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INFLUENCIA DE LA DISPERSIÓN DE MACROINVERTEBRADOS ACUÁTICOS SOBRE LA COMPOSICIÓN DE COMUNIDADES EN RÍOS DE PÁRAMO EN LA RESERVA ECOLÓGICA ANTISANA

Disertación previa a la obtención del título de Licenciada en Ciencias Biológicas

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Certifico que la disertación de la Licenciatura en Ciencias Biológicas de la candidata Ana Carolina León ha sido concluida con conformidad con las normas establecidas; por lo tanto, puede ser presentada para la calificación correspondiente.

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1. RESUMEN

La dispersión tiene un efecto importante en el ensamblaje de las comunidades porque interviene en procesos de colonización, flujo génico y divergencia evolutiva. La dinámica y estructura de cualquier comunidad depende de la entrada y salida de individuos. En este estudio buscamos entender la importancia del vuelo de insectos adultos sobre el ensamblaje de las comunidades acuáticas de ríos altoandinos. Para esto, medimos la distancia de vuelo de macroinvertebrados adultos con trampas Malaise, colocadas a lo largo de un transecto perpendicular a un río en la Reserva Ecológica Antisana, REA en los Andes de Ecuador. Con la información obtenida de los muestreos estimamos dos indicadores de vuelo: 1) eficiencia de vuelo, calculada a partir del ajuste de los datos de distancia de vuelo a ecuaciones de probabilidad de dispersión, y 2) capacidad de vuelo, equivalente a la longitud relativa del ala (Relative Wing Lenght, RWL) de los insectos capturados. Con esta información, y con datos obtenidos en estudios previos sobre la fauna acuática en 51 sitios de la reserva, analizamos la relación entre los indicadores de vuelo y la estructura de las comunidades, por medio de análisis de regresión lineal. Los análisis de regresión no mostraron relaciones significativas entre el vuelo (eficiencia o capacidad) y la distancia geográfica, la similitud ambiental, y la similitud en el grado de influencia glaciar de los macroinvertebrados adultos. Por otro lado, encontramos relaciones significativas con la estructuración espacial de los insectos y su tamaño (largo). A medida que aumenta la longitud del insecto, la distancia promedio y la semejanza medioambiental disminuyen. De manera similar, encontramos una tendencia significativa con taxones más largos presentes en un menor número de sitios. Estos resultados podrían deberse a que a una escala pequeña, la dispersión podría tener un "efecto masivo", que significa que los dispersores activos o fuertes también podrían tener una baja limitación ambiental produciendo una homogenización de la

estructura de la comunidad en sitios adyacentes independientemente de sus condiciones ambientales. No está claro el efecto del tamaño de los adultos macroinvertebrados en la dispersión y es necesario que en estudios futuros se hagan más mediciones morfológicas para clarificar estas dudas y así comprender a profundidad el efecto de la dispersión en la estructuración de las comunidades.

Palabras Clave: Andes, dispersión, ensamblaje de comunidades, macroinvertebrados, ríos altoandinos

2. ABSTRACT

Dispersal has an important effect on community assemblage, because it affects colonization processes, gene flow, and evolutionary divergence. The dynamics and structure of any community depend upon inputs and outputs of individuals. In this study, we wanted to gain insight into the importance of adult aquatic insect dispersal on the structure of aquatic communities in high altitude Andean catchments. For this, we measured aquatic insects dispersal distance with Malaise traps placed along a transect perpendicular to a stream at the Antisana Ecological Reserve (REA), in the Ecuadorian Andes. With this information, we estimated two indicators of flight: 1) flight efficiency, which was calculated from the adjustment of flight distance data to dispersal probability equations, and 2) flight capacity, equivalent to the relative wing length (RWL) of the captured insects. With this information, and with data obtained from previous studies on aquatic fauna in 51 sites at REA, we analyzed the relationship between flight indicators and spatial distribution of insects using linear regression analyses. Regression analyses showed no clear relationship between flight (efficiency or capacity) and geographical or environmental structuring of adult macroinvertebrates. On the other hand, we found significant relationships between spatial structuring and length of macroinvertebrate taxa. As insect length increased, mean overland distance and mean environmental similarity decreased (with high significance). In a similar fashion, we found a significant tendency for longer taxa to be present in a lower number of sites. The most probable explanation for our results might be that at small spatial scales dispersal can have a “mass effect” on community assemblage, meaning that active or strong dispersers should compensate environmental filtering, homogenizing communities at adjacent sites, independent of their environmental conditions. The relationship between body size and spatial structure of communities is not clear. Future studies should

measure additional morphological characteristics of insects in order to clarify remaining questions and thus understand the degree of the effect of dispersal in community assembly.

Key Words: Andes, dispersal, community assemblage, aquatic insects, high Andean streams.

3. MANUSCRITO PARA PUBLICACION

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TITULO: Influence of dispersal for macroinvertebrate community assemblage in high altitude Andean streams of the Antisana Ecological Reserve.

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INTRODUCTION

Dispersal is a key component of aquatic insects population dynamics (Rundle *et al.*, 2002), because the dynamics of any ecosystem depend upon inputs and outputs of individuals as well as on intrinsic processes (Peckarsky, Taylor & Caudill, 2000; Bohonak & Jenkins, 2003). Dispersal is defined as the movement of individuals from one area or habitat to another. In the case of insects, this process is fundamental to locate potential partners and for females to find favorable oviposition sites that ensure their reproductive success (Hauer & Lamberti, 2006). Also, it avoids inbreeding and allows insects to locate new sites with low density and few resource competitors, and it is a potential escape from unfavorable conditions like limited resources, predators, pathogens and parasites (Bilton *et al.*, 2001). Dispersal occurs in rates that are species specific, provides gene flow that affects the genetic structure of populations and helps maintain genetic diversity among and within them (Hauer & Lamberti, 2006). Moreover, from a metacommunity perspective, dispersal of individuals between communities helps maintain connectivity between them and allows the recolonization of extinct patches (Heino, 2013; Heino *et al.*, 2013).

