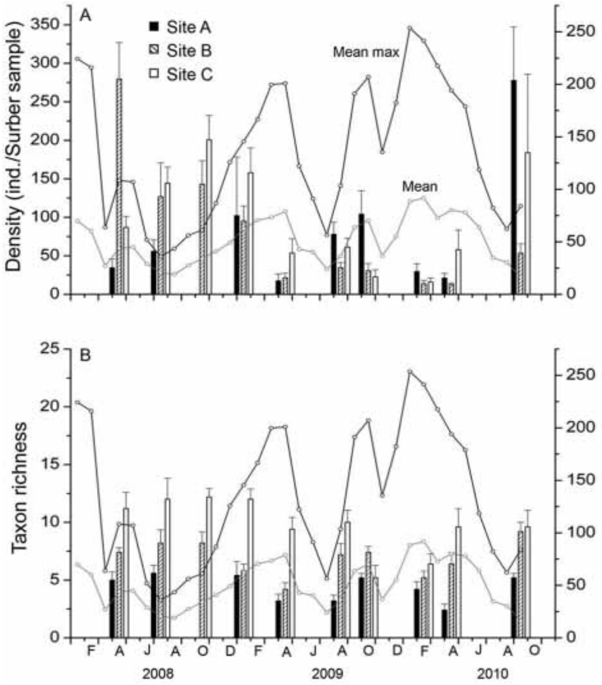

Figure 3. Mean (±1 SE) density of individuals (A) and taxon richness per Surber sample (B) at the 3 sampling sites during 2008–2010. Monthly mean and mean maximum discharge are superimposed. Ind. = individuals.

specific (Lancaster and Hildrew 1993, Snook and Milner 2002). Macroinvertebrate taxa differ with respect to a wide array of biological/functional traits that determine their realized abiotic niches and competitive interactions (Lamouroux et al. 2004, Statzner et al. 2004). In glacier-fed streams, resilience and resistance traits (e.g., small size, high adult mobility, habitat and feeding generalist, clinging behavior) are particularly dominant in species assemblages living close to glaciers. Such traits provide an obvious advantage for coping with harsh and disturbed environmental conditions (Füreder 2007). Gradual replacement of these traits by others along the stream (Ilg and Castella 2006) may explain the observed asynchrony among sites.

Even though differences were nonsignificant, mean CV in population (taxon) densities increased slightly and variability in community density decreased downstream. In other words, mean CV in population density was inversely related to CV in community density. Increased taxon richness downstream probably leads to a more moderated overall response because each species responds individually to flow. This result is in agreement with most model predictions for the diversity–stability hypothesis (Lehman and Tilman 2000). If we assume that community density may be used as a proxy for community biomass, then our finding of increasingly asynchronous variation of populations within downstream communities supports the notion that asynchronous species fluctuations driven by different responses among species to a temporally variable environment can stabilize community biomass (Cottingham et al. 2001, Loreau and de Mazancourt 2008, Allan et al. 2011).

Responses to flow

The effect of flow events was larger on density than on richness, a commonly observed response in streams (Giller and Malmqvist 1998). Short-term high-flow events in temperate streams are often stochastic and unpredictable

