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Impacto de las captaciones de agua en la integridad ecológica y posibles soluciones para el manejo del flujo de agua en ríos de páramo.

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Impacto de las captaciones de agua en la integridad ecológica y posibles soluciones para el manejo del flujo de agua en ríos de páramo.

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Dedicatoria

Con mucho cariño para Bárbara y Ezequiel

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Resumen

El manejo actual de las fuentes de agua que abastecen a la capital y sus alrededores, es sin duda alguna una de las principales preocupaciones para la dotación de agua futura, de un ecosistema que provee cerca del 85% del agua para el Distrito Metropolitano de Quito. Conocer el impacto que generan las captaciones y regulaciones del caudal en los ríos del páramo de Papallacta constituye la primera parte de esta investigación, seguida de la generación de modelos de hábitats viables como una herramienta para proponer caudales ecológicos en estos ríos. Los resultados demostraron que las captaciones causan un impacto negativo en la integridad del ecosistema, en la composición de la comunidad de invertebrados acuáticos y en la estructura poblacional de una especie de efímera: *Andesiops ardua*. La regulación del caudal mantiene algunos aspectos de la integridad ecológica, modifica la composición de la comunidad y altera la respuesta fenológica de la efímera en estos ríos. La generación de modelos de hábitats viables se realizó aguas arriba de las captaciones en los ríos que no sufren regulación. Se obtuvo que existen claras asociaciones entre la comunidad de invertebrados (riqueza y densidad) y las variables físicas del río. Los modelos de hábitats viables demostraron que la mayoría de invertebrados prefieren altas velocidad, bajas profundidades y sustratos grandes. La modelación a la respuesta a la descarga demostró que con el incremento de caudal dentro de un rango definido, la densidad de la mayoría de invertebrados aumenta.

Abstract

Current stream ecosystems management of water resources that supply the main city and surrounding towns is a major concern for the future water provisioning, from an ecosystem that provides nearly 85% from the drinking supply to the Distrito Metropolitano de Quito. To know the impact of intakes and flow regulation in páramo streams of Papallacta is the first part of this research, followed by generating habitat suitability models as a tool for calculation environmental flows in these streams. Our results demonstrated that intakes cause a deleterious impact on streams ecosystem integrity, invertebrate community composition and population structure of a mayfly *Andesiops ardua.* Flow regulation keeps some of the ecosystem integrity aspects but modifies the community composition and population structure of a mayfly. The habitat suitability models took place in upstream sites of stream with no regulated flow. Community density and richness were highly associated to physical variables; suitable models showed that several invertebrates preferred high velocities, shallow depths and cobbles substrates. Modeling habitats according to flow showed that flow increase between a defined flow range favor most taxa density increase and that these taxa could aid to understand flow variability through low velocities-depths preferences.

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Introducción

El uso y consumo de agua a nivel mundial incrementa en la medida que lo hace el desarrollo industrial y el crecimiento poblacional (WHO, 2008). En la actualidad el 95% de los recursos hídricos disponibles para el uso o consumo humano han sido intervenidos en algún nivel y las principales superficies de cuencas de los grandes ríos están bajo varios tipos de extracciones. La mayor demanda en la actualidad se concentra en la hidroelectricidad, el riego y el abastecimiento humano, sin embargo este orden no necesariamente responde al orden de importancia reconocido por la Naciones Unidas e implementado por varios gobiernos (WWWR, 2010). Por años la sociedad, los investigadores y los gestores han buscado un mecanismo de integración entre la demanda y la oferta, un mecanismo que reduzca la presión sobre el recurso sin desatender el abastecimiento. Estos acercamientos se han sintetizado en una temática que recoge la ecología y la hidrología de los ecosistemas con la finalidad de reconocer la capacidad de oferta natural del ecosistema y confrontarla con los tipos de usos. Los caudales ecológicos constituyen este concepto/herramienta que ha tenido acogida en varios países de los hemisferios del Norte y del Sur, sin embargo todavía no ha tenido una amplia aplicación en países de la región tropical y Andina. Los países de América Latina cuyas principales ciudades están abastecidas por fuentes que se ubican en las montañas que conforman los Andes, enfrentan a menudo una fuerte presión por el recurso hídrico y el suelo de este ecosistema (páramo). Los páramos en el caso del Ecuador como en Colombia y Venezuela, constituyen la principal fuente de agua para la capital y sus pueblos aledaños (Buytaert *et al*., 2006). La Empresa Pública Metropolitana de Agua Potable y Saneamiento posee en este ecosistema grandes infraestructuras de dotación de agua y proyectos futuros para suplir la demanda prevista hasta el 2050 (EPMAPS, 2005).

A pesar de la creciente demanda por el recurso y la importancia de los páramos para la dotación de agua, se conoce muy poco en cuanto al funcionamiento y diversidad del ecosistema acuático (Jacobsen 2008). En el año 2006 la EPMAPS propuso incorporar a su operación los caudales ecológicos como una medida de mitigación actual y de prevención para los futuros proyectos. Los métodos de aplicación para definir regímenes de caudales ecológicos son amplios y variados y dependen de las condiciones intrínsecas de las operaciones, el ecosistema y la capacidad e interés por el manejo (Tharme, 2003). En este caso, se decidió iniciar la investigación con una evaluación del impacto de las captaciones sobre los ecosistemas acuáticos como base para conocer la dirección de los impactos, sus niveles y las especies que formarían el objetivo de protección con el régimen de caudales ecológicos. Posteriormente, se construyó modelos para definir las condiciones que deben tener los hábitats en los ríos de manera que alberguen densidades óptimas a través de las preferencias por las variables hidráulicas o físicas de los propios hábitats.

La aplicación de esta investigación esta en presentar los impactos que tienen las captaciones en los diferentes componentes del ecosistema y contrastar esos resultado con los modelos de hábitats, para demostrar las condiciones que son viables para las taxa en estos ríos y bajo que caudales estas condiciones se podrían mantener de acuerdo a las variables físicas que conforman dichos hábitats.

INVERTEBRATE RESPONSE TO IMPACTS OF WATER INTAKE AND FLOW REGULATION IN HIGH ALTITUDE PARAMO STREAMS

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ABSTRACT

Freshwater ecosystems provide water for a wide range of humans needs (*e.g.* potable water for cities and towns). Nevertheless, water intakes and flow regulation in rivers and streams also represent a threat to the structure and function of aquatic ecosystems. We investigated the impact of intakes and reservoir regulation on the ecosystem integrity, invertebrate's community and population structure of flow sensitive taxa, in four high-altitude tropical streams of Ecuador. We monitored physical and chemical parameters as well as invertebrate benthos during two years in the streams from the water supply system of Quito. We found that water intakes have severe effects on ecosystem integrity; however, some of these effects were ameliorated through the constant contribution of flow from the upstream reservoirs. Flow alteration due to water intakes changes invertebrate's community composition with a major impact found in taxa richness at downstream sites, especially in streams with unregulated flows where several invertebrates were no longer present in the stream (i.e: *Contulma* sp. *Nectopsyche* sp. *Hydroptila* sp.). Our population analysis for a widely distributed mayfly *Andesiops ardua*, suggests that flow alteration and reduction could be responsible for phenological changes in this population. Although nymph developmental timing remained the same for upstream unregulated site, stage specific synchronicity was lost in downstream site. In conclusion, our study suggest that water intakes have a strong effect on aquatic insect communities, populations and overall integrity of these ecosystems; therefore, we propose that flow should be managed in a way that contributes to the maintenance of overall ecosystem integrity and consequently to the conservation of water services for the future.

Key words: Aquatic invertebrates, ecosystem integrity, flow regulation, intakes, páramo, tropical streams.

RESUMEN

Los ecosistemas acuáticos proveen agua para una serie de necesidades humanas (ej. agua potable para ciudades y pueblos). Sin embargo, las captaciones de agua y la regulación del flujo en ríos y arroyos también representan una amenaza para la estructura y el funcionamiento de los ecosistemas acuáticos. Hemos investigado el impacto de las captaciones y la regulación por reservorios en la integridad del ecosistema, la comunidad de invertebrados y la estructura poblacional de taxa sensibles al flujo, en cuatro ríos tropicales de altura del Ecuador. Monitoreamos parámetros físicos y químicos así como invertebrados del bentos, durante dos años, en ríos del sistema de abastecimiento para la ciudad de Quito. Encontramos que las captaciones tienen severos efectos en la integridad del ecosistema, sin embargo algunos de estos efectos se pueden aminorar a través de la contribución constante de flujo de los reservorios ubicados aguas arriba. La alteración del flujo debido a las captaciones cambia la composición de la comunidad de invertebrados, con mayor impacto en la riqueza de los sitios aguas abajo, especialmente en ríos no regulados, en donde varios invertebrados ya no se encuentran presentes en el río (ej: *Contulma* sp. *Nectopsyche* sp. *Hydroptila* sp.). Nuestro análisis de la población, con la efímera *Andesiops ardua*, sugiere que la alteración y reducción del flujo podría ser responsable de los cambios en la fenología de esta población. Aunque el patrón de desarrollo de los estadíos ninfales se mantuvo igual en el sitio aguas arriba no regulado, la sincronizidad de los estadíos se perdió en los sitios aguas abajo de la captación. En conclusión, nuestro estudio sugiere que las captaciones de agua tienen un fuerte efecto en las comunidades y poblaciones de insectos acuáticos y en general en la integridad de estos ecosistemas; por ello, proponemos que el flujo debería manejarse de una manera que contribuya al mantenimiento de la integridad ecológica en general y consecuentemente a la conservación del servicio de agua para el futuro.

Palabras clave: Captaciones, integridad ecosistémica, invertebrados acuáticos, páramo, ríos tropicales.

INTRODUCTION

The steep increase in demand of water for human use and consumption represents a major threat to the integrity of aquatic ecosystems and to the quantity of available water. Nowadays, managers face innumerable water conflicts, most of them related to overexploitation of water resources and degradation of aquatic ecosystems (Postel, 2000). Fueled by the urgency to attend human needs, water transfers and diversions have become an increasingly used practice with little or no accounting of environmental impacts. Access to safe drinking water is recognized as a universal right, but this goal set by the United Nations (WHO, 2003) should also consider the collateral effects of environmental impacts on aquatic ecosystems and their implications on present and future water availability. From this perspective, the extent to which water intakes affect the ecological integrity and functioning of streams and rivers, likely depends on many factors such as flow management regime, type and size of infrastructure, and interactions with other human disturbances. In this paper we analyze the impacts of water removal on the benthic macroinvertebrates communities of high-altitude Andean streams, a primary source of drinking water for a large population settled in the northern Andes of South America, and assess if these impacts can be modified by the use of dams (upstream reservoirs) to regulate the flow of water before the intake.

Water shortages and the loss of aquatic biodiversity and ecosystem function around the world (Dewson *et al.*, 2007a) have forced countries to manage water resources with a precautionary approach, promoting the exploration of different approaches for the determination and assessment of environmental flows. This concept seeks to maintain ecosystem functionality in space and time based on a flow regime that keeps enough water in the streams with a natural fluctuation through time (Tharme, 2003). Although the systematic application of this concept is relatively new, we already have good examples of efforts that incorporate environmental flows concepts and methodologies in the management of water resources at the national level such as the South African Water Act (Richter and Postel, 2004), the European Water Framework Directive (Acreman and Ferguson, 2010), the Australian Water Law (Tisdell, 2001) and the Clean Water Act (MacDonnell, 2009), among others. However, most preliminary efforts to manage environmental flows were largely limited to hydropower plants settings, with the objective of maintaining and restoring populations of economically relevant fish species (Jowett and Richardson, 1995) and only later there were new efforts that evaluate other biological (e.g. invertebrate) responses with a non-economic perspective (Gore *et al*., 2001). The need to set environmental flows also defined the path for the development of new methods and approaches. Temporal variation in hydrology represents a key variable to relate to ecosystem functioning as long as it maintains the natural stability of stream ecosystems (Poff and Zimmerman, 2010). But as a promising as it seemed, environmental flows assessment hasn't had the same widespread application in current projects of water diversion for human consumption, as it has had in hydropower generation settings. Therefore, assessment of environmental flows in water intake and flow regulation projects represent an extended field of research aimed at understanding biotic and ecological responses to artificial and natural alterations of flow regimes, and defining key flow regime requirements to maintain stream ecosystems integrity.

A wide range of responses to flow alteration has been reported for ecosystem components (*e.g*. fish, invertebrates, macrophytes and periphyton) in temperate streams from the northern and southern hemispheres (Hart and Finelli, 1999; Cortes *et al.,* 1998; Bunn and Arthington, 2002; Dewson *et al*., 2007b; Chessman *et al.,* 2008), whereas, few studies have assessed this topic for fish and invertebrate assemblages in tropical streams (Baptista *et al*., 2001; Anderson *et al*., 2006). As a general principle, the responses of benthic communities to flow alteration depend on the nature of hydrological cycles which, in temperate streams, usually exhibit clear and marked seasonality (Lytle and Poff, 2004), specially in intermittent streams where invertebrates are adapted to natural floods, droughts and supra – droughts (Lake, 2003; Acuña *et al*., 2005; Lytle *et al*., 2007; Stubbington *et al*., 2009; Fenoglio *et al*., 2010). In contrast, water regimes in tropical streams might be non-seasonal or have little seasonality (dry and wet seasons) related to the global climate inter-annual fluctuations (ITCZ), and, therefore, invertebrates might show distinct adaptations and life histories strategies that haven't been documented.

Notwithstanding, hydrographs from both zones are expected to change according to the nature of the hydrological disturbance, as has been shown in the responses of ecosystem components in temperate streams affected by dams (Hart and Finelli, 1999; Bunn and Arthington, 2002; Cortes *et al*., 1998; Vallania and Corigliano, 2007), irrigation withdrawals (Cortes *et al.,* 2002; Dewson *et al*., 2007b; Miller *et al.,* 2007;James *et al.* 2009) and water intakes for drinking supply (Chessman *et al*., 2009).

Environmental flow studies carried out in tropical streams are mainly related to the operation of dams for hydropower (Baptista *et al*., 2001; Anderson *et al*., 2006). This emphasis, however, does not reflect another increasing pressure on water resources, represented by the withdrawal of water for irrigation and human consumption. This has drawn our attention towards the need to look into water supply systems and the effects of water abstractions on aquatic ecosystems, with special attention paid to mountain ecosystems that are strategic in terms of water supply, and extremely sensitive from an ecological perspective. In this context, here we concentrate on water supply systems of high-altitude tropical streams of the Andean páramo ecosystems of northern South America.