Stream networks have a discontinuous and dendritic structure, which contributes to the diversity of the freshwater systems (Brown & Swan 2010). Because of their spatial configuration hydrographic networks have communities that are isolated from each other and remain connected by the flow of individuals along the streams and by dispersal through the air (Cottenie, 2005). However, dispersal through the landscape has often been ignored and thus its impact on local ecological processes has been underestimated. Aquatic macroinvertebrates have developed amazing adaptations to live, move, feed and reproduce in water (Merritt & Cummins, 1995) like posterior legs like oars, hooks, hairy body, claws, mouth brushes, device for catching food made by the insect or part of their body structure, cases made of different materials, etc. (Dominguez & Fernandez, 2009). These organisms colonize new habitats through diverse routes, which include: 1) The movement of organisms downstream, mainly passively (drift); 2) upstream movements along the sediment and 3) air dispersal by terrestrial adults (Grönroos *et al.,* 2013). Many macroinvertebrates have flying adults which are in charge of active aerial dispersal (Brown & Milner, 2012), while others are passively dispersed by vectors, such as wind or animals. Passive dispersal efficiency normally decreases with increasing size of the propagule (De Bie *et al.*, 2012; Vanschoenwinkel *et al*., 2008).

In stream communities, dispersal type and strength has been found to interacts with environmental heterogeneity to determine species composition, because differences in environmental conditions set a degree of co-occurrence of species (Heino, 2013; Bell, 2001; Reitalu *et al.*, 2008). In general, different species have different tolerance to environmental conditions and different niches (Chase & Leibold, 2003), so they should have different optimal sites along environmental gradients (niche position). As a consequence, any two species differing in environmental responses are expected to be, at least partially, segregated across a set of sites if there is variation in environmental conditions (Bradley & Bradley, 1985). As found by Heino (2013) adult flying insects with active dispersal over long distances, have a greater choice of habitat and hence, are most often found on sites with optimum environmental conditions , with low levels of random distribution. Instead, insects with aquatic adult and passive dispersal cannot perform habitat selection, and dispersal limitation prevents them from reaching environmentally suitable sites, which leads to a more random distribution (Heino, 2013; Cauvy-Fraunié *et al.*, 2015).

Within stream dispersal, such as drift and upstream larval movement, has been studied extensively (Waters, 1972; Soderstrom, 1987; Brittain & Eikeland, 1988; Allan, 2007). However, there are fewer studies about aerial dispersal of flying adults of aquatic insects among and within streams (Bilton *et al.,* 2001; Heino, 2013; Heino *et al.,* 2013; Kelly *et al.,* 2002; Kot *et al.,* 1996; Thompson & Townsend, 2006). Such information is particularly scarce in the tropics (Cauvy-Fraunié *et al*., 2015), and very little is known about its influence on community assembly processes in tropical mountain streams. Environmental conditions in these streams differ markedly from streams from temperate mountains, mainly due to lack of seasonality in temperature, but ample variations in diel temperatures (Kuhn *et al*., 2011). Also, previous studies have shown high spatial variation in environmental conditions, even between streams located at short distances (Jacobsen & Dangles, 2012). This variation is caused by the junction of streams from different origins (drainage basin, spring water and glacier melt) (Jacobsen, Schultz & Encalada, 1997; Cauvy-Fraunié *et al.*, 2014; Cauvy-Fraunié *et al.*, 2014)

In this study, we wanted to understand the influence of dispersal ability of adult aquatic insects on the structure of aquatic communities in an Andean catchment with glacier influence. Specifically, we wanted to understand if stronger, more efficient flyers, present a non-random distribution, as they are able to actively choose their oviposition sites, and if the opposite happens with weak flyers. For this, we measured adult dispersal with Malaise traps located at different distances along a transect perpendicular to a stream at the Antisana Ecological Reserve (REA in Spanish). Trapped adults allowed us to make estimations about flight ability (efficiency and capacity), which were later related to the distribution of aquatic insects collected in previous studies at 51 streams in the REA. This is the first study of terrestrial dispersal in glaciarized Andean catchments and provides preliminary information about its influence on metacommunity structuring in these stream networks. Such information is of prime importance, especially given the imminent retreat of glaciers and the reduction of glacial melt water contribution to streams, under ongoing global warming.

METHODS

Study area

The study was conducted in streams from the Antisana Ecological Reserve (REA in Spanish) in Ecuador (Figure 1), on the slopes of the Antisana Volcano, located at the eastern cordillera of the Ecuadorian Andes, 50 kilometers southeast from Quito, in the province of Napo (Bourdon *et al.*, 2002). In the study region, air temperature, humidity and radiation do not vary systematically during the year, while precipitation, cloudiness and wind speed have a seasonal variability (Cadier *et al.*, 2007). There is a high inter stream variability with respect to physical and chemical conditions, related to the confluence of waters from different origins: glacier (G), spring (S), and superficial drainage (D) (Andino. unpubl. data).

Adult dispersal

To measure the aerial dispersal of adult aquatic insects, we first selected a stream with high representation of taxa from the REA and with a relatively flat topography that allows insects to fly away from the stream. This selection was made with information from previous studies performed by the Limnology Laboratory of Pontificia Universidad Católica del Ecuador (PUCE). Also, we selected a stream that was located at a distance of at least c.a. 1.5 km from its nearest neighboring stream, to avoid collecting insects from other streams. The stream that fulfilled these requirements (marked on Figure 1 as stream 28) is located at 4005 m above sea level (a.s.l.), north of Lake La Mica, at 17M810863mE, 9941899mN.

On the selected stream we placed Malaise traps at 5, 25, 50, 100, 200 m from the stream, along a perpendicular transect which began at the edge of the stream. Malaise traps were scaled 5m from each other, in order to reduce interference between them. A two-week pilot test was conducted during May 2014, to monitor the effectiveness of the traps. The traps were deployed again on September 28, 2014. We collected insects every week until November 16 of the same year. Collected insects were kept in 75% ethanol and taken to the laboratory for identification to family or genus, using North and South-American macroinvertebrate keys (Merrit & Cummins, 1995; Domínguez & Fernández, 2009; Wilson & Sandoval, 1996; Brown *et al.*, 2009; Brown *et al.*, 2010; Triplehorn & Johnson, 2005; Holzenthal *et al.*, 2007).

Data analysis

Flight efficiency and capacity

We estimated the ability of collected adults to fly in two ways. First, we adjusted data on the proportion of individuals flying a given distance to two dispersal kernel models, to obtain indicators of flight efficiency: 1) an exponential model with one parameter (Crespo-Pérez *et al*., 2011, appendix 1) and 2) a Gamma model with four parameters (Nathan *et al*., 2012). Note that this procedure was only performed on taxa whose data on proportion of insects and distance followed a dispersal kernel form (see Nathan *et al*., 2012).