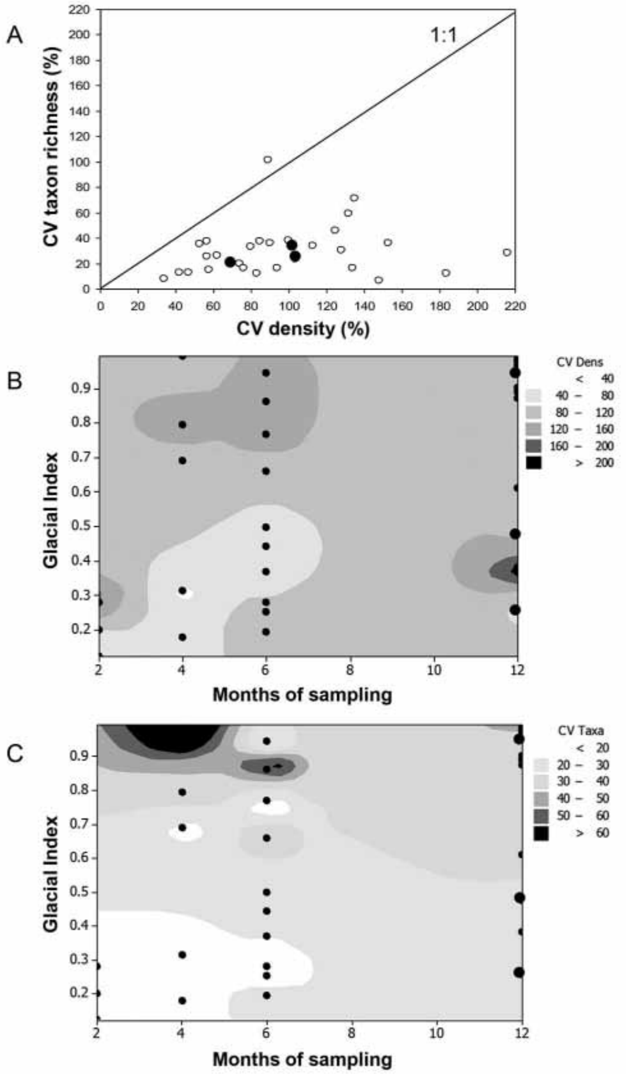

Figure 4. Coefficient of variation (CV) in taxon richness as a function of CV in density at various sites in different streams (A), and CV in density (B) and taxon richness (C) as a function of the Glacial Index (GI) and the number of months that the sampling covered. The GI was proposed by Jacobsen and Dangles (2012) as a proxy for environmental harshness. Values close to 1 are obtained close to large glaciers (see Methods for details). Large black dots = this study. Data from Brown et al. (2006), Robinson et al. (2001), Burgherr and Ward (2001), Lods-Crozet et al. (2001), Schütz et al. (2001), and this study.