The Andean páramo ecosystems are an emerging source of economic opportunities including cattle grazing for small farmers, community-based tourism, and hydropower generation and, at the same time, water supply for more than 10 million people from the main cities of Ecuador and Colombia (Buyatert *et al*., 2006). The potential use of these opportunities, however, depends on the balance between the maintenance of the ecological peculiarities on these ecosystems, and the demands and pressures that we are exerting on them. On one hand, páramo streams are characterized by permanent flows (Buytaert *et al*., 2006; Jacobsen, 2008), which mostly result from weather patterns and the extraordinary water storage capacity of the soils and vegetation of this ecosystem. On the other hand, growing population demands have increased pressure to extract more water from these poorly known ecosystem (Jacobsen, 2008) while, at the same time, aggressive agriculture, fire, and grazing threaten the integrity of soil and plant communities on which water regulation depends (Poulenard, 2001; Podwojewski 2002; 2008). Moreover, the Andean páramo has been recently acknowledged as a climate change regulator (Buytaert *et al*., 2006), but our understanding of its ecosystem functioning, resilience, and resistance to degradation is rather poor, and our attempts to collect information do not progress at the same rate as the construction of new intakes and other human activities.

Besides the ecological conditions of the páramo stream ecosystems and their surroundings, the impact of water diversions on benthic fauna will also depend on the type of flow regimes management implemented at the upstream and downstream sections of the water withdrawal infrastructure. From this perspective, a management alternative that could modify the impacts of water withdrawal is the establishment of upstream reservoirs intended to regulate water flow before the diversion point. Despite the potential benefits of this alternative, to this date we have very little information on the impacts of water regulation on the integrity and functioning of these ecosystems. In this context, our research seeks to address the current changes that might be taking place in high-altitude tropical streams used for water supply in the northern Andes. More specifically, we analyzed streams that are being used for the Water Supply System of Quito, inside the Cayambe – Coca National Park, that have no direct human disturbances other than water intakes and flow regulation. To cover as much of the potential effects of flow alteration, we propose a treatment template based on the type of flow management (unregulated and regulated streams) and the stream site (upstream and downstream of intakes). Our objectives have different ecological approaches on the same template: 1) to evaluate changes on ecosystem integrity, 2) to identify changes in invertebrate's community composition and 3) to identify changes on the population structure of a sensitive flow taxon.

FIELD METHODOLOGY

Study area

The study was conducted in high-altitude streams running through páramo ecosystems in the northern tropical Andes of Ecuador, roughly located at 69 km east of Quito city (Figure 1). The study streams belong to the catchments of Sucus-San Juan and Chalpi Grande, which drain into the Papallacta basin, in the headwaters of the Napo River basin, in Eastern Ecuador. The stream reaches selected for this study are located around 3700 m of altitude and surrounded by typical páramo vegetation dominated by a matrix of tussock grasses and sclerophylous shrubs (Luteyn, 1992; Sklenar, 2006). Headwater streams morphology is characterized by narrow and deep channels, steep slopes and high water velocities. Climatic patterns in the area are characterized by a mean daily temperature of 8.3°C and an annual precipitation of 1528 mm (INAMHI, 2008). The study area provides nearly 85% of the drinking water supply to the Metropolitan District of Quito through the diversion of water from the Atlantic system to the Pacific drain (EPMAPS, 2008).

Survey design

Our study had the dual purpose of evaluating the impacts of water intake on stream benthic fauna, and the extent to which these impacts could change as a result of two different management systems represented by “unregulated” streams which flow freely before the water intake, and “regulated” streams where flow is controlled by an upstream dam and then diverted by water intakes. In this context, we selected four streams, all with water intakes, two of them with an upper reservoir for flow regulation (Sucus and Mogotes streams) and two with natural unregulated flow (San Juan and Chalpi Norte), no upstream reservoirs. Within each stream we selected sampling sites located upstream and downstream of the water intakes (Fig. 1), with the specific location of each sampling point depending on accessibility and stream characteristics. Average distance between each sampling point and the water intake was ≈200 m, except for the downstream site of Mogotes stream that was located relatively far away from the intake (~1200 m), due to a vast area of wetlands immediately after the intake that made impossible to access to a closer site. We monitored all sites every three months from September 2006 to September 2008.

Hydrological sampling

Flow measurements were conducted on a monthly basis for several depth profiles at each stream section, with a Universal Current Meter Equipment F1 (Eijkelkamp, Agrisearch Equipment, Empresa Pública Metropolitanana de Agua Potable y Saneamiento EPMAPS, and Institut de Recherché pour le Developpment, IRD). During the research period hydrological data were obtained from calculations of point flow measurements and water level recording. Flow measurements at upstream sites were obtained from the monthly hydrological monitoring program conducted by the EPMAPS, for almost two decades. Downstream sites were sporadically measured until September 2006, when monthly point flow measurements started. Based on this information hydrographs were constructed using historical long-term data set from upstream sites and the available data from downstream sites.

Physical and chemical sampling

At each stream site we measured several physical characteristics including width, depth, velocity and dominant substrate type (Wentworth scale). Current velocity was estimated with a

Universal Current Meter Equipment F1, N°141702 propeller (Eijkelkamp, Agrisearch Equipment), while depth was measured with the current meter rod at each velocity profile, where we also reported substrate composition at the sampling area. We measured *in situ* pH, temperature, conductivity, and dissolved oxygen concentration with a Multiparameter Meter (HACH SensIon 156). Water samples for chemical analysis were collected in 500 ml glass bottle and a 1000 ml plastic bottle, previously rinsed with 10% HCl. Water samples were cooled and delivered to the laboratory during the next 4 hours. Chemical analyses were performed by the EPMAPS Water Quality Laboratory (Turbidity, PO_4, Cl^-, NO_3^-, Al, Fe^+) following standardized protocols.

Biological sampling

To assess the influence of water intake and regulation on benthic communities, we took three surber samples (net size 0.0625 m^2, 500 µm) every three months at each site, taking into account different mesohabitats (runs, riffles, pools and glides) to include as much habitat heterogeneity as possible. For the surber sampling we selected mesohabitats proportionately to their representation of the stream reach. Before placing the net, substrate composition of each mesohabitat was carefully described, and sampling was carried out by removing the surface substrate and scraping some of the cobbles. Gravel and fine gravel collected inside the net were transferred into a 5000 ml bucket to rinse-off the invertebrates attached to the substrate surface. When present in the surber sample, macrophytes were also added to the bucket and sifted again in the net to reduce the sample volume. Finally, we gathered all the invertebrates from the bucket in a small surber net (same characteristics) and then placed them in 0.8 lt jars, with stream water and 5 to 10 ml of 4% formaldehyde for preservation. In the laboratory (EPMAPS), invertebrates were identified to the lowest possible taxonomic level (genera), using 4x and 8x stereoscopes and available regional keys (Fernández and Domínguez, 2001).

DATA ANALYSIS

Ecosystem Integrity

To evaluate the effects of flow alteration on the ecosystem integrity of the streams, we evaluated through time hydrological, physical, chemical and biological variables. We constructed hydrographs for each stream using monthly discharge data at upstream and downstream sites, when data was available. Effects on flow caused by intakes and reservoirs were analyzed with repeated measures ANOVA, where the response variable was monthly discharge and the factors were *type of flow* (two levels: unregulated and regulated), *stream site* (two levels: upstream and downstream) and *time* was considered as a between-subject factor. Hydrological data was tested for normality and there was no need for transformation. Additionally, we analyzed physical variables (velocity, depth and substrate type) with a Non-Metric Multidimensional Scaling (NMMS) analysis to assess if sites cluster according to the intake and/or regulation effects on velocity, depth and substrate. Chemical variables were analyzed through a Principal Components Analysis (PCA), on previously normalized data (PRIMER – E, 2006). We evaluated if sites from streams with different type of flow cluster or not according to particles an ions present in the water column. The biotic quality of streams was evaluated using the Andean Biotic Index developed for Ecuadorian and Peruvian páramo streams (Acosta *et al.*, 2009). The Andean Biotic Index ABI is based on the BMWP-Col index of Colombia and adjusted for high altitude tropical stream invertebrate's taxa. ABI scores were analyzed with repeated measures ANOVA to compare water quality between streams and the perturbation level on the aquatic ecosystem through time (Appendix I).

Community composition

Effects of intakes and flow regulation in the community composition of invertebrates were evaluated through invertebrate density and taxa richness. We performed a one –way ANOSIM (PRIMER – E, 2006) between upstream sites of unregulated and regulated streams to assess potential differences in community assemblages. We performed a repeated measurement ANOVA for the selected community metrics, with time as the repeated measurement factor, type of flow with two levels (unregulated and regulated) and stream sites with two levels (upstream and downstream) as factors, and density/taxa richness as the response variable, to asses potential changes between levels of factors (STATISTICA, 2009). Data was tested for normality and transformed ln (x+1), when needed. To identify dominant taxa at stream sites according to the type of flow we performed a dominance plot (rank-abundance) analysis, from which we selected the dominant taxa present in all stream sites at all type of flows. We looked for variation through time, type of flow and sites for several taxa known as flow sensitive.

Population Structure

Effects of intakes and flow regulation were also analyzed at population level, using data of flow sensitive taxa. Among these, we searched for species that occurred in higher densities in our studied streams and that exhibit clearly differentiable nymphal stages to describe species phenology. Specifically, we selected the mayfly *Andesiops ardua*, and performed population structure analysis based on the comparison between different nymphal stages of this species. We classified the nymph stages according to the wing pad development into four stages (as in Delucchi and Peckarsky, 1989). We used the stage specific density to compare between dates at two streams with different types of flow: San Juan (unregulated) and Sucus (regulated), and within stream at upstream and downstream sites. We used a generalized linear model (GLM) with untransformed data to look into changes of stages' densities. The model was constructed for each stream with density as the response variable, type of flow (regulated and unregulated), stream sites (upstream, downstream), periods (2006 – 2007, 2007 - 2008) and nymphal stages (I-IV) as categorical predictors, and time as the continuous variable. We plotted density stages in several panels according to the date of sampling and the corresponding years to assess changes through time (Fig. 7). We used total density for each nymphal stage from the each sample at the sampling date. We added flow data from sampling dates that responded to the multiannual hydrographs previously constructed, and we drew the nymphal stage total density development for each site in one stream of either category.

RESULTS

Ecosystem Integrity

Overall physical, chemical and biological data suggest a decrease on ecological integrity at downstream sites of intakes in streams with unregulated flows. In contrast, downstream sites at streams with regulated flow showed an improvement of some ecosystem features but not for the integrity of the ecosystem as a whole. Here, we describe the main effects that the intakes and also flow regulation might have on physical, chemical and biological variables and hence on ecosystem integrity.

Although highly variable, monthly measurements of water discharge suggest that hydrological behavior of streams with unregulated flows have a soft bimodal distribution with a high peak during June – August (rainy season) and another lower peak during March and April. In contrast, hydrographs at streams with regulated flows presented a unimodal path with a single peak during June –August (Fig. 2). The hydrological behavior between streams with unregulated and regulated flow is significantly different (ANOVA; $F_{1, 42} = 3.8$, $p < 0.05$) and the differences between stream sites is highly significant (ANOVA; $F_{2, 76} = 11.6$, $p < 0.0001$). The mean monthly percentage of flow diverted by intakes in unregulated streams were of 94% (Chalpi Norte) and 84% (San Juan) and in regulated streams were of 83% (Sucus) and 30% (Mogotes). Regarding stream physical variables, substrate type wasn’t significantly different between types of flow and stream sites. Velocity differences were highly significant between types of flows and significant between stream sites (Table 1). Depth differences were significant between types of flow and stream sites. Upstream sites with unregulated flows had higher velocities and depths than downstream sites. Contrarily, upstream site of the stream with regulated flow (Mogotes) presented lower velocities and depth than downstream sites (Appendix II). Nevertheless, the NMDS showed that, in general, sites share many similar physical characteristics, specifically substrate type, as suggested by the lack of any clear cluster of samples, with the exception of all downstream sites of streams with regulated flows which roughly gathered in the lower part of Axis 2 (Fig. 3). Principal components analysis showed that chemical variables don’t vary between streams with unregulated and regulated flows and between stream sites, where only Turbidity slightly associates sites from unregulated streams PC1: 28.2%, PC2: 17.5% (Fig. 4). The biotic quality of streams evaluated with the ABI scores (Appendix I) showed significant differences for each factor and also with time interaction (Table 2). Hence, biotic quality of streams with unregulated flow decrease as well as the regulated stream Sucus, but this latter maintain a good biotic quality ABI score even under the intake presence in the stream. On the contrary, the regulated stream Mogotes shows a low biotic quality ABI score at upstream and a good biotic water quality at downstream (Appendix I).

Community composition

The invertebrate community assemblages differed among streams with different types of flow (ANOSIM: $R = 0.021$; $p < 0.05$). Density at downstream sites of streams with unregulated flows was always lower than at upstream sites, and density at downstream sites of streams with regulated flow was always higher than at upstream sites, except for one date in the first period (December) for Chalpi Norte and one date in the second period (September) for San Juan (Fig. 5) Significant differences in density were observed for streams with different types of flow with and without date interaction. Highly significant differences were observed in stream unregulated and regulated streams and sites through time (Table 3). Taxa richness was significantly different within factors and through time, with lower taxa richness at downstream sites of streams with unregulated flows and one stream with regulated flow (Sucus), and lower taxa richness at upstream sites of one stream with regulated flow (Mogotes). Similar taxa richness pattern though time was observed for both time periods (2006 – 2007 and 2007 – 2008) in all streams (Fig. 5).

Downstream sites at streams with unregulated flows exhibited lower invertebrate richness, with the absence of 11 taxa in San Juan, and 16 taxa in Chalpi Norte; downstream sites at streams with regulated flow showed invertebrate richness decreased for Sucus (31 taxa) and increased for Mogotes (16 taxa).

The dominance-rank curves showed that upstream sites of streams with unregulated flows had a higher percentage of taxa from the Chironomidae family and a greater contribution from *Hyalella* sp. and *Andesiops ardua* (Fig. 6). We found ten taxa present at all sites, and from that, more than 50% of the dominance was composed by several Trichoptera genera (Table 4). Oligochaeta was the only taxon that increased its density at downstream sites of unregulated flows but was not considered as a flow sensitive taxon (Table 4). Density of dominant taxa at upstream and downstream sites of streams with unregulated flows showed a clear pattern of hydrological association, with high densities at upstream sites where flow is available and lower densities at downstream sites where flow is lower (Fig. 6).