Exponential model:

$$P = \exp(-\varepsilon\delta)$$

where P is the proportion of insects flying a given distance, δ is distance, and ε is flight efficiency.

Gamma model:

$$P = a\exp\left(\frac{\delta - b}{c}\right)\left(\frac{\frac{\delta - b}{c} + d - 1}{d - 1}\right)^{d-1}$$

where *P* is the proportion of insects flying a given distance, δ is distance, and *a*, *b*, *c* and *d* are parameters to be estimated. Of these, parameter *c*, gives the amplitude of the curve and was used as an indicator of flight efficiency. For both models (Exponential and Gamma), we obtained P and δ from the data and estimated the value of the parameters, for each taxon, by non-linear least squares, using Microsoft Excel's Solver ®.

Second, we estimated flight capacity of all taxa of adult aquatic insects collected on Malaise traps, by calculating the Relative Wing Length (RWL) (Malmqvist, 2000) of 30 individuals of each taxon, which corresponded to forewing length divided by body length. For this, we used a graduate stereoscope Zeiss Stemi 200-C.

Macroinvertebrate community assemblage: relationship between flight efficiency and capacity and stream distance and environmental heterogeneity

We studied the relationship between flight efficiency and capacity of our sampled flying adults and the distribution of their larvae at 51 stream sites at REA (Figure 1). We obtained data on larvae distribution from previous studies by the Limnology Laboratory of Pontificia Universidad Católica del Ecuador (PUCE) (Cauvy-Fraunié *et al*., 2015). Larvae from that data set were collected with a Surber sampler, once between May 2009 and January 2010, in the morning before glacial flood (see Cauvy-Fraunié et al., 2015 for more information on larvae collection). As mentioned by these same authors, temporal variability in community composition in the study streams is low, so differences in sampling dates have probably little effect on our results.

To understand if stronger fliers show stronger spatial structuring, we compared flight efficiency and capacity to 1) the mean overland distance between all sites where each taxon is present (i.e. shortest distance in a straight line between pairs of sites); 2) the mean environmental similarity; and 3) the mean similarity in level of glacial influence between all sites where each taxon is present. We analyzed the relationship between the flight ability variables (efficiency and capacity) and the geographical distance and environmental similarity variables with linear regression analyses. Additionally, to understand if insect size is related to their spatial distribution, we regressed mean length of each taxon to mean overland distance, mean environmental similarity, mean glacial similarity, and the number of sites where each is present.

We calculated overland distances between sites with ArcGIS (version 10.0), using the *Analysis/Proximity/Point distance* tool. Environmental similarity between sites was calculated with the Bray-Curtis similarity index with the software PAST (Paleontological Statistics, version 2.17c). The index was calculated with data on stream slope, height, width, conductivity, temperature, turbidity, pH, chlorophyll A concentration, amount of Coarse Particulate Organic Matter (CPOM), and substrate stability (calculated with the Pfankuch index, Pfankuch 1975; Andino, unpubl. data). For glacial influence we used the index calculated by Cauvy-Fraunié *et al*., (2015). Briefly, these authors used Non-centered Principal Component Analysis (NPCA) with the environmental variables more strongly related to glaciality (temperature, conductivity, turbidity and substrate stability), to create an index scaled between 0 and 1 (1=higher glacier influence, 0=no glacier influence). Similarity in glacier influence between pairs of sites was calculated as the absolute difference between their glacier indices, subtracted from one.

RESULTS

Adult dispersal

Over the nine weeks of sampling, we found 22 taxa of flying adult macroinvertebrates with our Malaise traps (Table 1). We collected a total of 4626 individuals, of which 49.11% belonged to Orthocladinae and 23.08% belonged to Tanypodinae (Diptera: Chironomidae) (Table 1). It is important to note that the study by Cauvy *et al*. 2015, collected 45 taxa that have flying adults in the same stream (Appendix 1).

We were able to adjust dispersal kernels only to eight taxa: *Allaudomyia, Blepharicera,* Diamesinae, *Molophilus, Neotrichia, Prionocyphon,* Orthocladinae, and Tanypodinae (Figure 2). The remaining taxa presented only a few individuals that reached a single distance; others presented variable numbers of individuals at each distance, with no apparent pattern, and therefore, could not be adjusted to any of the models. In general for the eight taxa with the adjust dispersal kernel, as the distance from the stream increased the proportion of individuals decreased, but the form of the kernel varied among taxa. The Gamma model performed better than the exponential model (higher R^2 values for all taxa, except *Allaudomyia*, where both models presented the same R^2 value, Figure 2), and allowed to model cases with higher probability at intermediate distances and lower probability at short distances (e.g. *Blepharicera* and *Molophilus*). In the following we only present results for the flight efficiency parameter of the Gamma model (i.e. parameter *c*). Relative wing lengths of all 22 taxa can be seen in Table 2.

Macroinvertebrate community assemblage: relationship between flight efficiency and capacity and stream distance and environmental heterogeneity

Data on larvae distribution in the 51 stream sites showed that many of the taxa collected with our Malaise traps, are distributed in many of the sites, with varying abundances (Figure 3 shows the distribution of four of these taxa). Also, some of the taxa (9 out of 22) seemed to be restricted to only a few sites. For example, Hydroscaphidae is present only in streams 28 and 45, which are relatively far away from each other (2368.58 meters, Appendix 1).

Regression analyses showed no clear relationship between flight (efficiency or capacity) and geographical or environmental structuring of macroinvertebrates. Specifically, we found a slight tendency (but not significant) for mean environmental similarity to increase with higher flight efficiency, *c* (Figure 4b). Relationships between flight capacity (RWL) and mean overland distance and mean environmental similarity were very weak and non-significant (Figure 4c, 4d). The same was true for both flight measurements and their relationship with mean glacier influence similarity (Figure 4e. 4f).

Length of macroinvertebrate taxa showed stronger, significant relationships with community structuring (Figure 5). For instance, as insect length increased, mean overland distance and mean environmental similarity decreased (with high significance). In a similar fashion, we found a significant tendency for longer taxa to be present in a lower number of sites. No clear relationship was found between insect length and mean glacier influence similarity.