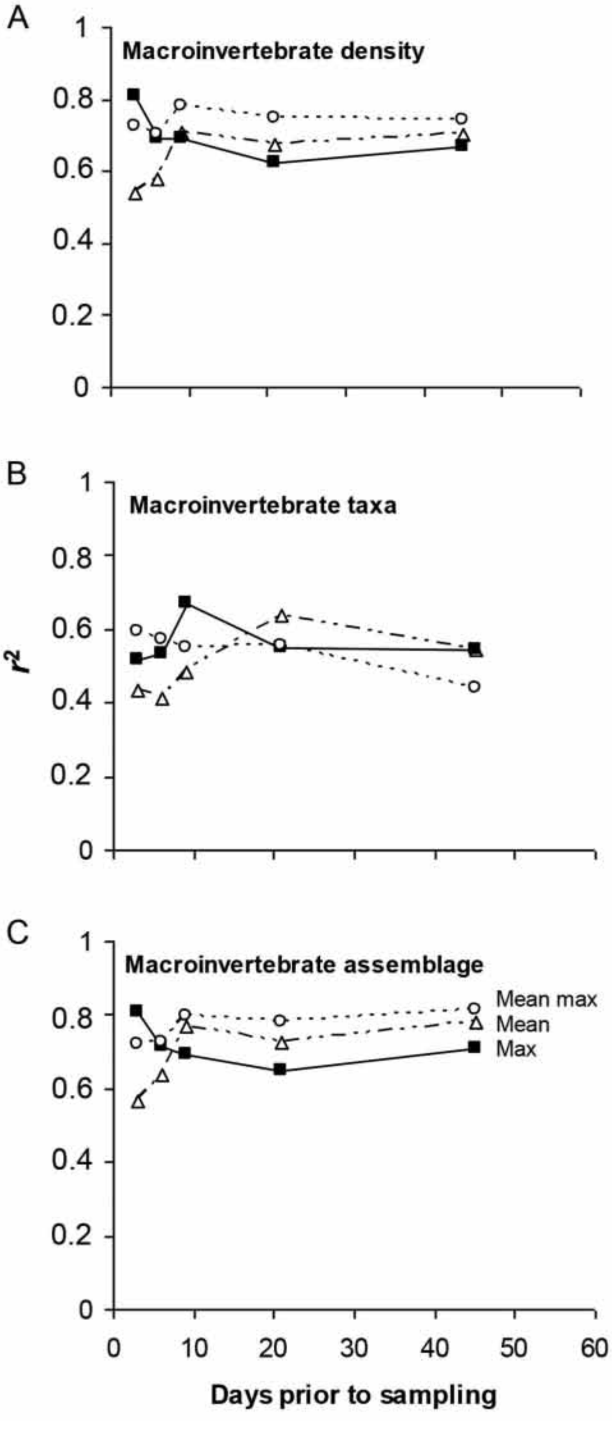

Figure 5. r^2 values from exponential regressions of density (A), taxon richness (B), and nonmetric multidimensional scaling (NMDS) axis-1 coordinates (C) against mean, maximum, and mean maximum discharge during the last 3, 6, 9, 21, and 45 d before sampling of benthic macroinvertebrates.

(Resh et al. 1988). In contrast, benthic macroinvertebrates in tropical glacier-fed streams are subjected to quite predictable increases in hydraulic stress mostly on a daily basis that follows the diel freeze–melt cycle of the glacier (even though the magnitude of these diel fluctuations may be quite variable and largely unpredictable). If macroinvertebrates had adapted to this predictable regime, we might not expect to find a large effect of daily fluctuations in discharge on the macrofauna. However, we did indeed find significant relationships between faunal metrics and all 3 discharge parameters (mean, maximum, mean maximum), calculated for periods from 3 to 45 d prior to sampling (Fig. 5A–C). These discharge parameters were all highly correlated across all period lengths (all $r_p > 0.85$). Consequently, we could not distinguish between short-term and longer-term effects of flow on the fauna. However, these results enhance the robustness of our finding that flow events do indeed drive temporal variability in the fauna of equatorial glacier-fed streams.

If disturbance level varies among sites, simple CVs in faunal metrics may not allow us to disentangle the effect of disturbance level from that of taxon richness on community stability, even if we increased explanatory power by including more sites. Regressions between quantified disturbances (flow events) and faunal metrics should better reflect relative community response. However, the slopes of these regression lines, i.e., the effect of flow events on the faunal metrics, also did not differ significantly among the 3 stream sites (Fig. 6A–C). The explanatory power of flow was not significant for any faunal metric at site A, probably because of overriding effects of other stochastic disturbances in the highly unstable morainic environment at site A.

We did not calculate mean boundary shear stress at the reach scale because the DuBoys equation is applicable only under uniform flow conditions in wide channels ($W/H > 20$) (Schwendel et al. 2010), but the lower mean current velocity, depth, and slope at site A compared to site B should lead to lower shear stress at site A. That combined with a higher skewness index (~refugia space) at site A suggests that a given flow event had less effect on the fauna at site A than at site B. Likewise, if we assume that the lower mean current velocity, higher skewness index, and lower CV in water depth at site C probably diminished the effect of a given flow event on the fauna at site C (thereby reducing the regression slope) compared to site B, then regression slopes for density (Fig. 6A) and community composition (Fig. 6C) should be similar for the 3 sites. In contrast, site C, the most taxon rich, should be the most variable with respect to taxon richness. Thus, these results do not support our expectations of reduced influence of glacial runoff along the stream or the predictions of the diversity–stability hypothesis that high taxon richness should reduce community variability as a response to disturbance. Again, relationships between flow and community metrics seem to be the outcome of a complex interaction between habitat-specific characteristics and differing communities composed of species with different resilience/resistance traits (Füreder 2007).