Population Structure

In all sites and conditions, *Andesiops ardua* exhibited multiple nymphal stages throughout the year, suggesting either multi-voltine population structure or alternatively, very slow nymph developmental rates (Figs. 7&8). Nevertheless, the population structure of *Andesiops ardua* was different between streams with different types of flow: unregulated flow of San Juan stream (Fig. 7) and regulated flow of Sucus stream (Fig. 8), and between sites and dates. In the unregulated stream (San Juan), nymph development followed the same pattern from one year to the next, with a clear density peak in December of both years (Fig. 7b). Hence, although on every single date we found all nymphal stages, there were more stages I on December of each year, and more black wind pads (last developmental stage) on July (Fig. 7b). After the intake, in the downstream section of San Juan (Fig. 7a), flow and nymphal density were greatly reduced, and there was a clear change in nymphal stage composition (Fig. 7c). Nymph stage I, was almost completely absent in the downstream section of the intake (Fig. 7c), suggesting that flow reduction might affect some nymph stages more than others. While, both sections, upstream and downstream of the intake had an overall peak density in December of both years (2006 and 2007), there is a evident shift in nymph developmental time downstream of the intake suggesting that flow reduction is affecting *Andesiops ardua* phenology and population structure.

In the regulated stream (Sucus), all stages were present through the year, similarly that in a natural unregulated San Juan stream. However, nymph developmental time was completely different, with higher abundance of stages I in June of both years (Fig. 8b). Flow measurements at downstream sites indicate a reduction of almost 1/3 from its natural conditions, compared to upstream sites (Fig. 8a). Contrarily, nymphal densities were higher in the downstream site compared to the upstream site of the regulated stream. Moreover, there was a change on nymphal peak month compared to upstream site, with a peak in March. The two-year period of observations of this taxon suggest that intakes and regulated flow generate an effect on this taxon's phenology and population structure.

DISCUSSION

Ecosystem integrity

Our results demonstrate that overall ecosystem integrity of the studied páramo streams were negatively affected by water intakes, especially in streams with unregulated flows. Ecosystem integrity in streams with regulated flows is influenced by the reservoir regulation which generates a temporary buffer condition for intakes, and natural high and low flows caused an erratic base or permanent flow that somehow mimics the flow upstream and has increased the ecosystem resilience to face artificial and natural low flows. This result is consistent with the patterns previously reported by Cortes *et al*. (1998) and Lytle *et al*. (2007), who found that ecosystems features such as invertebrates, algae and water quality respond positively to permanent flows. The high percentage of flow removal in streams with unregulated and regulated flows reflects the need to attend the city's water demand, during the dry season from the Pacific drain that matches the rainy season from the Andean páramo. Several consequences of decreased flow revised in Dewson *et al*. (2007a) match our results for different levels of impacts according to the extent or percentage of flow removal.

Regarding to the effects of intakes and flow regulation in stream physical variables, we found that velocity was a clear indicator of flow alteration, a similar pattern that has been previously suggested by Wilcox *et al.* (2006). Velocities were lower at downstream sites of intakes in streams with unregulated flows and lower at the upstream site of the streams with regulated flows (Mogotes). This latter pattern might be caused by reservoir regulation, and is consistent with the results reported by Cazaubon and Giudicelli (1999) who found that reservoir could have residual or compensation flows that are unlikely to be similar to natural flows. Our results also suggest that depth reflects the effect of flow reduction caused by intakes in streams. Lower depths were found at downstream sites of streams with unregulated flows, but no generalization was feasible at downstream sites of streams with regulated flows (Mogotes). Streams in this research have similar substrate types, although sediment accumulation at downstream sites due to intake flushes, might explain partly the observed density of Oligochaeta.

We found that water chemistry wasn't affected by intakes and reservoir regulation. Cazaubon and Giudicelli (1999) found that under permanent flows, water quality doesn't change; therefore, under different types of flow alteration, responses could depend on the upstream management of flows. Although, changes in temperature due to flow alteration could be expected in some cases as reported in Miller *et al.* (2007), we didn't find that temperature, pH, conductivity, and/or dissolved oxygen concentrations were responsible for any difference between streams and sites.

Biotic quality of streams, evaluated through the Andean Biotic Index that uses invertebrate's identity, was an optimal indicator of the ecosystem disturbance caused by intakes because, as suggested by Baptista *et al*. (2001), ultimately impact of intakes affects the stream biota. ABI scores at downstream sites of streams with unregulated flows were poor as a result of highly resistant taxa that subsist a 90% of flow removal (e.g. Oligochaeta, Chironomidae). Contrarily, at downstream sites of streams with regulated flows, we found high ABI scores accounting for a biotic quality improvement (e.g. *Atopsyche* sp. *Metrichia* sp. *Andesiops ardua*). The most obvious difference between downstream sites of streams with unregulated and regulated flows reflects the distinction observed in physical variables (velocity and depth), according to the type of flow. The availability of habitats observed at downstream sites of streams with regulated flows are maintained or even increased by the flow control of the reservoirs. The flow levels registered in these sites can increase the input of food resources, explaining the higher biotic quality (Biggs *et al*., 2005; Takao *et al*., 2008). The biotic community at downstream sites of streams with unregulated flows should be similar as the upstream sites if habitats became available and water chemistry creates suitable conditions under certain flow variability (Miller *et al.,* 2007). Overall ecosystem integrity changes on páramo streams are a synergistic result of the effects of flow variability reduction and water quantity removal.

Community composition

Our results demonstrated that the composition of invertebrate's communities at páramo streams is affected by the presence of water intakes and flow regulation from reservoirs. We found differences in community assemblages between streams with unregulated and regulated flows, caused by the base (permanent) flow releases in streams with regulated flows, as reported by Bunn and Arthington (2002), Fleituch (2003) and James *et al.* (2008). Bunn and Arthington (2002) and Lytle *et al*. (2007) found that communities are adapted to flows by synchronization of phenology to variability. Our results suggest that densities at upstream sites of streams with unregulated flows show clear synchronization with timing of natural low flows in September and December. At the downstream sites densities appear to be lower but still synchronized to flows in a different scale. Upstream sites of streams with regulated flows had no response to low flows of December as seen in unregulated flows, but high densities found in September do respond to the expected pattern of natural low flows from the beginning of the low flows season. At downstream sites of streams with regulated flows, densities are clearly synchronized with flows as expected during natural low flows (Lytle *et al.*, 2007), and also presented higher densities than upstream sites throughout the year. Although, we have little to no information on high-altitude invertebrate's response to flow disturbances, we found that at downstream sites of streams with unregulated flows, density maintain its synchronization pattern to flows as in upstream sites, even when densities were lower and belonged mostly to resistant taxa. But in the case of streams with regulated flows, an unsynchronized response is observed at the upstream site while synchronization to flow was clear at downstream sites.

Invertebrate's richness at páramo streams was reduced by the effects of water intakes at downstream sites of streams with unregulated flows. Interestingly, overall taxa richness was higher in streams with regulated flows than in streams with unregulated flows, demonstrating that flow regulation has a stronger effect than intakes. We suggest that higher invertebrate's richness found at upstream and downstream sites of streams with regulated flows are partly due to the higher stability of available habitats which result from the permanent presence of flow in this sites as seen by Baptista *et al.* (2000), Fleituch (2003), Miller *et al.* (2007), and Effenberger *et al.* (2008). Biggs *et al.* (2005) also suggest that effects of flow removal in a large temporal scale might reduce the small scales variation.

Our inter annual analysis shows that intakes and flow regulation from reservoirs cause invertebrate's richness community to decrease and increase (Miller *et al.,* 2007; James *et al.,* 2008) and that these patterns are sustained in time concomitantly with Sttubington *et al.* (2009) who observed that inter annual diversity depends on water volume. As previously documented in literature the wide range of responses from different sites could be the result of differential sensitivities of different invertebrate species, whose life strategies could allow them to respond to artificial flow regimes (Poff *et al*., 1997; Boulton, 2003). We observed that flow sensitive taxa disappeared at downstream sites of streams with unregulated flows (i.e. *Contulma* sp*., Baetodes* sp.*,* *Ochrotrichia* sp., *Atopsyche* sp.) and were replaced by resistant taxa such as Chironomidae and Oligochaeta, which is consistent with observed results from Miller *et al.* (2007), who reported species replacement in response to alteration of flow patterns.

Dominant taxa at upstream sites of streams with unregulated flows (i.e. *Andesiops ardua* and *Hyalella* sp.*)* showed a clear density decrease but no disappearance at downstream sites, while a great part of the community was almost extirpated. Downstream sites of streams with unregulated flows were dominated by worms (Annelidae) and only few insect species. The reasons for these changes in richness as well as the lower densities found in these sites could be attributed to insufficient food resources and scarcity of refugia, resulting from reduced flow regimes (Hart and Finelli, 1999; Biggs *et al.,* 2005; Fenoglio *et al*., 2010). In this instance, from our findings we can confirm that prolonged dewatering of streams reduce habitat availability and refugia causing severe effects on invertebrate community composition, a pattern reported in many ecosystems around the world (Armitage and Cannan, 2000; Matthaei and Townsend, 2000; Miller *et al*., 2007). Therefore, water intake effects evaluated in páramo streams with unregulated flows, where the disappearance of several invertebrate taxa is a consequence of flow removal, has major implications in the invertebrate's community composition of the Andean páramo ecosystem. Erratic or constant discharges can mitigate the impact of flow removal by reservoirs but intakes have demonstrated to cause an immediate effect downstream (Cortes *et al.,* 2002; Biggs *et al.,* 2005; McIntosh et al 2002).

Flow sensitive taxa appears to dominate upstream sites of streams with unregulated flows, a pattern that can be attributed to high velocities, diverse substrate and suitable depths; similar physical characteristics were found at downstream sites of streams with regulated flows, where the invertebrate community also shared some of the flow sensitive taxa (*Anomalocosmoecus* sp.*, Andesiops ardua* and *Hyalella* sp.*).*This suggests that not only changes in density affect the community composition but it might be taking place a species replacement or loss, favoring resistant taxa (Cortes *et al*., 2002). Downstream sites of streams with regulated flows apparently favor taxa that could completely dominate the community (e.g. *Anomalocosmoecus* sp.). Holomuzki and Biggs (2000) found that Limnephilidae tend to go to the hiporreic zone to avoid high flow disturbances, which is interesting because *Anomalocosmoecus* sp. (Limnephilidae: Trichoptera) at this stream site has been observed to persist through the entire year, even during severe natural high flows and gate opening at the intakes (Figure 2) . Specifically, we found that at upstream site of Sucus (stream with regulated flow), invertebrate richness is higher than any other site, and downstream sites of both streams with regulated flow account for high richness than registered at upstream and downstream sites of streams with unregulated flows. Several authors have suggested that high invertebrate richness is strongly related to habitat heterogeneity (Baptista *et al.*, 2001; Cortes *et al.,* 2002; Boulton, 2003, Effenberger *et al.*, 2008), what could aid to understand what is taking place in this stream as the result of permanent flow and habitat availability in the stream. The effect of flow alteration could be favoring only few populations' density, as reported elsewhere by Cazaubon and Giudicelli (1999), Lytle and Poff (2004) and Vallania and Corigliano (2007).

Population structure

Andesiops ardua has a widespread distribution in the Andean páramo streams (Domínguez and Fernández, 2009) and is a dominant flow-sensitive taxon in this ecosystem. We expected a population response to flow alteration as suggested by Raddum *et al.* (2000), who found mayflies life cycles influenced by flow regimes and temperature. Our findings demonstrate that intakes and reservoir regulation cause different levels of effects on the life-history and phenology of *Andesiops ardua*. Acuña *et al.* (2005) suggest that nymphal stages vary with natural high and low flows, which is consistent with our findings related to all nymphal stages decrease with high flows and increase with low flows. Several authors have found that flush discharges cause drift that increase downstream populations (James *et al.,* 2008; James *et al.,* 2009), which can help us to understand densities of certain nymphal stages in downstream reaches. We observe a temporal displacement of the pattern argued before in the regulated stream (upstream and downstream), a respond that can be compared with similar findings of Delucchi and Peckarsky (1989) for regulated streams.

Our findings demonstrate that, in an overall view throughout two years of data from nymphal stages densities of *Andesiops ardua* population, the phenology of this species has been altered from an upstream site pattern to a downstream site pattern in an unregulated stream (San Juan). A similar respond present the regulated stream (Sucus) but in an opposite direction. It has been suggested that many invertebrates from the tropical and subtropical streams could be multivoltine, univoltine and bivoltine, but as mentioned before for different aspects of high-altitude tropical streams invertebrates, little evidence has been documented on the effects of flow alteration in aquatic insect's life-histories. Life histories and phenology of *Andesiops ardua* could share some aspects of low latitude voltinism and high altitude insect's development (Delucchi and Peckarsky, 1989; Jackson and Sweeney, 1995; Harper and Peckarsky, 2006); this might induce two alternative patterns of phenological behavior of *Andesiop*s *ardua* population: 1) a univoltine life cycle with an extremely slow growth of all nymphal stages, and 2) a multivoltine life cycle with synchronized events of adults oviposition. As reviewed by Jacobsen (2008), several authors have observed these suggested possibilities for different ephemeropterans in the tropics. However these suggested patterns can only be observed in the upstream site of the unregulated stream (San Juan). At the downstream site of this stream (San Juan), there is no clear phenological pattern and we can only see a density reduction. In the case of nymphal stages development in a regulated stream (Sucus), there is also no explainable phenological pattern in both upstream and downstream sites, while at this latter the density has increased. Lytle *et al.* (2008) has suggested that population adaptation to flow alteration depends on the individual genetic plasticity, therefore we might expect that the observed *Andesiops ardua* population respond to the flow alteration in some way, but we are not yet able to identify the phenological direction of change and to which extent. We are also aware of our data limitation, where the periodic three months sampling haven't enable us to observe if any synchronized oviposition is taking place and when has this occurred. The resulted water reduction at the downstream site of the unregulated stream (San Juan) reduces nymphal stages densities and alters the phenological behavior observed upstream. The inexplicable pattern occurring in the regulated stream (Sucus), both (upstream and downstream) sites suggest an alteration of phenological behavior and an effect on nymphal densities.

CONCLUSIONS

Based on our findings we conclude that water intakes and reservoir regulation change the ecosystem integrity of páramo streams. The negative effect of water intakes is reflected on the impoverishment of ecosystem integrity in streams with unregulated flows. Our evidence suggests that impacts of water withdrawal could be ameliorated via presence of permanent discharges as a flow regime from the upstream reservoirs. This result however was not constant and this ambiguity is reflected in increases of biotic quality, while other ecosystem features remained unchanged, like substrate and temperature. Invertebrate's community composition changed due to water removal at páramo streams with deleterious consequences on the community assemblages, taxa distribution and community density. The loss of flow sensitive taxa and an increase in density of resistant taxa can lead to further effects on ecosystem functioning. Limited scale of habitat improvements by constant presence of flow may have maintained the ecosystem richness, favoring some resilient invertebrate populations, but flow alterations will sustain habitat changes limiting diversity. Therefore we suggest that due to the impact of water intakes, a continuous input of flow should be maintained permanently in streams to avoid this habitat loss and consequently community impoverishment. If flows are released permanently into streams as in regulated streams, then continuous flow and the natural flow recharge of this ecosystem will improve ecological integrity and ecological features, as the distance to the intake increase. We observed this pattern in downstream site of Mogotes stream, and the maintenance of a resilient and resistant community that support good biotic quality and high richness in Sucus stream.