DISSCUSION

Measuring and modeling dispersal of adult aquatic insects

Studying insect dispersal is difficult because it involves detection of movements by capturing specimens. Moreover, studying aquatic macroinvertebrate dispersal might present additional difficulties, because methods may require modifications for use in water (Bilton *et al.,* 2001), and most of the macroinvertebrates have a small size which makes it easier for them to escape (Verberk, Siepel & Esselink, 2008; Cummings *et al*., 1995). There are some techniques for measuring dispersal of adult aquatic insects, like capture-mark-recapture (this requires marks that will not be lost in water), or simple capture methods with sticky traps, light traps and Malaise traps, located at varying distances from a source (i.e. a stream) (Winterbourn *et al.*, 2007). In this study we used Malaise traps to capture adult aquatic insects, as this method has been successfully used in a previous study to collect aquatic insects and measure their dispersal (Peterson *et al*., 2004). This method presented some problems that complicated our ability to answer our study questions. First, the irregular topography of the reserve made it difficult for us to locate a site with a wide and open space that allowed measuring dispersal over long distances. Therefore, we were able to locate the farthest trap only at 200 m from the stream. Future studies should find alternative ways to measure dispersal at longer distances, like capture-mark-recapture methods (Harabis & Dolny, 2011; Van De Meutter, Stoks & De Meester, 2006; Beirinckx *et al.*, 2006; Schtickzelle, Baguette & Le Boulenge, 2003). Second, our Malaise traps did dot capture the 45 flying taxa present in the stream (collected with Surber samples), maybe because emergence periods did not match the dates when we sampled for adults. Published information about tropical macroinvertebrate phenology and life cycles is very scarce (Porst *et al*., 2012; Durance

& Ormerod 2007; Johnson *et al*., 2012; Clarke *et al*., 1997; Bonada *et al*., 2007) and, even more so for high altitude sites (but see Ríos-Touma *et al*., 2011). More studies should be conducted in order to better understand discrepancies between aquatic and terrestrial collections of macroinvertebrates. Third, the strong winds in the study region might have influenced our results, as it may have passively transported insects to our traps. We have no information about the influence of wind on the flight of high Andean aquatic insects, but previous studies in other areas have shown that insect distribution is affected by wind (Pasek, 1988). Future studies should measure wind strength and consider it as a possibly strong driving factor of insect dispersal. Finally, lateral dispersal might not be significantly influencing community assemblage. Most of the flight activity could be taking place along the stream, rather than laterally away from the stream channel (Petersen *et al.,* 2004). Therefore, for future studies it would be very useful to study migration along the stream, because even though there have been many empirical studies about this type of migration (Allan & Castillo, 2007; Kopp, Jeschke & Gabriel, 2001), none have been done in the tropical Andes and there are still many questions about its effect on population persistence and community assemblage (Kopp *et al.,* 2001; Speirs & Gurney, 2001).

Modeling dispersal requires adjusting mathematical functions to dispersal data. Several mathematical functions have been used for this purpose – for example, Gaussian, Negative Exponential, Exponential Power, (Inverse) Power-law and Gamma (Nathan *et al.,* 2012). These functions describe dispersal in different ways, have different numbers of parameters, each one potentially operates at different scales and/or generates a different dispersal kernel. In this study, we tested two types of functions that differed in their number of parameters. The higher number of parameters in the Gamma function allowed modeling greater forms of dispersal kernels for short, intermediate, and long distance dispersal (Furstenau & Cartwright, 2016). This proves that this is a more flexible model that model, that results in better-adjusted curves than the Exponential model. Other studies have also used this model successfully to model dispersal of seeds (Levin *et al*., 2003; Pegman, Perry & Clout, 2016), pollen (Klein, Desassis & Oddou-Muratorio, 2008), birds (Van Houtan *et al*., 2007), macroinvertebrates (Johnson *et al*., 2012), and mosquitos (Winskill *et al*., 2015).

Dispersal and community assembly

There are only a few studies relating dispersal to community assembly and even less about dispersal of insects from lotic communities (Heino, 2013; Petersen *et al.,* 2004; De Bie *et al.,* 2012; Beirinck *et al.,* 2006; Bilton *et al.,* 2006; Gronroos *et al.,* 2013). As reported by Heino *et al.,* (2015), there are many aspects influencing community structure that remain unexplained, For instance, the influence of dispersal is very poorly understood (Cauvy-Fraunié *et al.,* 2015), and a better understanding of dispersal ability and strength of benthic with flying adults would allow better understanding of community dynamics (Poff *et al.,* 2006). In this study, we wanted to breach this gap by measuring the distance traveled by adult aquatic insects and the influence of flight ability in the composition of lotic communities. Specifically, we wanted to prove if weak dispersers show a random spatial structure, because of their inability to actively reach sites with suitable environmental conditions, and if strong dispersers – that are able to actively fly to sites with optimum conditions – have a non-random distribution and a high level of spatial structuring (Cauvy-Fraunié *et al.,* 2015). However, our results showed non-significant relationships between flight ability and the spatial and environmental structure of sites were taxa are present. A possible explanation for this might be that at small spatial scales dispersal may have a “mass effect” on community assemblage. This means that active or strong dispersers should also show low environmental filtering, homogenizing community structure at adjacent sites, independent of their environmental conditions (Leibold *et al.,* 2014). On the other hand, we found significant relationships between insect length and spatial and environmental structure of the sites at which they are present. Longer insects occur in closer (lower overland distance) and environmentally different sites. Also, longer taxa are usually present in a lower number of sites. These results are opposed to those found by Hildrew, Raffaelli & Edmonds-Brown (2007) that says that larger insects associated with freshwaters have more control over their flight direction and speed, and achieve long-distance dispersal. Nevertheless, the effect of body size and dispersal mode shows in metacommunity structure is not yet clear. These traits should be considered when developing a predictive framework for metacommunity dynamics. Our results are indeed puzzling, because according to studies on tolerance of macroinvertebrates to environmental conditions, taxa with longer development times, small body sizes or both, are more tolerant to unfavorable environmental conditions than shorter lived, bigger taxa (Verberk, Siepel & Esselink, 2008). This means that bigger taxa should be present in more environmentally similar sites, and shorter taxa should be present in more different sites, which is not the case in our study. More studies should be conducted in order to clarify these remaining questions. More precise morphometric measurements of insects could maybe help to clarify these questions.