Future investigators of temporal variability in communities along glacial-fed streams could take advantage of

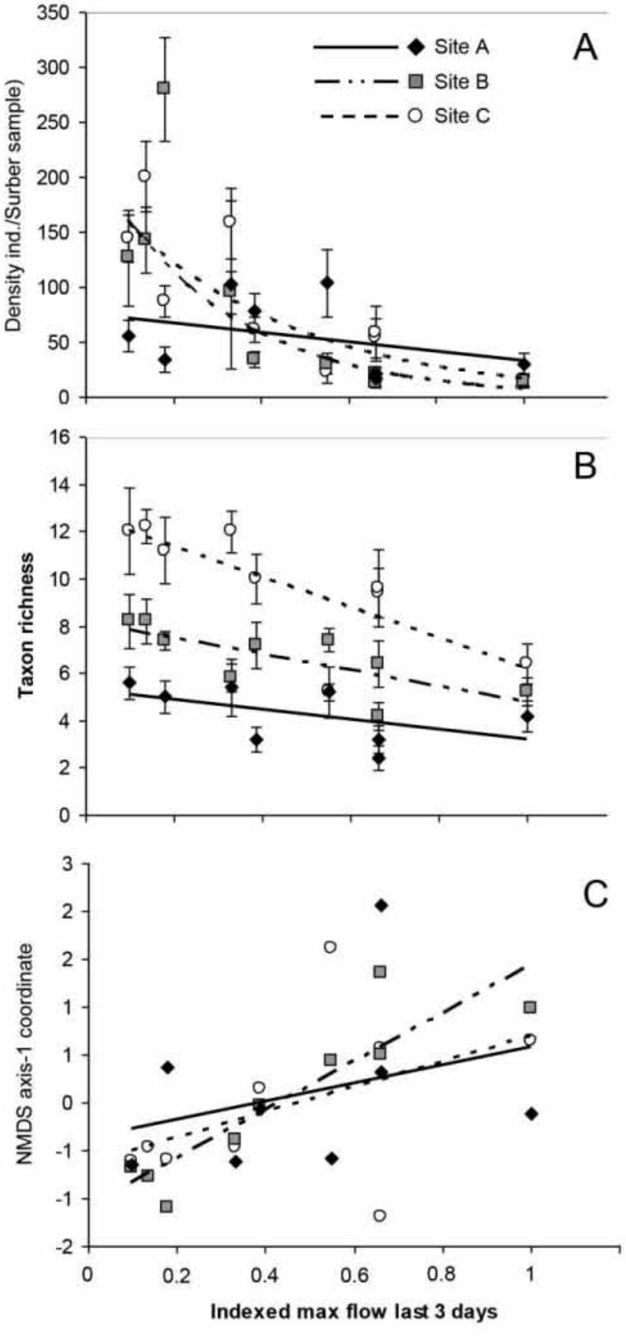

Figure 6. Linear regressions of faunal density (A), taxon richness (B), and nonmetric multidimensional scaling (NMDS) axis-1 coordinates (C) as functions of indexed maximum (max) flow during the last 3 d before sampling benthic macroinvertebrates. Error bars denote SE. Ind. = individuals, max = maximum.

this perfect model system and design studies specifically to test the diversity–stability hypothesis (which was not our goal). We also need to know how species specialized and endemic to glacier-fed streams depend upon and respond to hydrologic regime (Cauvy-Fraunié et al. 2013). Many glaciers are shrinking, and all monitored tropical Andean glaciers are shrinking quickly (Vuille et al. 2008). Glacial shrinkage certainly will cause changes in the hydrological regime of meltwater streams (Milner et al. 2009), but the nature of such changes may be highly stream- and region-specific. Therefore, predicting effects of glacial shrinkage on aquatic communities will be challenging. Nevertheless, understanding how benthic communities respond to hydrological regime and disturbances is a prerequisite for subsequent predictions of consequences of tropical glacier melting on diversity, composition, and stability of communities in glacier-fed streams.