Population structure of taxa such as *Andesiops ardua* is an example of flow sensitive taxa that have attributes that allow them to colonize a widespread range of conditions. Bond and Lake (2003) suggest that this advantage aid populations to seek for suitable conditions and become more resilient. At the long-term, however, local impacts can have severe indirect effects on flow sensitive taxa (i.e: *Ochrotrichia* sp. *Contulma* sp. *Austrelmis* sp.) as suggested by Effenberger *et al.* (2008) for the habitats distribution and availability for different taxa. Ecuadorian high-altitude páramo streams have high aquatic invertebrate's richness (Jacobsen *et al.,* 1997), even though invertebrate's taxonomy is still under revision (Domínguez and Fernández*,* 2009). For these reasons, any negative effect on the community composition and the population structure of aquatic invertebrates from this ecosystem, represent a potential loss of biodiversity.

Current management of intakes and reservoirs fed by páramo streams located in a National Park with the highest level of protection should consider an environmentally sound operation. The evidence found on the negative effects of flow removal supports our recommendation to change the current management to continuous flow contributions that maintain the habitat stability and availability of downstream reaches. In a environmental flow context the flow variability should be maintained, but we propose that this must be manage to a certain degree from the natural flow, in order to have ecosystem integrity improvement by the stream reaches restoration. The volume of water that should be contributed to the downstream sites from intakes and reservoirs should take into account more accurate hydrological information and sustained research on invertebrate community and population responses to flow alterations.

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TABLES

Table 1. Repeated measures ANOVA for velocity, depth, and substrate as response variables with two factors of two levels: type of flow (unregulated/regulated) and site (upstream/downstream) of streams located in the páramo of Papallacta, Ecuador. Highly significant differences for velocity are shown for streams with different type of flow and significant differences for sites from water intakes. Significant differences for depth are shown for streams with different type of flow and for sites from intakes. No differences of substrate are shown for sites and streams with different types of flow.

		Velocity			*Depth*			*Substrate*		
	d.f	*MS*	*F*	*p - value*	*MS*	*F*	*p-value*	*MS*	*F*	*p-value*
Time	1	1626	6.3	0.000	1821	743	0.000	10.8	2.5	0.11
Time*Flow type	1	24.2	11.4	0.000	25.8	10.5	0.001	19.9	4.3	0.03
Time*Site	1	22.0	8.6	0.003	18.5	7.58	0.006	8.4	1.9	0.16
Time*Flow type*Site	1	5.1	2.0	0.158	2.3	0.95	0.329	0.7	0.1	0.68
Error	76	2.5			2.4			4.3		

Table 2. Repeated Measures ANOVA for Andean Biotic Index (ABI) scores for streams located in the Papallacta páramo, Ecuador. Differences of ABI scores are highly significant for the flow type (unregulated/regulated) and flow type with stream site (upstream/downstream) interaction, stream sites shown no differences through time.

	Andean Biotic Index			
	d.f	*MS*	*F*	*p-value*
Time	1	9182	380	0.0000
Time*Flow type	1	5209	21.5	0.0000
Time*Site	1	1.4	0.05	0.9391
Time*Flow type*Site	1	2124	8.79	0.0041
Error	76	241.6		

Table 3. Repeated measurements ANOVA models for density and taxa richness of invertebrate's community of headwater streams of the páramo of Papallacta, Ecuador. Results for between subjects considered flow type (unregulated and regulated) and sites (upstream and downstream) and within subjects analysis included time interaction with mentioned factors. Significant differences on density were found for flow type and date interaction and no differences were observed between sites through time. Richness differences occurred in all treatments with highly significant values among sites and flow type with time interaction.

	Density				*Taxa Richness*			
	d.f	*MS*	*F*	*p-value*	*d.f*	*MS*	*F*	*p-value*
Within subjects								
Time	1	2095484	174	0.000	1	732.5	50.2	0.000
Time*Type of flow	1	8388200	7.0	0.009	1	157.9	10.8	0.001
Time*Stream site	1	1039002	0.8	0.321	1	186.2	12.8	0.000
Time*Type of flow* site	1	6041695	5.0	0.026	1	84.5	5.8	0.017
Error	76	1198676			76	14.5		

Table 4. Results on mean density (m^{-2}) ± SE (standard error) of dominant taxa present at upstream and downstream sites of water intakes in streams with unregulated and regulated flows, of the páramo of Papallacta, Ecuador.

			Stream with unregulated flows				*Stream with regulated flows*			
			Upstream		*Downstream*		*Upstream*		*Downstream*	
Order	Family	Taxa	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Diptera	Chironomidae	Chironomidae	34	7	36	5	69	14	47	10
Amphipoda	Hyalellidae	*Hyalella* sp.	17	5	2	1	17	6	19	4
Haplotaxida		Oligochaeta	8	2	26	7	28	21	17	12
Ephemeroptera	Baetidae	*Andesiops ardua*	7	2	0	1	2	0	9	2
Diptera	Simulidae	*Simulium* Sp1.	3	1	2	0	2	1	3	1
Trichoptera	Hydroptilidae	*Ochrotrichia* sp.	3	1	0	0	2	1	1	1
Trichoptera	Limnephilidae	*Anomalocosmoecus* sp.	2	1	0	0	13	2	9	2
Trichoptera	Leptoceridae	*Nectopsyche* sp.	2	1	0	0	2	1	0	0
Trichoptera	Anomalopsychidae	*Contulma* sp.	2	1	0	0	2	1	0	0
Trichoptera	Hydroptilidae	*Hydroptila* sp.	1	1	2	1	2	1	1	1

Table 5. A General Linear Model results for *Andesiops ardua* nymphal stages at upstream and downstream sites of intakes in streams with different types of flow from the páramo of Papallacta, Ecuador. Repeated measures ANOVA for stages density of all effects show only differences between periods (years) of nymphal stages density. Significant differences also show the effects interaction of flow type, site and period.

	d.f.	*MS.*	*F*	*p-value*
Date	1	2384.9	0.53	0.46
Flow type	1	4849.1	1.08	0.0.29
Site	1	693.2	0.15	0.69
Period	2	21435.8	4.7	0.009
Nymphal Stage	3	7392.6	1.6	0.18
Flow type * Site	1	6771.4	1.5	0.22
Flow type * Period	2	160.1	0.03	0.96
Period * Site	2	256.3	0.05	0.94
Flow type * Site * Period	2	21823.5	4.87	0.008
Flow type*Site*Stage	3	2041.53	0.455781	0.71
Flow type*Period*Stage	6	408.57	0.091215	0.99
Site*Period*Stage	6	330.78	0.073848	0.99
Flow type*Site*Year*Stage	6	1913.59	0.427218	0.85
Error	155	4479.20		

FIGURES

Figure 1. Study streams located in the páramo of Papallacta in the Cayambe-Coca National Park, at the site of the Municipal Water Supply Company of Quito (EPMAPS at approximately 69 km northeast from Quito city in the headwaters of Napo River basin, Ecuador. Streams with unregulated flows are the San Juan and Chalpi Norte (represented in circles); and regulated flows are the Sucus and Mogotes (represented in squares). Sampling sites are located upstream (black markers) and downstream (white markers) of water intakes at 3.700 m of altitude. These markers (black and white, circles and squares) will be used consistently in the following graphs.

Figure 2. Mean monthly point discharge measurements of páramo streams (± SE) of a) Unregulated flow (Chalpi Norte and San Juan) with two flow peaks in March and July and b) Regulated flow (Sucus and Mogotes) with one peak in July. Hydrographs include data collected during the research period (2006 – 2008) at upstream and downstream sites; the later represent the few data available in two-year sampling period. Flows at downstream sites have lower values than at upstream sites for both flows. Bars indicate standard errors (SE) where enough data were available for proper calculation.

Figure 3. Non-Metric Multidimensional Scaling (NMDS) of physical variables at upstream and downstream sites of intakes in streams with different type of flow. Unregulated downstream sites cluster in the bottom part of MDS2 (33.7%) (diagonal ellipse), while regulated downstream sites remain distributed along MDS 1 (44.6%), with no separation from regulated upstream sites and unregulated downstream sites (horizontal ellipse). Data from unregulated upstream sites distribute erratically along the plot showing the multiple combinations of physical variables in the natural reach.

Figure 4. Principal components analysis (PCA) for chemical variables at upstream and downstream sites of intakes in streams with different types of flow. PC1: 28.2 % indicates that streams don't vary chemically between sites and types of flow.

Figure 5. Mean invertebrate's community density (± SE) and mean taxa richness (± SE) at upstream and downstream sites of water intakes in páramo streams with different type of flow (unregulated and regulated).

Figure 6. Dominance-rank curves of Andean invertebrates at páramo streams. Downstream sites of streams with unregulated flows present higher dominance of species concentrated in a few taxa. The lower dominant species curve was found at downstream sites of streams with regulated flows.

Figure 7. Time series diagrams along a sampling period of two years of San Juan stream (non-regulated stream) for a). Mean discharge measurements, b). Mean nymphal stages density of *Andesiops* ardua (± SE) in upstream site of the intake and c). Mean nymphal stages density of

Andesiops ardua (± SE) in downstream site of the intake. In **a).** Unregulated stream San Juan, presents a natural flows hydrograph for upstream site (black circles) and an artificial flows hydrograph for downstream site (white circles). In **b)** and **c)** each different nymphal stage has a different color code (stage I: black, stage II: dark gray, stage III: gray, stage IV (blackwind pad stage BWP): white).

Figure 8. Time series diagrams along a sampling period of two years of Sucus stream (regulated stream) for a). Mean discharge measurements, b). Mean nymphal stages density of *Andesiops ardua* (± SE) in upstream site of the intake and c). Mean nymphal stages density of *Andesiops ardua* (± SE) in downstream site of the intake. In **a).** Regulated stream Sucus, presents only artificial flows hydrographs for upstream (black squares) and downstream (white squares) sites from the intake. In **b)** and **c)** each different nymphal stage has a different color code (stage I: black, stage II: dark gray, stage III: gray, stage IV (blackwind pad stage BWP): white).

Figure 1. Rosero et al.

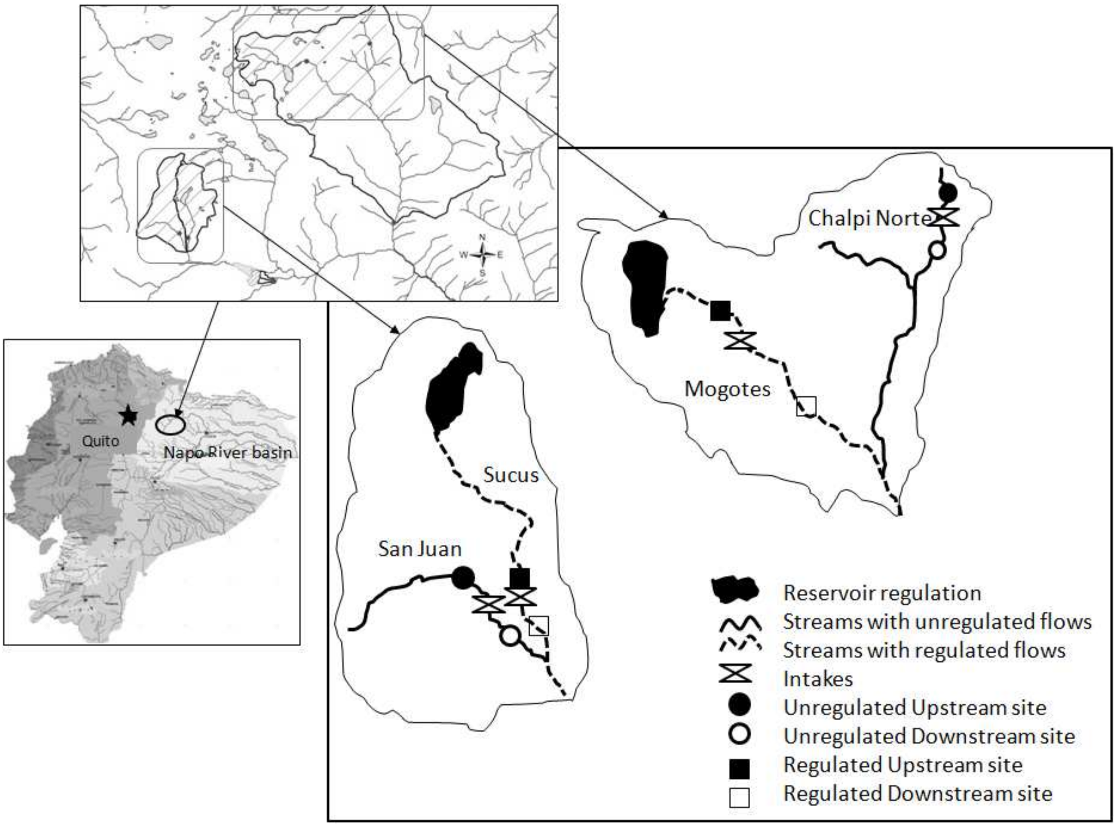


Figure 2. Rosero et al.