Avenues for future research

This is a pioneer study about aquatic insect flight in a high altitude Andean catchment. This study provides preliminary information about the influence of dispersal on community assemblage. Nevertheless, more studies are urgently needed about dispersal abilities of benthic species, in order to fully understand the importance of active and passive dispersal for community composition and assemblage (Bilton *et al*., 2001). In this study, we estimated flight ability with dispersal kernels and wing measurements but were not able to make a clear distinction between active and passive dispersers. Therefore, we suggest that future studies focus on such differentiation, and relate their distribution to wind strength and direction. This would provide more insight about dispersal dynamics, the role of stochastic, passive dispersal and their influence on community structure.

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4. NORMAS PARA PUBLICACION

Instrucciones para autores

A single file should be prepared containing the title page. Summary, Text, Acknowledgments, References and tables (see guidelines below).

Additional files may be created for each figure. Microsoft Office 2007/2010 file formats (i.e. .docx. .xlsx etc.) are acceptable on S1M.

- Please leave the right-hand margin unjustified

- Turn the hyphenation option off

- Use tabs. Not spaces to separate data in tables

(a) ***Title page.*** This should include the title. List of author's names, Institute or laboratory of origin, Name, Postal address and email address of the author to whom proofs should be sent. an abbreviated title for use as a running head line and five keywords, which should be relevant for literature searching and each normally comprising not more than two words.

(b) ***Summary.*** All papers should include a summary. In short numbered paragraphs, limited to about 3% of the length of the text, and in any case to not more than 500 words. This should provide a concise statement of the scope of the work and its principal findings and be fully intelligible without reference to the main text.

(c) ***Introduction.*** This should contain a clear statement of the reason for doing the work. Outlining essential background information but should not include either the results or conclusions.

(d) ***Methods***. This should be concise but provide sufficient details to allow the work to be repeated.

Product and manufacturer names: Where specific named materials/products are mentioned or named equipment used (including software packages). These should be identified by their manufacturer. Followed by the manufacturer’s location (e.g. town. state. country), or a source reference should be given if a standard or replicated procedure is being followed.

(e) ***Results.*** This should not include material appropriate to the Discussion.

(f) ***Discussion.*** This should highlight the significance of the results and place them in the context of other work.

(g) ***Acknowledgments.***

(h) ***References.***

(i) ***Tables.***

(j) ***Figure legends.***

(k) ***Illustrations***. The original drawings should not be sent until the Editor requests them. Please see section ‘Tables. Figures and Illustrations’ for further information on electronic submission of artwork.

There are no formal limits to the length of papers, but page space in the journal is tight, and most papers (except review articles) should be no longer than 9.000 words in total (text plus references. excepting Figs and Tables).

5. FIGURES

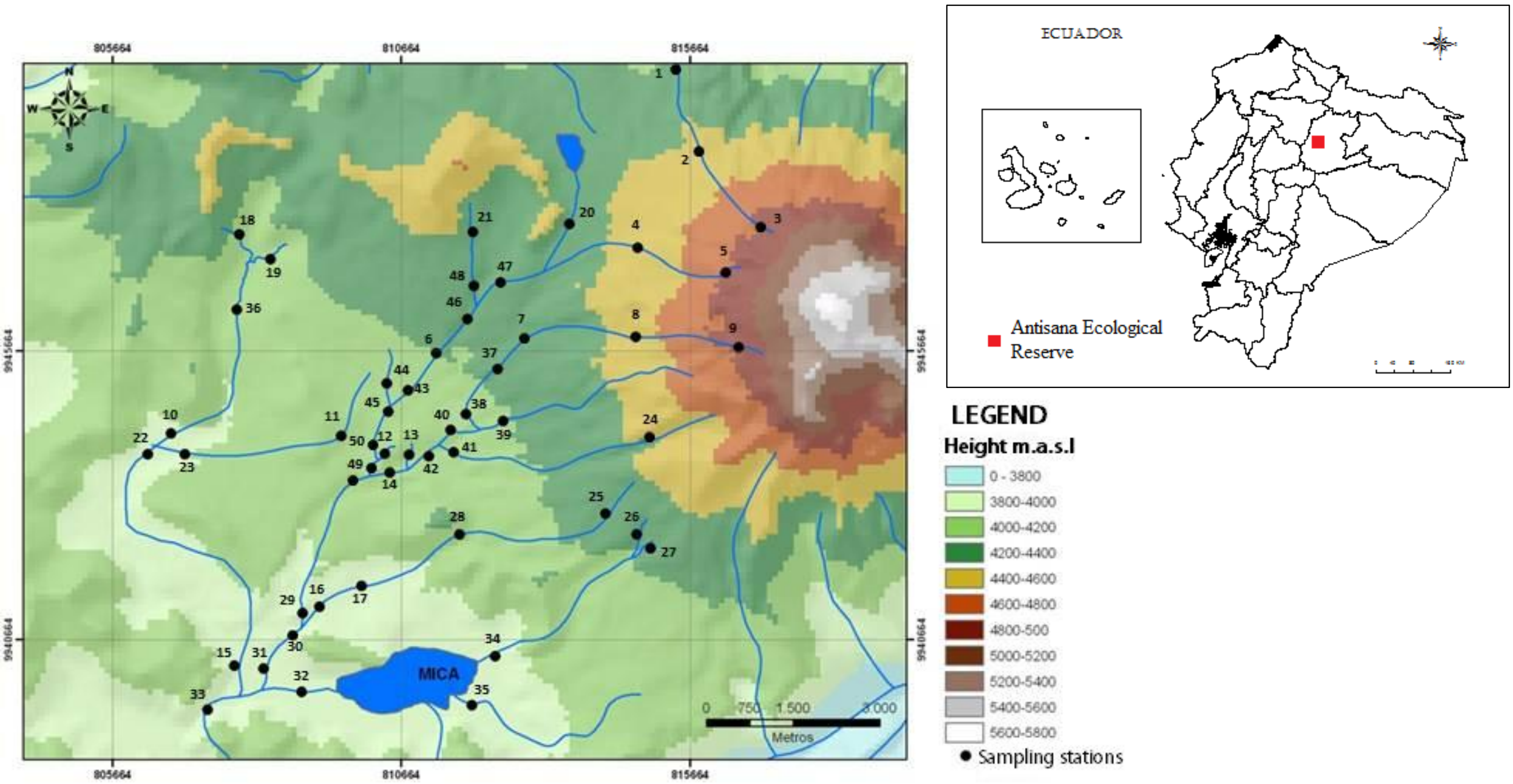

Figure 1. Map of 50 points in several streams of the REA sampled between 2008 and 2014 by the Limnology Laboratory of PUCE. Map modified from Espinosa (unpubl. data).