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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).

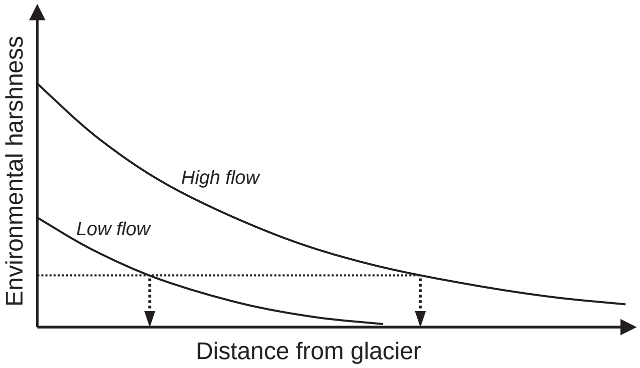

Fig. 1 Conceptual diagram illustrating how the same level of environmental harshness in glacier-fed streams will be found at different distances from the glacier, depending on actual flow (discharge), assuming that environmental harshness declines along the stream and increases with flow.

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.

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

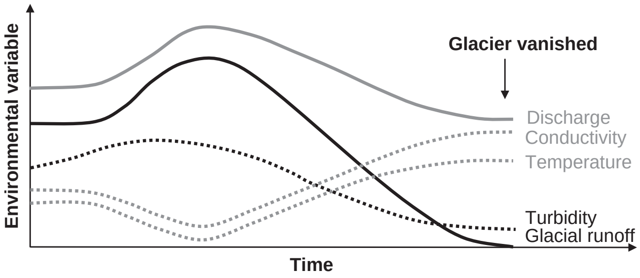

Fig. 2 Conceptual diagram illustrating the expected temporal changes in selected environmental parameters at any point along a glacier-fed stream during glacial shrinkage.

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

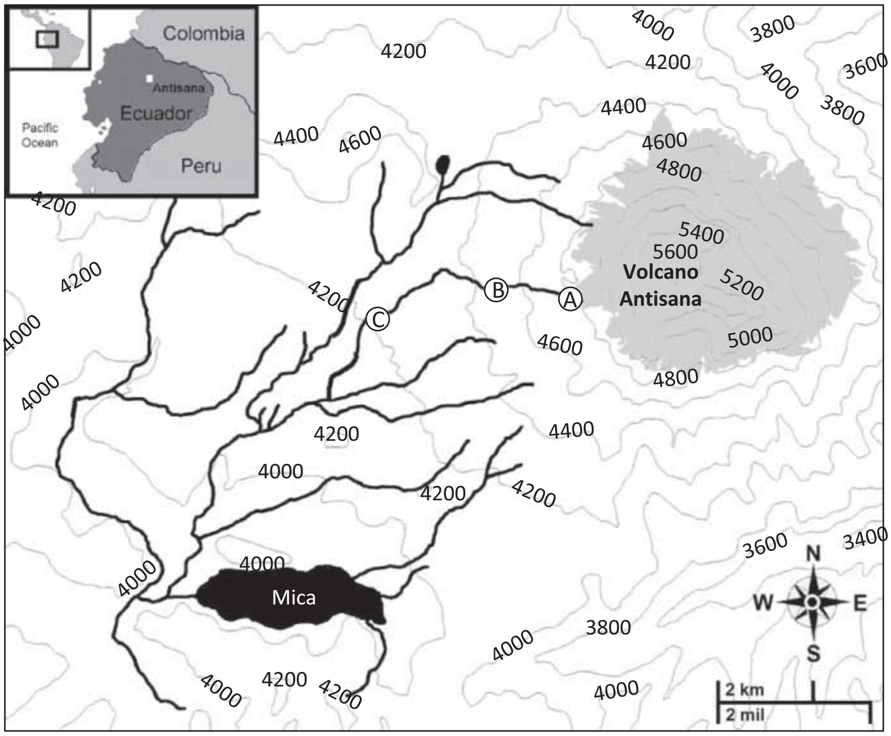

Fig. 3 Map of the Antisana stream system. Letters A, B and C indicate the locations of the three study sites along the stream draining the Crespo glacier.