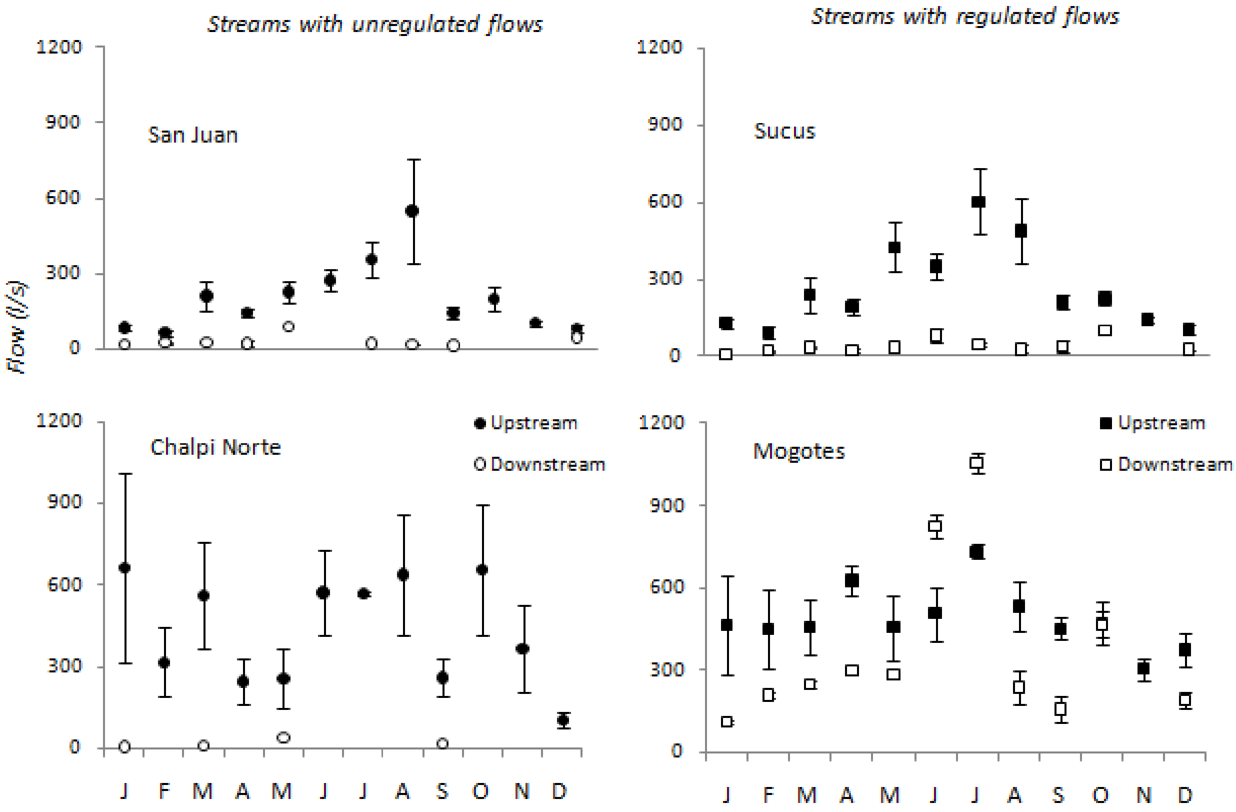


Figure 3. Rosero et al.

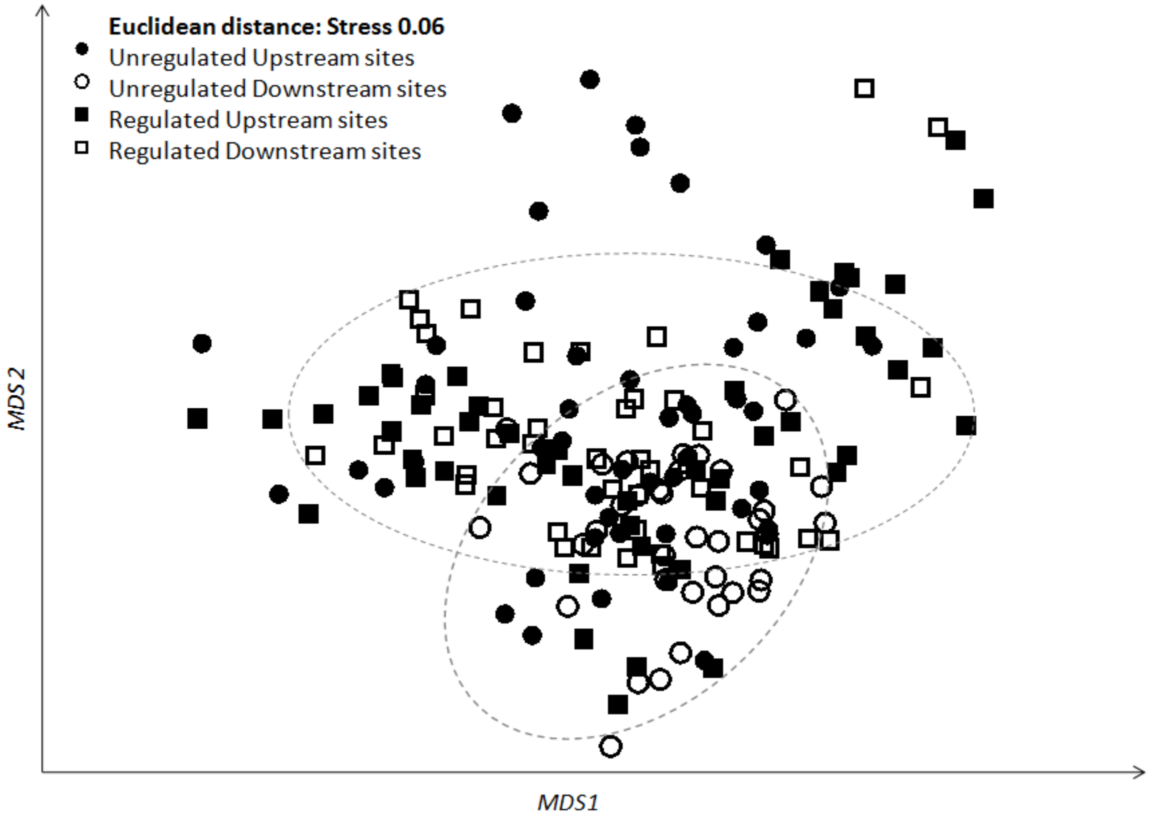


Figure 4. Rosero et al.

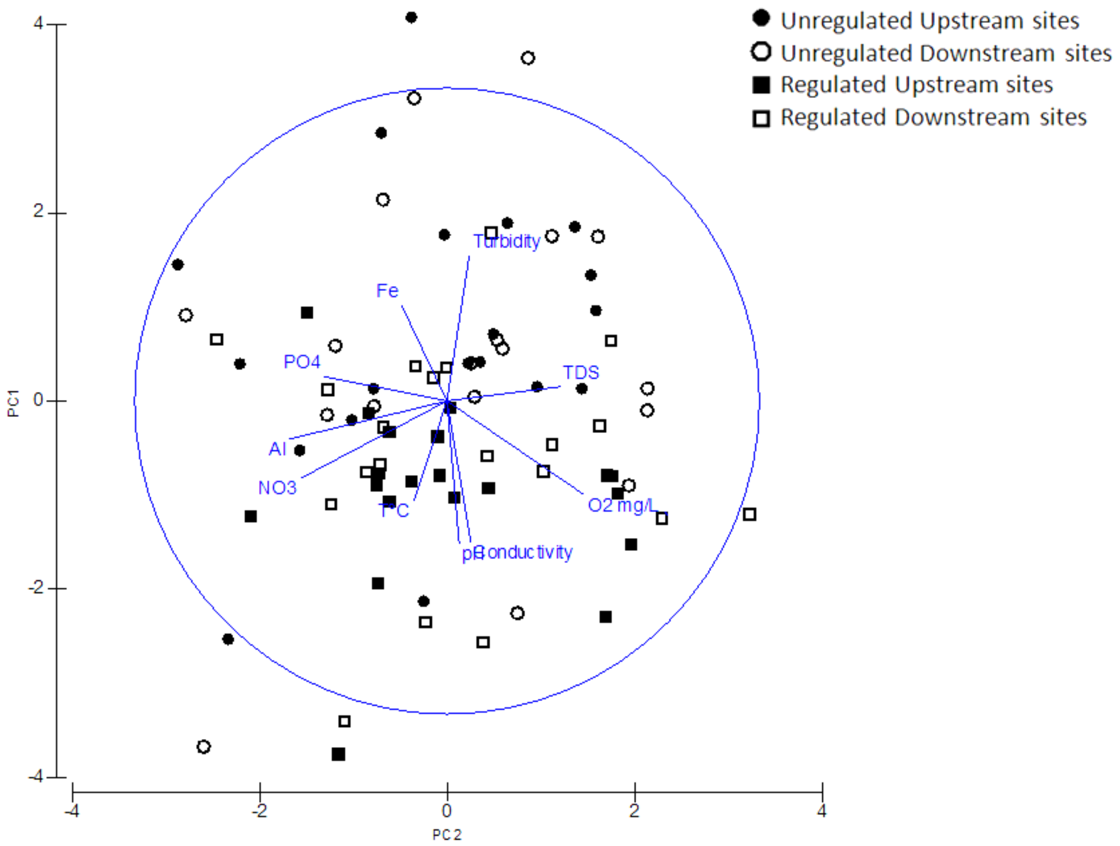
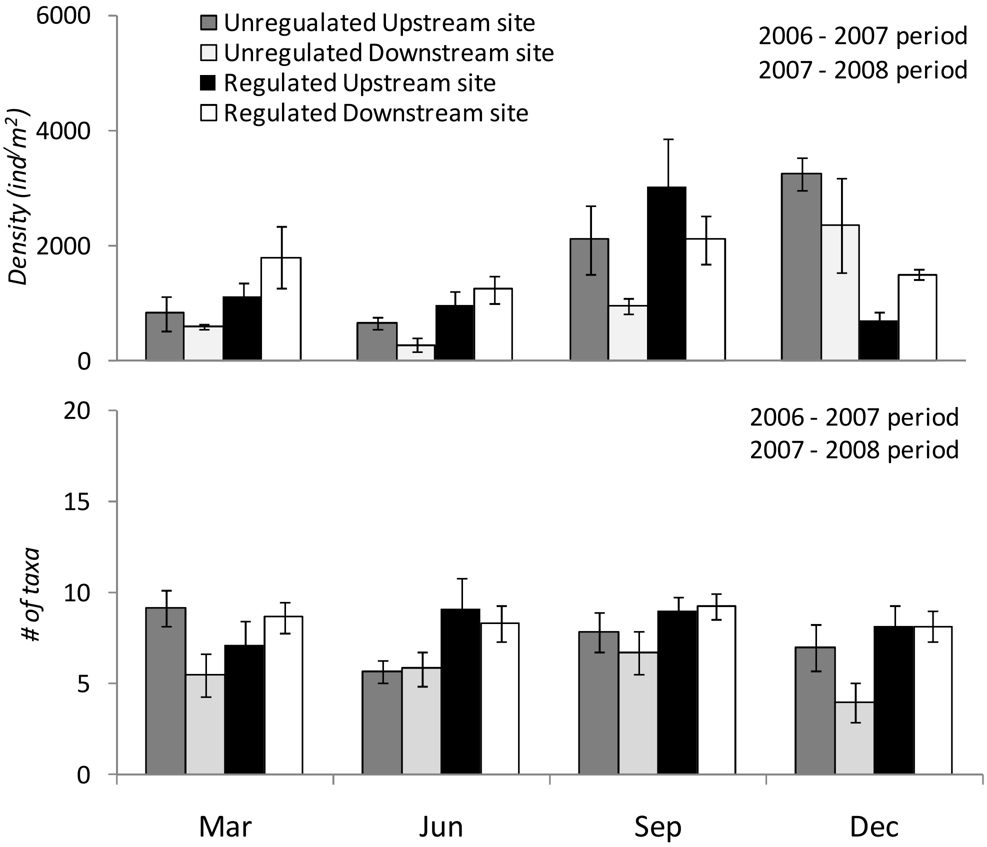


Figura 5. Rosero et al.



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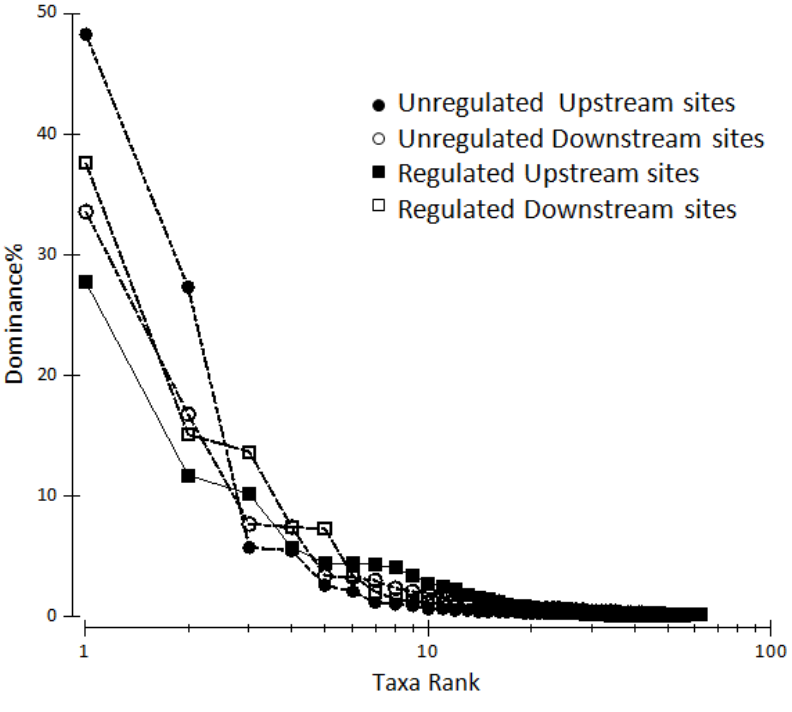

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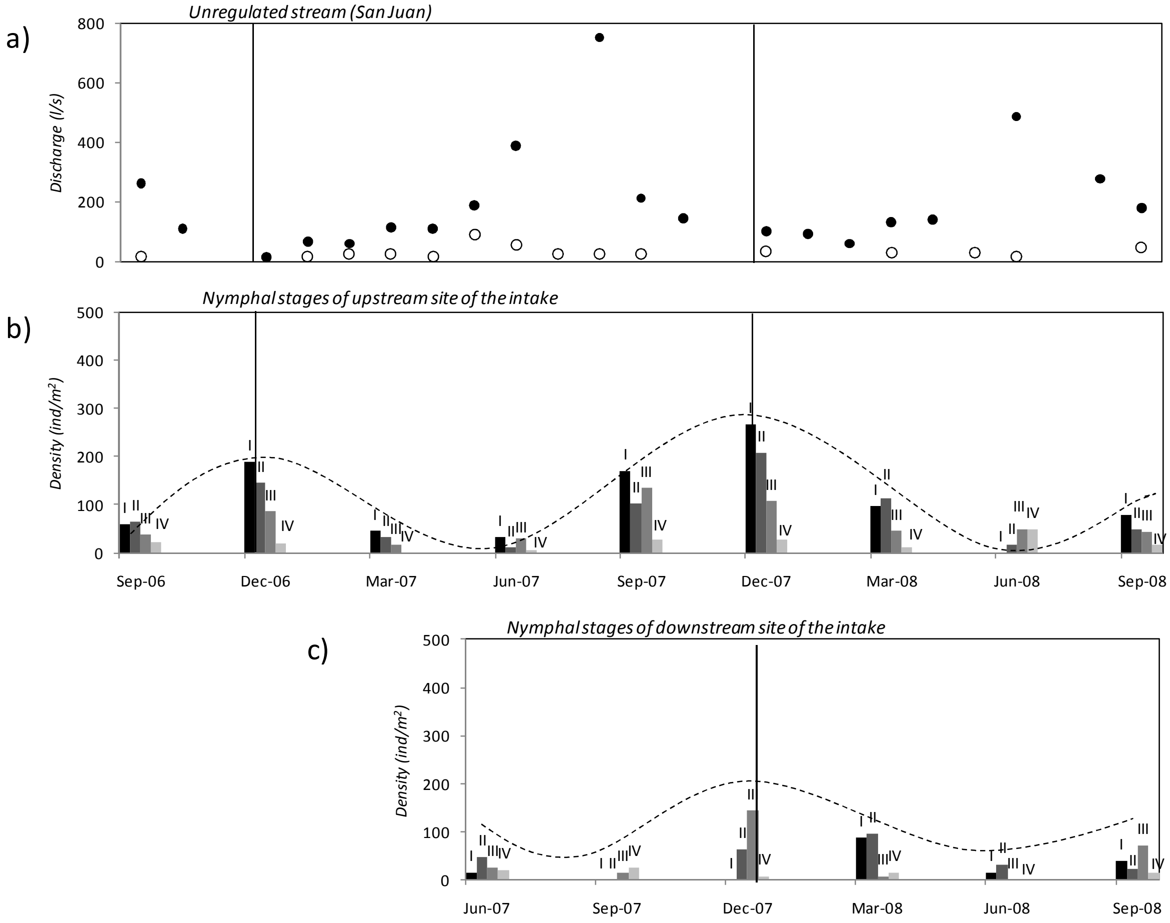