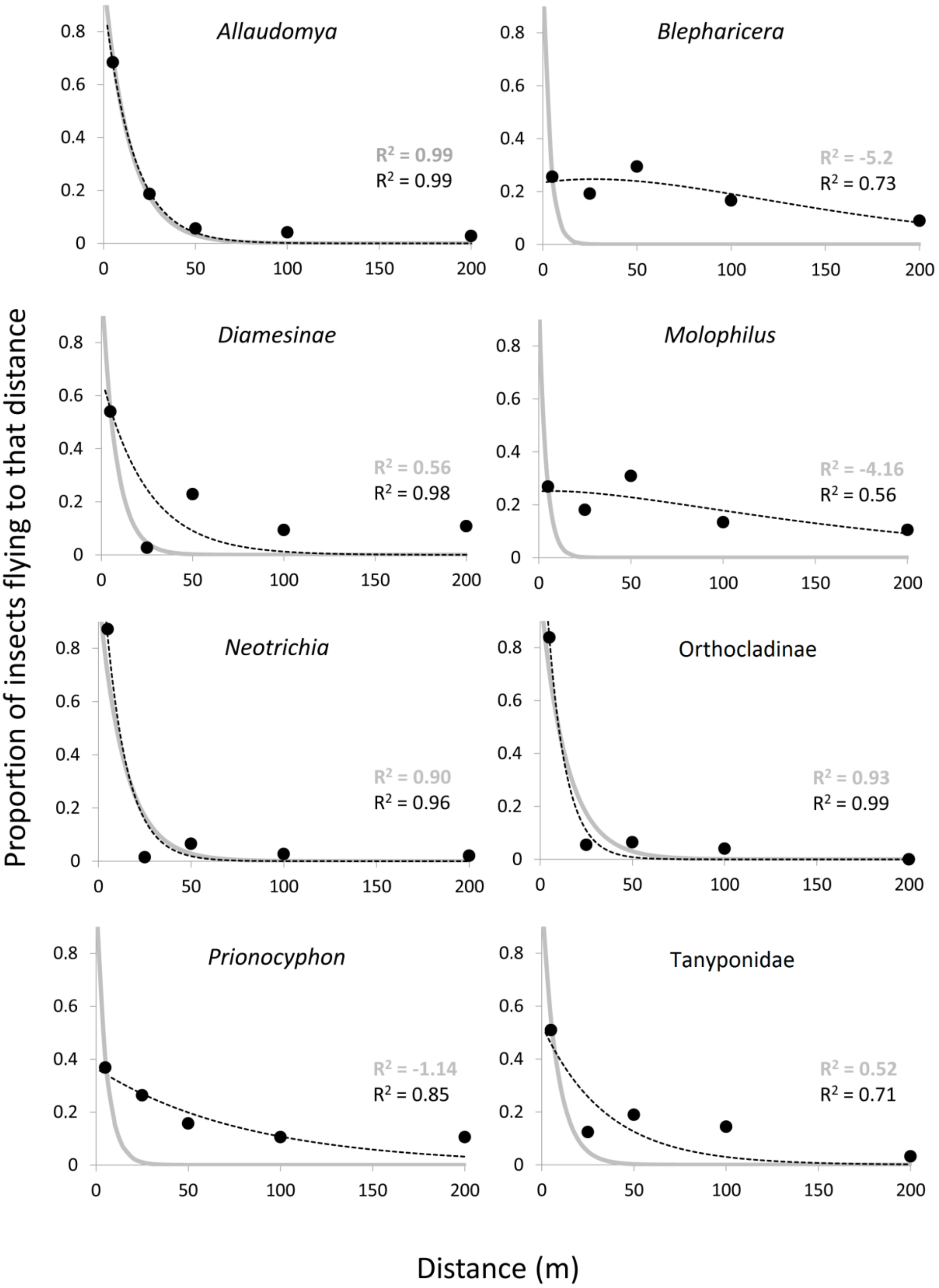

Figure 2. Dispersal probability of adult aquatic insects. Dots correspond to the proportion of insects caught at each distance from the stream. Continuous gray lines correspond to the adjusted Exponential model to the data. Dotted black lines represent the Gamma model adjusted to the data.