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

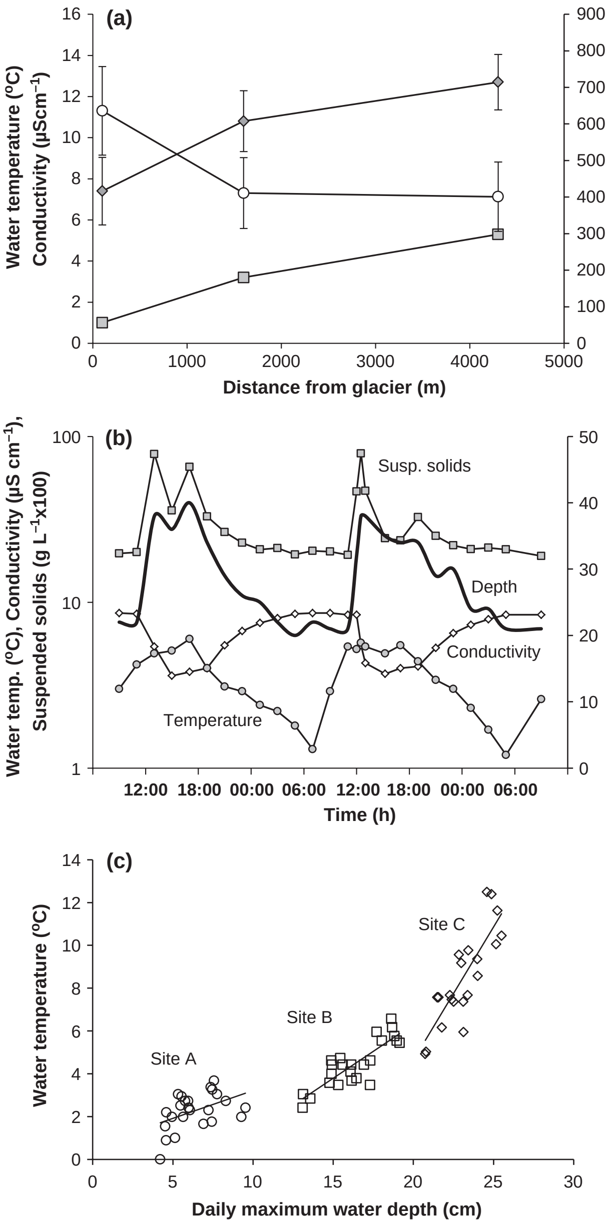

Fig. 4 Spatiotemporal variability in environmental parameters in the Ecuadorian, glacier-fed Crespo stream. (a) Mean water temperature, turbidity and conductivity at the three study sites versus distance from the glacier. (b) Water depth (thick line), suspended solids (filled squares), conductivity (open 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).