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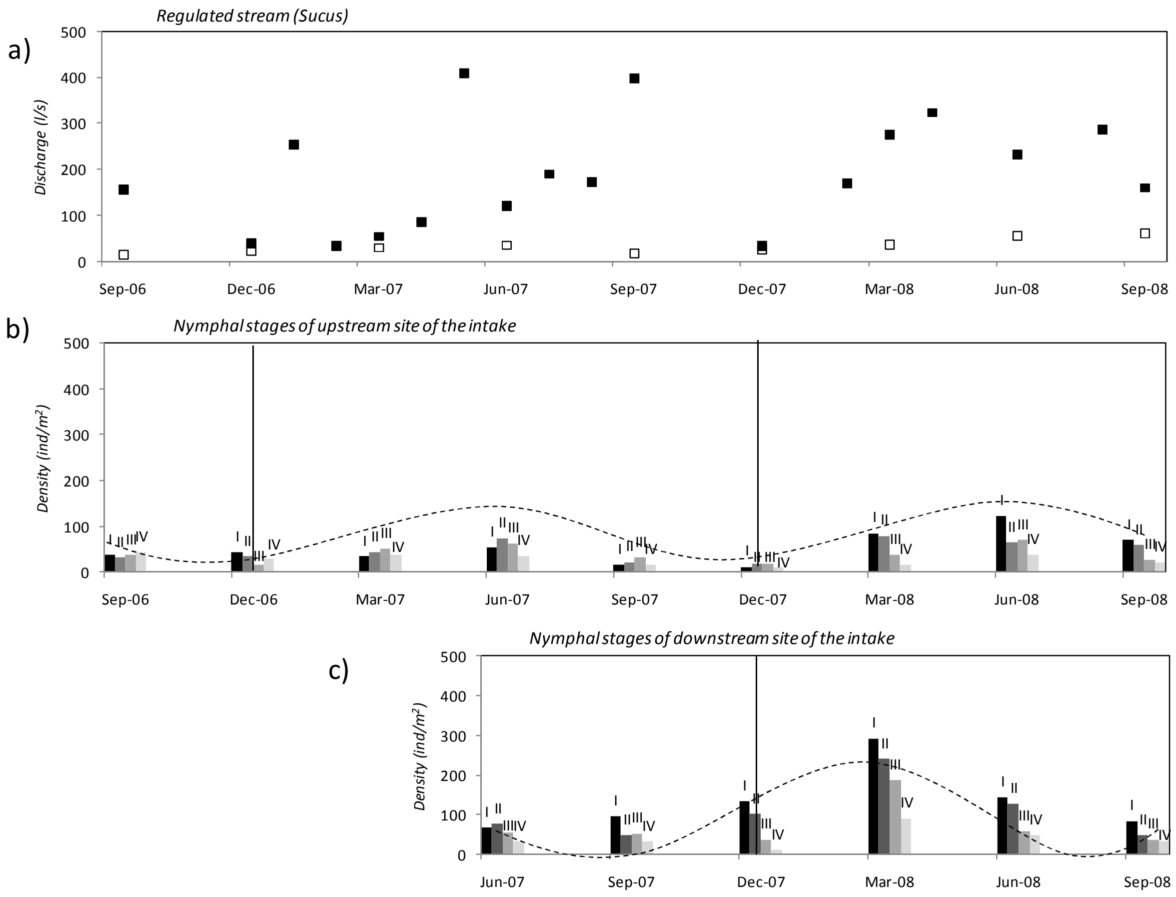

Appendix I. ABI scores for invertebrates families of Andean páramo streams in Papallacta, Ecuador.

Order	Family	Score
Turbellaria		5
Oligochaeta		1
Hirudinea		3
Gasteropoda	Limnaeidae	3
	Planorbiidae	3
Bivalvia	Sphaeriidae	3
Amphipoda	Hyalellidae	6
Acari	Hydracarina	4
Ephemeroptera	Baetidae	4
	Leptohyphidae	7
	Leptophlebiidae	10
	Oligoneuriidae	10
Plecoptera	Grypopterygidae	10
	Perlidae	10
Coleoptera	Elmidae	5
	Hydrophilidae	3
	Psephenidae	5
	Ptilodactylidae	5
	Scirtidae	5
	Staphylinidae	3
Trichoptera	Odontoceridae	10
	Anomalopsychidae	10
	Helicopsychidae	10
	Hydrobiosidae	8
	Hydroptilidae	6
	Leptoceridae	8
	Limnephilidae	7
Lepidoptera	Pyralidae	4
Diptera	Blepharoceridae	10
	Ceratopogonidae	4
	Chironomidae	2
	Culicidae	2
	Dolichopodidae	4
	Empididae	4
	Muscidae	2
	Psychodidae	3
	Simulidae	5
	Tabanidae	4
	Tipulidae	5
	Limoniidae	4

Appendix II. Mean environmental values (±SE) of Andean páramo streams in Papallacta, Ecuador. Substrate type indicates dominant substrate from stream reaches upstream and downstream from intakes.

	Unregulated Flows				*Regulated Flows*			
	(San Juan)		*(Chalpi)*		*(Sucus)*		*(Mogotes)*	
	Upstream	*Downstream*	*Upstream*	*Downstream*	*Upstream*	*Downstream*	*Upstream*	*Downstream*
Location (°W, °S)	812799 9960130	812863 9959924	823368 9971572	823500 9971000	813090 9960130	813075 9959925	819692 9970577	822320 9969900
Altitude (m.a.s.l.)	3740	3738	3820	3818	3760	3758	3800	3782
Discharge ($m^3.s^{-1}$)	0.238 (0.03)	0.038(0.005)	0.412 (0.07)	0.399 (0.1)	0.255 (0.056)	0.033 (0.006)	0.293 (0.072)	0.017 (0.005)
Width (m)	1.52 (0.06)	2.04 (0.17)	6.95 (0.37)	4.9 (0.24)	1.73 (0.04)	1.82 (0.16)	1.25 (0.07)	1.71 (0.14)
Veocity ($m.s^{-1}$)	0.52 (0.06)	0.29 (0.06)	0.52 (0.07)	0.13 (0.02)	0.64 (0.07)	0.33 (0.05)	0.26 (0.04)	0.59 (0.02)
Depth (m)	0.46 (0.04)	0.21 (0.01)	0.34 (0.07)	0.31 (0.02)	0.28 (0.03)	0.24 (0.06)	0.32 (0.03)	0.36 (0.03)
Substrate type	Cobble	Pebble	Cobble	Cobble	Cobble	Boulder	Pebble	Gravel
pH	7.72 (0.22)	8.02 (0.10)	7.21 (0.18)	7.05 (0.16)	8.06 (0.13)	8.24 (0.10)	7.33 (0.14)	7.61 (0.16)
Conductivity (uS/cm)	63.66 (23.74)	57.59 (17.87)	24.17 (10.33)	31.80 (12. 96)	75.40(20.93)	87.30 (21.68)	31.46 (9.63)	39.79 (14.03)
Temperature (°C)	7.73 (0.48)	8.19 (0.48)	7.62 (0.21)	7.58 (0.15)	8.96 (0.55)	8.3 (0.38)	8.12 (0.27)	7.62 (0.18)
Dissolved Oxygen ($mg.l^{-1}$)	7.2 (0.09)	7.34 (0.14)	6.75 (0.19)	7.12 (0.36)	7.14 (0.19)	7.34 (0.11)	7.12 (0.08)	7.45 (0.16)

Generating habitat suitability models for aquatic insects as a tool for calculating environmental flows for high-altitude tropical streams

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Abstract

Habitat loss in stream ecosystems occurs probably faster than in terrestrial ecosystems when human demands compromise water flow from the stream environment. We designed an eco-hydraulic survey to generate a tool for environmental management in current and upcoming water projects in high altitude páramo streams. We proposed to evaluate relationships between aquatic invertebrate communities and stream physical variables, to select representative taxa to build habitat suitability models, and to relate models (and taxa) to flow variability. These taxa specific models could be used to determine environmental flows and consequently, to manage water allocations. We measured aquatic invertebrate community composition (i.e. richness and density) and related it to habitat characteristics. We selected ten representative taxa to build habitat suitability models using generalized additive models (GAMs) with taxa specific invertebrate density as response variable, and stream, depth, velocity and substrate type as predictors. We found that suitable habitats for invertebrates are commonly characterized by high velocities, medium depths and large substrates. We integrated flow to the suitability models and observed density of *Andesiops ardua*, *Ochrotrichia* sp., and *Hyalella* sp. to increase with the flow, while density of *Anomalocosmoecus* sp., Hydroptilidae sp.1, *Neoplasta* sp., and Simuliidae sp.1, to remain constant as flow increases. The initial flow increment cause a positive effect on invertebrate's density, but high flows are not necessarily suitable habitats for rare/less abundant taxa and *Austrelmis* sp. *Anomalocosmoecus* sp., *Neoplasta* sp., and *Andesiops ardua* are few interesting taxa to be considered in the design of environmental flow regimes due to the responses they present that are not related to flow increments. Instream habitat models from suitable habitats for invertebrates served as a tool to assess environmental flow ranges for high altitude streams. Suitable models could sustain the ecological integrity of stream ecosystems, through the evaluation of fauna (invertebrates) response to flow amount and variability and consequently, to further reduce potential threats to habitat loss in páramo stream ecosystems.

Key words: Aquatic insects, Ecohydraulics, flow variability, habitat suitability models, páramo.

Introduction

One of the major threats to aquatic ecosystems and their biotic communities is the withdrawal of water for a diverse set of human activities including irrigation, hydropower generation, industry, and human consumption (Allan and Castillo, 2007). Postel (1996) estimated 70% of total world's runoff to be consumed by humans by the 2025. In the last decades, for example, it has been estimated that least 80% of the water from the Mekong River watershed, has been used for irrigation and that near 90% of Brazil electricity demand is been provided by the Paraná River watershed (WWDR3, 2009). The magnitude of current water demand across the world, and its huge impacts on the functioning and biodiversity of stream ecosystems, raise many questions about the future persistence of healthy aquatic ecosystems, but also about their potential to keep supplying water for critical human needs (Postel, 2000). From this perspective, recent years have witnessed active efforts for the development of research and management tools intended to balance the integrity of aquatic ecosystems with the human needs that they sustain (Poff *et al.*, 2009).

Among these attempts are these relatively new approaches to water management, commonly known as "Environmental Flows" (Poff *et al.*, 2003; Alan and Castillo, 2007). Although the methodologies and focus vary greatly (Tharmes, 2003), the general approach is aimed at controlling the extraction of water from aquatic ecosystems, in such a way that allows the maintenance of a volume of water and a temporal flow regime that resembles natural conditions and permits the persistence of biotic communities and ecosystem processes (Poff *et al.*, 1997; Bunn and Arthington, 2002; Lytle and Poff., 2004). In doing so, this approach intends not only to conserve the biotic integrity of the ecosystem, but also its capacity to supply water for human needs in the long-term (Poff *et al.*, 2003). Despite the obvious appeal and promising perspectives of these methodologies, there are still very few examples of their implementation and many questions remain about appropriate ways to define the water volumes and temporal regimes to be preserved under different conditions (Poff and Zimmerman, 2010). Key among these obstacles is the uncertainty about the relationships between water flow, ecological interactions, and the response of different organisms to alterations of the hydrological regimes (Postel and Richter, 2003; Poff *et al.*, 2007).

In trying to develop tools for the design, calculation and implementation of environmental flows, active research is begin carried out on the modeling of the species-specific response to changes in flow regimes (Jowett and Duncan, 1990; Jowett *et al*., 1991; Jowett, 2003, Merigoux and Dolédec, 2004; Dolédec *et al*., 2007; Gibbins *et al*., 2010). Although it must be recognized that water flow is only one of the environmental factors affecting stream organisms, and that the influence of ecological interactions must not be ignored (Lancaster & Downes, 2011), the modeling of the impacts of flow on aquatic species is critical, as flow regime influence habitat distribution and community dynamics through its physical variables (Winemiller *et al*. 2010; Jowett and Biggs, 2008). Although habitat modeling could include monitoring changes in physical (substrate, depth, velocity, temperature, etc.) and ecological variables (food resources, predation and behavior); hydraulic variables are being widely used to model habitats (Dolédec *et al*., 2007; Guisan *et al*., 2002; Armitage and Cannan, 2000). Hydraulic preferences of organisms reflect the frequency of use and the level of occupation by populations for groups of physical variables that create suitable habitats (Jowett, 1997).

Recent studies of stream habitat modeling (Jowett and Davey 2007) use an innovative approach for the development of models of hydraulic preferences applied for stream invertebrates. Jowett and Davey (2007) applied general additive models (GAMs) with several ecohydraulic metrics and highlighted the ability of GAMs to combine several variables additively in order to obtain the contribution of all variables to the biota response. GAMs developed and validated with physical/hydraulic variables could account for most of the patchy distribution of invertebrates on habitats (Winemiller *et al*., 2010; Guisan and Zimmermann, 2000). In this context, the construction of habitat suitability models (using GAMs) based on species tolerance and responses to hydraulic variability could become a useful tool for the design and monitoring of environmental flow regimes.