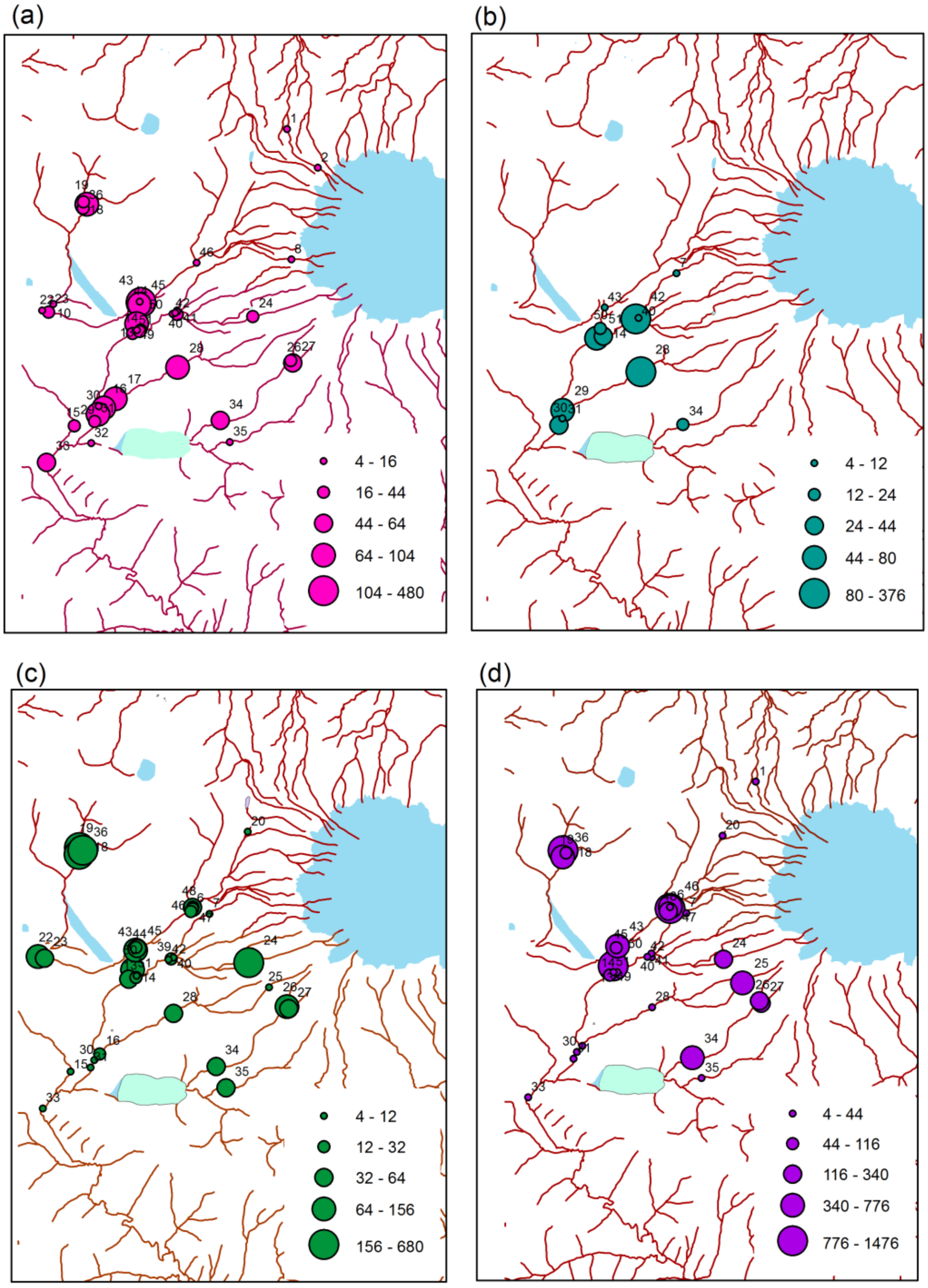

Figure 3. Spatial distribution and abundance at 51 sites of the Antisana Ecological Reserve of: (a) *Molophilus* (b) *Blepharicera* (c) *Prionocyphon* (d) *Allaudomyia*. Colored circles and numbers next to them represent the abundance of each taxon at each site. Lines represent the streams. The central light blue shape represent the glacier at Antisana and the small light green shapes, represent lakes of the area.

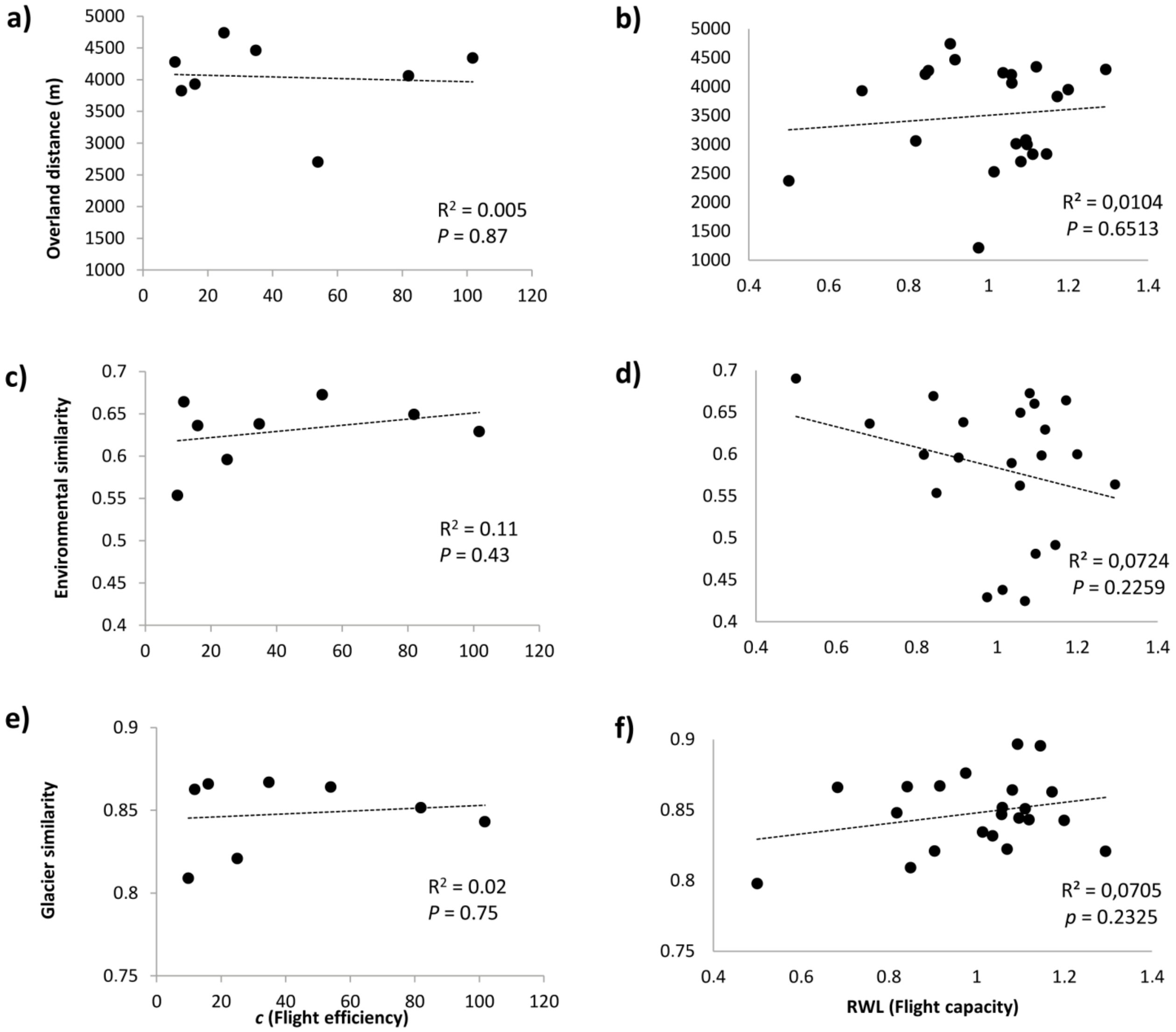

Figure 4. Relationship between flight efficiency (**a**, **c** and **d**) and capacity (**b**, **d** and **f**) of taxa collected with our Malaise traps, and their spatial distribution in the sites of the Antisana Ecological Reserve**.** Dots represent each taxon and dotted lines represent regression lines . **a**, **c** and **d** include only the eight taxa for which we could adjust dispersal kernels (see main text). The other graphs include the 22 taxa that were collected with our Malaise traps.