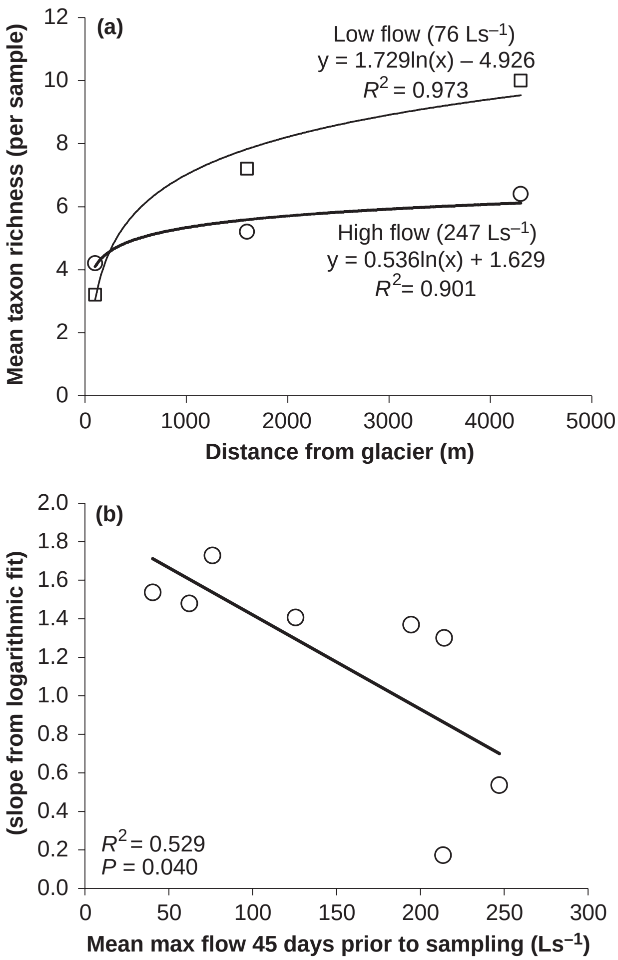

Fig. 5 Taxon gain along the Ecuadorian Crespo stream and its relation to flow. (a) Taxon richness as a function of distance from the glacier. Data from two sampling occasions with different mean maximum flow during the 45 days prior to sampling are shown. A logarithmic function is fitted to the data. (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

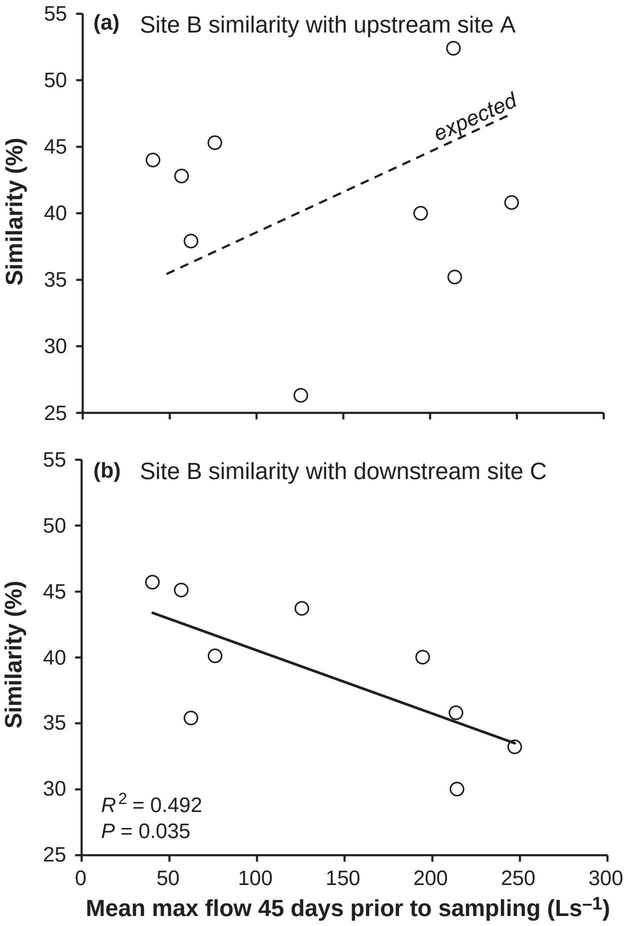

Fig. 6 (a) Similarity (Bray–Curtis on log $x + 1$-transformed data) between benthic macroinvertebrate assemblages at site B on each sampling occasion and the 'mean assemblage' at site A (all dates from site A pooled) versus mean maximum flow (measured at site B) 45 days prior to sampling. The expected 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.

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).