The high-altitude ecosystems of the northern Andes (páramo ecosystems) offer a striking example of the pressures that human populations are exerting on aquatic environments (Rosero, 2011). The streams and lakes that drain páramo ecosystems have been recognized as critical environment for a diverse biota (Jacobsen, 2008; Sklenar and Ramsay; 2001), but at the same time, they provide most of the water used for human consumption, irrigation and energy generation in vast areas across the Andes, including at least 9 millions of people in large cities such as Mérida, Bogotá, Quito, and Cuenca (Buytaert, 2006). Although recent years have seen a rapid recognition of the strategic role that páramo ecosystems play in the regulation of water supply (Buytaert *et al.,* 2006), management efforts have concentrated in terrestrial habitat protection (FONAG, 2009) and there is still little experience in direct management of stream flows and approaches for the design of environmental flows for these ecosystems. Moreover, little is known about the species-specific responses of high-altitude stream invertebrates to changes in flow regimes (and other associated variables), and the potential use of such information in the design of effective management strategies. In this context, our study analyzes biotic and ecohydrological data from high-altitude streams that are currently used for drinking water supply systems in northeastern Ecuador, with the objectives of: 1) identifying associations between invertebrate communities and stream physical variables; 2) identifying representative taxa for the development of habitat suitability models according to their hydraulic preferences, and 3) assessing the effect of flow variability on habitat suitability models of representative taxa. Ultimately, our goal is to use this case study to explore the possibility of using habitat suitability models for the design of environmental flow regimes in high-altitude páramo ecosystems.

Methods and materials

Study area

The study is located in the northern tropical Andes páramo of Ecuador. The páramo ecosystem is a life zone that ranges from 3500 to 4000m of altitude and is uniquely located in the Andes mountain chain. Our study area is located at 69 km northeast of Quito inside the Cayambe – Coca National Park. The streams are located at ≈ 3700m above sea level and are part of the Quijos catchment in the headwaters of Napo River Basin System, one of the main basins in Ecuador that drains into the Amazon River. The Quijos River upper catchment is formed by three sub-catchments: San Juan – Sucus, Chalpi Grande and Papallacta that feed a main stream Papallacta at different altitudes (Fig. 1). Overall, stream sites in this area have good biotic quality and ecosystem integrity (Rosero, 2011); chemical conditions of headwater páramo streams present low temperatures ≈ 9 °C, and high dissolved oxygen concentrations ≈ 7 $mg l^{-1}$with saturation percentages of ≈ 65 (Table 1). Our study streams are part of the Water System for Quito and surrounding towns and stream reaches are located upstream from water intakes and have no upper regulation. Although the streams are located inside a protected area, and most of the land is under conservation management, there is some cattle presence inside stream banks during some periods (but see Rosero, 2011).

Field methods and data analysis

We designed an eco-hydraulic survey in order to sample aquatic invertebrates in a wide range of different physical characteristics from several habitats in streams with similar flow and geo-morphological conditions during the “low-flow” season of December 2009. We selected two representative streams reaches from San Juan and Chalpi Norte streams (Fig. 1), located upstream from water intakes. Stream reaches had non- modified morphology and also were non-affected by the downstream impoundments.

We collected the ecohydraulic samples in reaches of 15 m length, alternating mesohabitats when possible, by dividing streams width in four lanes of different depths (0.1, 0.2, 0.3, and 0.45 m) (Jowett & Richardson, 1995). In order to warrant an adequate sample size over the range of depths and velocities in streams with common substrate types, we collected 25 samples per lane in a total of 8 lanes (forming a virtual grid along the stream). At each site on the grid, we registered dominant substrate from the sampling area before performing benthic sampling, and also described the percentage of substrate composition using the Wenthworth scale, in order to further obtain a Substrate Index (as in Jowett and Duncan, 1990). At the same sites, we collected invertebrates using a Hess sampler (net surface 0.02 m^2, 350 µm) and stored invertebrates in 500 ml jars with stream water and 1 – 2 ml of 4% formalin before transport to the laboratory for further analysis. At each site, we measured velocity and depth afterwards at the center of the Hess cylinder surface using a current meter and a measured rod (Flow Probe, Global Water Institute). We also registered the presence of algae, macrophytes, and/or moss as microhabitats and classify sample locations as cascades, runs, riffles, and pools as mesohabitats.

In the laboratory, we identified invertebrates with available regional keys (Fernández and Domínguez, 2001; Domínguez and Fernández*,* 2009), to the lowest possible taxonomic level, usually to genera and in some cases to family or subfamily.

1) Associations between invertebrate communities and physical variables

We described, characterized and made associations between invertebrate communities and their physical variables, by calculating the invertebrate community density (No. m^{-2}) and richness (*S*), and related these values with their corresponding habitat (physical) types.

We classified habitat types into mesohabitats and microhabitats by assessing them visually. We characterized mesohabitats by differences in velocity: where “pools” were mainly identified by the absence of moving water, “runs” by the presence of higher velocity but with no water splashes, “riffles” were characterized by high velocity with water splashes and continuous bubbles, and finally “cascades” were characterized by bubbles and splashes in a steep change of slope. Regarding microhabitats, we classify them as a categorical variables taking into account the presence of algae, moss, and macrophytes as substrate cover from the surface sampled. Habitat’s physical variables: depth and velocity were classified into five categories (Table 2), while dominant substrate type was classified into six categories (sand, fine gravel, gravels, cobbles, boulders, and bedrock), where dominant substrate was estimated from the percentage of cover.

2) Taxa used for habitat suitability models according to their hydraulic preferences

From the invertebrate community data (see above), we selected dominant and rare taxa as representative invertebrates from the Andean páramo streams. Our criteria for dominant taxa were an average density over 200 ind $\cdot$ m^{-2} or presence in 70% of the total samples of each stream, and for rareness we considered average densities under 150 ind $\cdot$ m^{-2} or 40% presence at reach mesohabitats.

For the development of hydraulic preferences analysis and habitat suitability models we used taxa density, registered velocity and depth, and we used a substrate index, calculated from the percentages of substrate composition in the sample surface (see above). For example, low substrate index of 3 indicates substrate dominated by sand, and high substrate index of 7 indicates substrates dominated by boulders (as in Jowett and Duncan, 1990).

We calculated depth, velocity and substrate type preferences for representative taxa by weighting the number of taxa present in each sample by the sampling variable average. This preliminary analysis was the first assessment to identify preferences of physical/hydraulic conditions to evaluate differences or similarities of the stream reach average conditions.

We developed habitat suitability models where specific invertebrate density per Hess sample was the response variable (*N*) and depth, velocity, and substrate index were the continuous predictors and stream was the categorical predictor. We did not include microhabitat as a categorical predictor (algae, moss and macrophytes) in this analysis as this might co-variate with flow and it was our intention to understand the contribution of physical variables to invertebrate density distribution. We used generalized additive models where no data transformation from variables was required, and models used Poisson distributions with logarithmic link functions to model density of organism within a unit of space in (*N)* samples:

$$log_{(N)} = r + \mathrm{s}_1 (v) + \mathrm{s}_2(d) + \mathrm{s}_3(\mathrm{S}) + (v \times d)$$

where, each variable has a parametric linear component and nonparametric nonlinear component fitted by cubic splines (Jowett and Davey, 2007). We allowed two degrees of freedom for velocity (v), depth (*d*), substrate index (*S*) and three degrees of freedom for velocity x depth (*v x d*) interaction. Model statistics assumed over dispersion as occurs often with invertebrate density, but in order to avoid undue influence from outliers we excluded a few data from the total data set to maintain the observed biological response. We used contour plots to evaluate the model predictions beyond the observed data and according to the hydraulic preferences. We plotted density to velocity – depth axes for a substrate index. We developed models using the statistical software Time Trends (Jowett, 2010).

3) Flow variability on habitat suitability models of representative taxa.

We calculated stream discharge (*Q*) in several stream transects by applying standard methods measures (as in Hauer and Lamberti, 2006). Additionally, we measured bank width and wetted perimeter during four days of sampling and calculated the stream reach area. Finally, we registered the water level from a limnimetric strip in order to calculate flow from the discharge calibration curve from 2006 – 2008 (Rosero, 2011), and compared observed flow to historical monthly data from 1989 – 2005 (EPMAPS, 2005).

To model how different flows regime might affect invertebrate hydraulic preferences (based on habitat suitability models), we conducted simulations with representative taxa from our mentioned surveys (see above), using the River Hydraulics and Habitat Simulation software RHYHABSIM (Jowett, 1999). We selected a 90% return period flow (0.2 $m^3.s^{-1}$) to simulate the habitat suitability response to flow increases, due to an unavailability of continuous historical data of higher flows events and floods. We expressed the effect of flow variability until this flow as the change in invertebrate density present at a surface of suitable habitat per stream length. We analyzed representative invertebrate's suitable habitats for each stream separately (San Juan and Chalpi) to evaluate specific-taxa response to flow variability.

Results

1) Associations between invertebrate communities and physical variables

The benthic community in our study streams comprised a total of 42 taxa with 13 orders, 27 families and 33 genera (Appendix 1). Richness and density of Andean páramo invertebrates varied between streams according to the ecological and physical dominant characteristics in streams (Table 2). Of the 200 sampled mesohabitats, runs were the most common mesohabitat, present in 88 locations, and cascades were the least common, present in only 17 locations. Invertebrate richness was highest in riffles while density was highest in cascades; runs, and pools were similarly lower in richness and densities (Table 2). Algae were the most common microhabitat, present in 83 samples, while macrophytes were the least common, present only in 10 samples from the total set. Invertebrate richness and density were highest in moss and lowest in algae and macrophytes. Invertebrate richness was the highest in depths between 0.23 – 0.31 m, and density was the highest in depths between 0.05 – 0.139 m. Richness and density were highest in a velocity range of 1.1 – 1.64 $m{\cdot}s^{-1}$, and in gravel substrates (Table 2). Less than 20% of the samples were in sand were we found low richness but relatively high density, mainly comprised of Oligochaeta, Nematoda, Turbellaria, Glossiphoniidae, Chironomidae and Lymnaeidae. No bedrock locations were registered in these streams (Table 2).

2) Taxa used for habitat suitability models according to their hydraulic preferences

The five most dominant and the five rarest taxa in these Andes páramo streams belonged to four insecta and one non insecta orders of invertebrates: Ephemeroptera, Trichoptera, Coleoptera, Diptera and Amphipoda (Table 3). Orthocladiinae (Diptera) were the most abundant subfamily and common in both streams. *Andesiops ardua* (Ephemeroptera) and *Hyalella* sp. (Amphipoda) were the second most abundant taxa in San Juan and Chalpi Norte, respectively. Least abundant invertebrate taxa were similar between streams but varied in density and contribution into the community (Table 3).

Each taxa weighted by reach depth showed that most representative invertebrate prefer depths ≈ 0.18m, which is the average sample depth of stream reaches. Taxa weighted by the reach velocity showed that Simuliidae sp.1, *Austrelmis* sp., Ceratopogonidae sp.1 and *Neoplasta* sp. prefer high velocities > 1.32 $\mathrm{m{\cdot}s^{-1}}$, that were higher than the reach average velocity 1.26 $\mathrm{m{\cdot}s^{-1}}$. *Andesiops* sp., *Hyalella* sp., Hydroptilidae sp.1 and *Ochrotrichia* sp. prefer lower velocities < 1.21 $\mathrm{m{\cdot}s^{-1}}$, and *Anomalocosmoecus* sp., and Orthocladiinae were present in velocities similar to the average velocity of the reach, indicating either a preference for the reach velocities or no specific velocity preference (Table 4). Taxa weighted by reach substrate index showed that only Ceratopogonidae sp.1, Hydroptilidae sp.1, and *Ochortrichia sp*., preferred substrates of gravel (SI = 5) than the average reach substrate estimated as cobbles (SI = 6)(Table 4).

The generalized additive model analysis showed that depth suitability curves for representative taxa follow three types of patterns: continuous decrease, decrease up to 0.3m and then increase, and increase up to 0.35 m and then decrease (Fig. 2). The depth suitability curve for *Andesiops ardua* decrease almost linearly as an example of the first pattern mentioned; only depth suitability curves for *Hyalella* sp. and *Anomalocosmoecus* sp. decrease and then increase, and suitability curves for the remaining taxa decrease when depth increases (Appendix 2). The velocity suitability curves follow three patterns: an increase up to 1 $\mathrm{m{\cdot}s^{-1}}$ and then decrease, a decrease up to 1.5 $\mathrm{m{\cdot}s^{-1}}$ and then increase, and continuous increase up to 1.5 $\mathrm{m{\cdot}s^{-1}}$(Fig. 2). The velocity suitability curve for *Andesiops ardua* follow the pattern of increase up to 1.5 $\mathrm{m{\cdot}s^{-1}}$, the velocity suitability curves for *Anomalocosmoecus* sp*., Austrelmis* sp*.,* Ceratopogonidae sp.1,Hydroptilidae sp.1 decrease up to 1 $\mathrm{m.s^{-1}}$ and then increase*,* and *Hyalella* sp., *Neoplasta* sp., *Ochrotrichia* sp*.,* Orthocladiinae, and Simuliidae sp.1, follow the pattern of continuous increase (Appendix 2). Substrate suitability curves for representative taxa showed two similar increase patterns and one decrease pattern (Fig. 2). *Andesiops ardua, Anomalocosmoecus* sp*., Austrelmis* sp.*,* *Hyalella* sp.*,* *Ochrotrichia* sp.*,* and Simuliidae sp.1*,* were most abundant in substrates of gravels, cobbles and boulders (SI = 4 – 6), while Ceratopogonidae sp.1, Hydroptilidae sp.1, and *Neoplasta* sp., were most abundant in substrates of fine gravel and gravel (SI = 3). Orthocladiinae density was less consistent than other taxa but high densities were observed in substrates of cobbles (Appendix 2).

The contour plots indicate that GAMs predicted densities for dominant taxa are symmetrical in velocities of 1.8 $m \cdot s^{-1}$ and depths of 0.25 m. Predicted densities for rare taxa are also symmetrical but in a wider range of velocity – depth (Fig. 3 & 4). Contour shapes show that highest densities occurred in velocities lower than 2.5 $m \cdot s^{-1}$ and depths under 0.35 m, in cobbles substrates (SI = 6) for both groups (dominant and rare). Contours of *Andesiops ardua*, *Austrelmis* sp., *Hyalella* sp., *Ochrotrichia* sp. and Orthocladiinae show that high density is distribute in similar hydraulic conditions (Fig. 3), while *although in lower density Anomalocosmoecus* sp.*,* Ceratopogonidae sp.1, Hydroptilidae sp.1, *Neoplasta* sp., and Simuliidae sp. 1 present a a more disperse distribution in different hydraulic conditions (Fig.4).

3) Flow variability on habitat suitability models of representative taxa

Flow varies from 0.08 to 0.4 $m^{3} \cdot s^{-1}$ in San Juan stream and from 0.1 to 0.4 $m^{3} \cdot s^{-1}$ in Chalpi Norte stream. The historical low flow seasons in these streams showed that flow is reduce to 0.2 $m^{3} \cdot s^{-1}$ which is also the 90% return period flow. The flow registered in December 2009 was: 0.16 $m^{3} \cdot s^{-1}$ in San Juan stream and 0.18 $m^{3} \cdot s^{-1}$ in Chalpi Norte stream.

The habitat suitability models for representative invertebrates integrated to flow showed that, overall density increase when flow increase as habitats are availables (Fig. 5). Initial increment of flow suggest a positive effect on the density of most taxa, but a further increment cause a negative effect on *Austrelmis* sp. Orthocaldiinae, *Hyalella* sp., *Ochrotrichia* sp., *Andesiops ardua*, and *Austrelmis* sp., that show a density decrease with flow in San Juan and Chalpi Norte streams. Orthocladiinae have the highest densities and it's apparently associated with flows that exceeded 0.05 $m^{3}.s^{-1}$. *Austrelmis* sp., show increment until thresholds not higher than 0.018 $m^{3} \cdot s^{-1}$, when density started to decrease *Andesiops ardua* and *Ochrotrichia* sp., also show a density increase but in different scales for each stream, the higher density increment for both taxa are in San Juan stream (Fig. 5). *Anomalocosmoecus* sp., Ceratopogonidae, *Hydroptilidae* sp.1, *Neoplasta* sp., and Simuliidae sp.1, constitute the rare/less abundant taxa that showed an initial increment of density and then a sustained or stable density in higher flows. *Neoplasta* sp., showed similar density response to *Andesiops ardua* in Chalpi Norte stream.. Density of rare/less abundant taxa initially increased at suitable habitats when flow changed between 0.1 and 0.2 $m^3.s^{-1}$,

Discussion

Our study identified important associations between invertebrate community (and specific taxa) and the physical variables of habitats. Higher community richness and density were found in gravels of shallow, fast flowing waters with moss. Modeling of suitable habitats for representative taxa in high – altitude streams identified specific taxa preferences for high velocities as the result of low depths in cobbles substrates; these velocity -depth suitability increased for certain taxa (mainly dominant) and decrease for others less tolerant. Ultimately, the effect of flow variation on suitable habitats favored almost all taxa density.

Flow increase in high altitude streams causes the direct increment of hydraulic conditions such as depth and velocity of habitats. This flow increase creates new and different habitats for invertebrates, as seen in our study, that favor specific – taxa responses in density as the conditions are suitable. Therefore, our results demonstrate that suitability is the result of habitat's hydraulic variables interaction, where flow defined the extent to which each variable influence the taxa response.

1) Associations between invertebrate communities and physical variables

Invertebrates in high – altitude streams are associated to depths, velocities, and substrates that create mesohabitats and favor microhabitats that ultimately reflect a wide range of tolerances to hydraulic conditions (Statzner and Higler, 1986). These hydraulic conditions in headwaters tropical streams settle runs, riffles and cascades, mesohabitats known for hosting high invertebrate densities also in other latitudes (Jowett, 2003). Substrate defined basically the type of mesohabitat where invertebrate refuge, hold or feed; we have found that great richness and densities are associated to large substrates as reported before elsewhere (Winemiller *et al.*, 2010;

Quinn and Hickey 1990; Minshall, 1984). Specifically, high altitude streams showed that gravels and cobbles represent an important substrate for the community, probably due to the opportunity for shelter, refugia, or feeding resources (mosses) (Principe *et al*., 2007; Wallace *et al.,* 1997).

The high community richness and density associated to large substrates, high velocities and shallow waters showed to strength when moss was present on the substrate. The presence of a energetic/feeding source could account partly for the community association to physical variables when this source is present; although we know that tropical invertebrates share several feeding strategies and trophic levels (Tomanova *et al*., 2006), we are aware that richness and taxa in this combination clearly improved the community association to physical characteristics of habitats. However, other energetic/shelter sink sources might seem to offer this benefit, we found that algae and macrophytes were microhabitats with low richness and densities Armitage and Cannan (2002). .

2) Taxa used for habitat suitability models according to their hydraulic preferences

Suitability models for representative taxa from high altitude tropical streams represent to a great extent the community response to the physical/hydraulic conditions of habitats. Depth suitability decreased for almost all invertebrates and it was clearly related to the velocity suitability increase for several taxa, which has been reported by Jowett and Davey (2007) and also found in Andean páramo streams. Some groups like *Ochrotrichia* sp., Simuliidae sp.1, and Ceratopogonidae sp.1 could account as depth tolerant taxa and could be monitored to evaluate responses of depth increase in the stream channel. Tolerances and suitability could be related to life history traits (breathing, locomotion, and morphology) and these adaptations should be part of a further research as observed by Sagnes *et al*. (2008), who recorded different life stages and sizes of several trichopterans according to specific depths from a wide range.

Velocity suitability of several taxa from high – altitude streams agrees with observation of different altitudes and latitudes. TheAndean Limnephilidae: *Anomalocosmoecus* sp., showed preferences for low velocities which agree with findings of Holomuzki and Biggs (2000) that observed, in the southern hemisphere, that Limnephilidae move into the hyporheic zone when flow increases as a response to their preference for low velocities. We also found that Orthocladiinae in our study streams were abundant in shallow water and in moderate – high velocities and this response is comparable to findings from Collier (1993) in New Zealand. Merigoux and Dolédec (2004); Jowett (2000) showed similar hydraulic preferences for invertebrates as seen for the Andean páramo steams. Groups of invertebrates that showed velocity suitability increases should be taken into account for setting hydraulic sensitive taxa (eg. *Austrelmis* sp., *Ochrotrichia* sp., *Neoplasta* sp., Simuliidae sp.1). *Andesiops ardua* (Ephemeroptera) also show an interesting suitability increase up to 1 $m{\cdot}s^{-1}$ which contrast with its substrate suitability increase with large substrates; this pattern although could be partly compared to findings in the northern hemisphere by Encalada and Peckarsky (2006) that found that *Baetis bicaudatus* preferred large substrates for oviposition, and these substrates could be available with low depths and medium - high velocities.

Almost all representative taxa in high-altitude tropical streams showed a preference for large substrate as suggested by Minshall (1984). Jowett *et al.* (1991) found cased trichopterans in New Zealand related to medium to high substrates, which is similar to observed Andean trichopterans: *Anomalocosmoecus* sp. (high substrates), Hydroptilidae Sp1 (medium substrates), and *Ochrotricha* sp., (medium to high substrates), which reflects consistency of substrate suitability. Also, invertebrate’s densities in medium to large substrates in high –altitude tropical stream could be explained from taxa morphological adaptations, in order to be attached to large substrates with respective high velocities (eg. *Andesiops ardua, Ochrotrichia* sp, *Anomalocosmoecus* sp., Simuliidae sp.1), as seen for ephemeropterans and trichopterans form the northern and southern hemisphere (Dolédec *et al*., 2007; Collier *et al*., 1995).

Partly, the distribution of invertebrates according to the hydraulic preferences could be explained by life history traits and patchiness in suitable habitats (Shoffner and Royal, 2008: Hoffman *et al*., 2006, Jowett and Richardson, 1995). Models can only explain a proportion of the variation on invertebrate distribution and a great remainder of the variation is fundamental to understand habitats occupancy and to understand that not all habitats are necessarily occupied to its full capacity. Winemiller *et al*. (2010) suggested that life histories traits may enable invertebrates to utilize a variety of habitats and thus result in a more uniform distribution within the stream.

Habitat suitability models for representative taxa in páramo streams overlap between taxa, which could support suitable habitat models extrapolation to streams of similar characteristics (Leathwick *et al*., 2006). Guisan and Zimmermann (2000) suggest that dominant species modeling approaches to the community assemblage modeling, when species distributions overlap in the habitats. Suitable habitats for representative taxa should account for hydraulic conditions from a wide range of combinations, what suggest that habitat heterogeneity could support a specific-taxa suitability increase responses as well as increase community associations. High altitude tropical streams include a mosaic of habitats where the most common (riffles and cascades) respond for the suitable hydraulics that host high community and specific taxa densities.

3) Flow variability on habitat suitability models of representative taxa.

Suitability models vary with flow as the response of hydraulic variables changes. Several taxa in high altitude streams increased density when flow increased, showing that models reflect the increase of available/suitable hydraulic conditions for invertebrates to colonize or occupied to its full extent (Begon *et al*., 2006). We have observed this synergistic hydrological effect until the final increase or decrease of the taxa density from a suitability model. The effect of flow variability should account the hydraulic/physical variables interaction, in order to provide adequate responses of biota to flow (Poff *et al*., 2003).

The proposed model has been integrated to a range of flows, limited in historical data from high flows and events, what could be seen as a drawback to set environmental flows. The 90% return period flow only reflects partly the flow variability in these streams ecosystems. Although, the low flow season ecological data to build up suitability models, indicate the observed densities of taxa to natural low flows, further extrapolation and integrate calculated GAMs to flow to simulate density with flow through the hydraulic variables (Jowett and Davey, 2007).

The natural wide range of flows from these streams allows proposing a range of flows from 0.1 to 0.2 $m^3.s^{-1}$, that will maintain density increase of dominant and rare taxa in suitable habitats of streams. Doledec *et al*. (2007) proposed a range of flow in order to keep hydraulic preferences that contribute to taxa density. This proposed environmental flow range response to the low flow season ecohydrological data that is basically where streams present less variation in flow. Key research complements are needed to propose environmental flow regimes that show the monthly and daily hydrological variation and how invertebrates could response to it, as well as other ecosystem components, in order to keep the ecosystem integrity and function. This preliminary research has shown a way to propose environmental flows through habitat suitability models defined by GAMs, based on the low flows season natural response of invertebrates. We suggest a further integration of long term hydraulic and hydrological data to this tool to update and improve instream habitat models and set environmental flow regimes.

The community analysis and the taxa- specific models could contributed to a general goal of assisting in the management of water withdrawal from Andean páramo streams. Information based on the understanding of ecohydraulics could improve future decisions and maintain high altitude tropical streams conditions to provide not only high water quality for main cities, but also provide suitable habitats for communities, that maintain trophic and biogeochemical cycles. Suitable habitats could aid to restore and manage streams in a highly water depended ecosystem in Ecuador.

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Tables

Table 1. Physico-chemical parameters at páramo streams in the tropical Andes of Ecuador, variables were calculated from monthly spot readings taken during the day.

	San Juan	*Chalpi Norte*
Physical variables		
Altitude (m asl)	3740	3820
Flow (m^3/s)	0.089	0.094
Width (m)	1.15	1.28
Depth (m)	0.28	0.37
Chemical variables		
pH	7.62	7.21
Conductivity (uS/cm)	65.6	25.7
Temperature (^{o}C)	9.1	8.9
Dissolved oxygen concentration (mg.l^{-1})	7.2	6.7

Oxygen Saturation (%)	65	63
Alkalinity (mg.l^{-1} $CaCO_3$)	35	35
Chloride (mg.l^{-1})	2.65	8.62
Ammonia (mg.l^{-1})	0.07	0.03
Nitrates (mg.l^{-1})	0.2	0.3
Nitrites (mg.l^{-1})	0.006	0.003

Table 2. Habitat characteristics and variable ranges of Andean páramo streams, expressed by the number and percentage of samples registered from total locations, *N* = 200; invertebrate mean richness and abundance ± SE registered for high – altitude tropical streams.

	Habitats		*Invertebrate community*			
	n	*%*	*Mean Richness*	*±SE*	*Mean Density*	*±SE*
Mesohabitat						
Pool	23	11.5	7	0.5	2150	355
Riffle	72	36	9	0.5	2250	290
Run	88	44	7	0.2	2150	135
Cascade	17	8.5	8	0.5	3200	785
Microhabitat						
Algae	76	38	7	0.2	2400	290

Moss	83	41.5	9	0.5	2700	405
Macrophytes	31	15.5	8	1.1	1750	390
Depth (m)						
0.05 – 0.136	63	31.5	8	0.2	2600	270
0.137 – 0.223	97	48.5	7	0.2	2150	160
0.224 – 0.319	31	15.5	9	0.3	2350	315
0.32 – 0.406	6	3	6	1.2	1300	395
0.407 – 0.493	3	1.5	7	1.8	1550	115
Velocity (m/s)						
0 – 0.54	27	13.5	7	0.6	2600	270
0.55 – 1.09	57	28.5	7	0.3	2000	160
1.1 – 1.64	43	21.5	8	0.4	2600	315
1.65 – 2.19	61	30.5	6	0.2	2200	395
2.2 – 2.74	12	6	5	0.6	2500	115
Substrate Index						
3 (sand)	17	8.5	6	0.6	2200	445
4 (fine gravel)	13	6.5	8	0.6	1650	320
5 (gravel)	42	21	9	0.5	2400	360
6 (cobble)	69	34.5	7	0.3	2050	225
7 (boulder)	59	29.5	8	0.2	2450	240
8 (bed rock)	0	0	0	0	0	0

Sand= 0.062 - 2mm, fine gravel = 2 – 4mm, gravel = 4 – 64 mm, cobbles = 64 – 256 mm, boulder = 256 – 1024mm.

Table 3. Representative taxa (dominant *d*, and rare *r*) from the invertebrate community of high-altitude tropical Andes páramo streams, percentages of samples in which taxa occurred and an average taxa density ±SE, over the 100 samples in each stream.

	San Juan				*Chalpi Norte*			
Taxa	%	Ind m^{-2}	±*SE*	dominant /	%	Ind m^{-2}	±*SE*	dominant /
Andesiops ardua	93	567	70	*d*	65	132	12	*d*
Austrelmis sp.	83	313	33	*d*	47	99	8	*d*
Anomalocosmoecus sp.	35	112	8	*r*	49	135	11	*r*
Ceratopogonidae sp.1	32	130	8	*r*	43	87	6	*r*
Hyalella sp.	47	239	25	*d*	87	603	128	*d*
Hydroptilidae sp.1	33	83	5	*r*	13	66	3	*r*

Neoplasta sp.	27	58	27	*r*	58	125	9	*r*
Ochrotrichia sp.	79	300	32	*d*	86	461	61	*d*
Orthocladiinae	95	604	48	*d*	97	1146	78	*d*
Simuliidae sp.1	45	150	15	*r*	37	88	7	*d*

Table 4. Andean páramo invertebrate preference defined by averaged physical variables sample locations (N = 200), and averaged sample variables weighted by number of taxa.

	Depth (m)	*Velocity (m/s)*	*Substrate index*
Average sample	0.18	1.26	6 (cobble)
	Average sample variables weighted by number of taxa		
Andesiops ardua	0.17	1.21	6
Anomalocosmoecus sp.	0.17	1.27	6
Austrelmis sp.	0.17	1.33	6
Ceratopogonidae sp.1	0.17	1.32	5
Hyalella sp.	0.17	1.21	6
Hydroptilidae sp.1	0.17	1.16	5
Neoplasta sp.	0.19	1.34	5

Ochrotrichia sp.	0.18	1.23	6
Orthocladiinae	0.18	1.28	6
Simuliidae sp.1	0.18	1.37	6