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

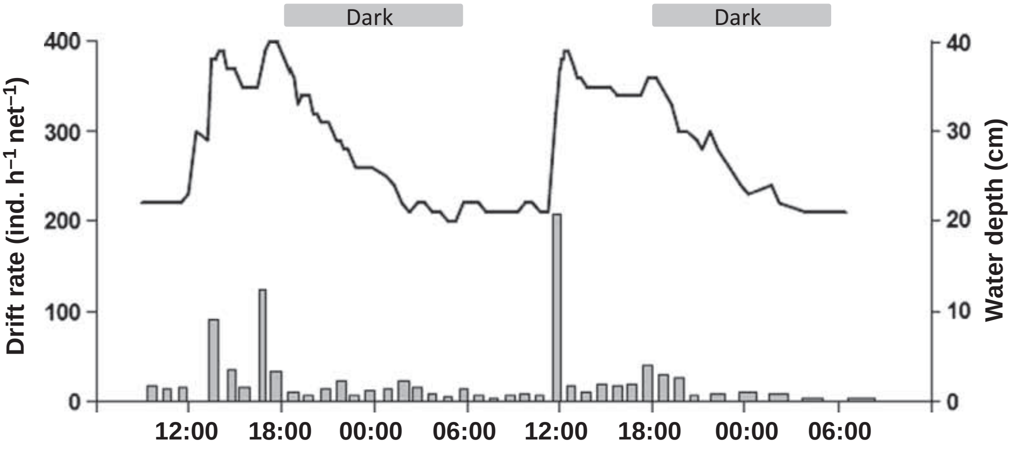

Fig. 7 Mean drift rate (from two nets) measured approximately hourly together with continuous data on water depth during a 48-h period at site B.

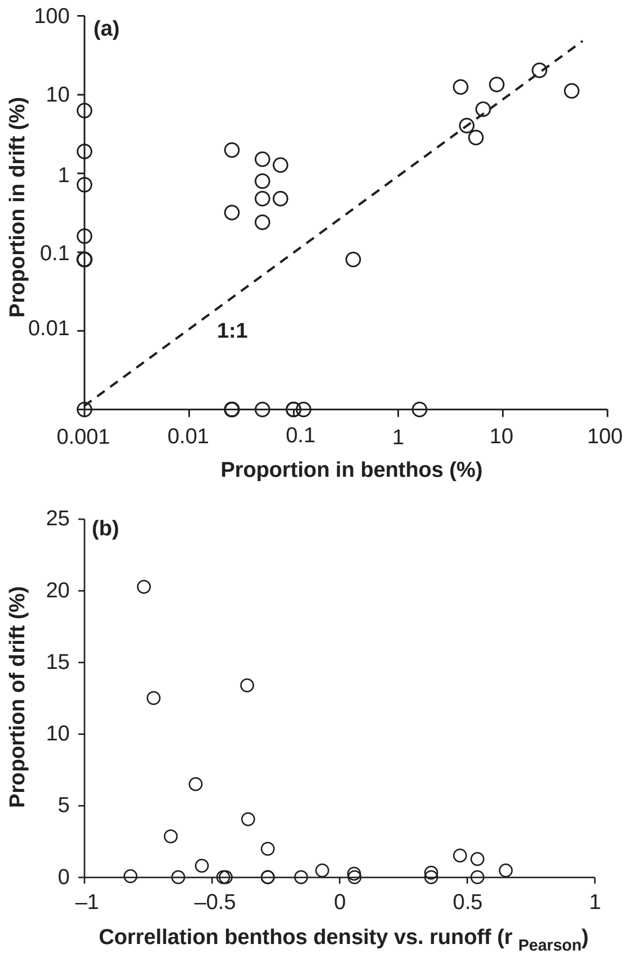

Fig. 8 Drift in relation to benthos. (a) Overall proportion of each taxon in drift versus benthos, all samples pooled. (b) Overall proportion in drift versus the effect of flow on the density of the taxon in benthos (Pearson's correlation coefficient). Only taxa occurring on at least two sampling dates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