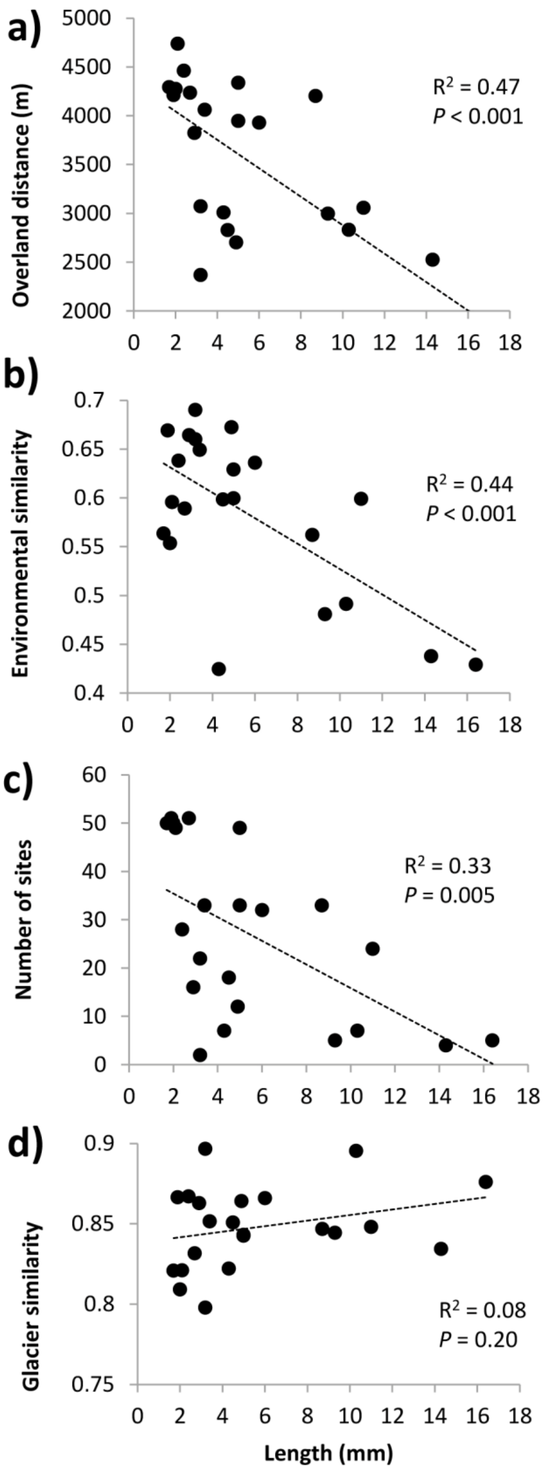

Figure 5. Relationship between body length (mm) and **a)** mean overland distance; **b)** mean environmental similarity; **c)** number of sites at which each taxon is present; **d)** glacier similarity between sites where each taxon is present. Dots represent each of the 22 taxa caught. Lines represent regression lines.

6. TABLES

Table 1. Families and genera found in the Malaise traps during nine weeks of sampling.

Taxa				Numbers caught
Order	**Family**	**Subfamily**	**Genus**	
	Ceratopogonidae		*Alluaudomyia*	282
	Blephariceridae		*Blepharicera*	78
	Empididae		*Chelifera*	13
Diptera		Chironominae		15
		Diamesinae		74
	Chironomidae	Orthocladinae		2272
		Tanypodinae		1068
	Limoniidae		*Geranomyia*	31
			Molophilus	171
	Simuliidae		*Simulium*	93
Plecoptera	Gripopterygidae		*Claudioperla*	18
	Anomalopsychidae		*Contulma*	1
	Hydrobisidae		*Cailloma*	5
	Helichopsychidae			8
Trichoptera	Glossosomatidae		*Mortoniella*	12
	Hydrobiosidae		*Atopsyche*	11
	Leptoceridae		*Nectopsyche*	13
	Hydroptilidae		*Neotrichia*	400
			Ochrotrichia	8
Coleoptera	Hydroscaphidae			7
	Scirtidae		*Prionocyphon*	19
Lepidoptera	Pyralidae		*Synclita*	27
			TOTAL	**4626**

Table 2. Insect size variables of the 22 taxa collected with Malaise traps.

Species	**Body length (mm.)**	**Forewing Length (mm.)**	**Relative wing length (wing length/body length)**
Alluaudomyia	6	4.1	0.683333333
Atopsyche	5	6	1.2
Blepharicera	4.9	5.3	1.081632653
Cailloma	8.7	9.2	1.057471264
Chelifera	2.7	2.8	1.037037037
Chironominae	1.9	1.6	0.842105263
Claudioperla	11	9	0.818181818
Contulma	9.3	10.2	1.096774194
Diamesinae	2.1	1.9	0.904761905
Geranomyia	10.3	11.8	1.145631068
Helichopsychidae	14.3	14.5	1.013986014
Hydroscaphidae	3.2	1.6	0.5
Molophilus	5	5.6	1.12
Mortoniella	3.2	3.5	1.09375
Nectopsyche	4.3	4.6	1.069767442
Neotrichia	2.9	3.4	1.172413793
Ochrotrichia	4.5	5	1.111111111
Orthocladinae	2	1.7	0.85
Prionocyphon	3.4	3.6	1.058823529
Simulium	1.7	2.2	1.294117647
Synclita	16.4	16	0.975609756
Tanypodinae	2.4	2.2	0.916666667

Table 3. Data on flight efficiency (*c*) and capacity (Relative wing length, RWL) and of the spatial distribution of the 22 taxa collected with our Malaise traps.

Species	***c***	**RWL**	**Overland Distance**	**Environmental Distance**	**Glacier Similarity**	**Number Of Sites**
Allaudomyia	15.99	0.68333333	3930.32269	0.63611544	0.31666667	32
Atopsyche	-	1.2	3946.57272	0.59964538	-0.2	33
Blepharicera	53.97	1.08163265	2703.80024	0.67238424	-0.0816327	12
Cailloma	-	1.05747126	4203.33295	0.56212677	-0.0574713	33
Chelifera	-	1.03703704	4237.59138	0.58909814	-0.037037	51
Chironominae	-	0.84210526	4213.64455	0.66907752	0.15789474	51
Claudioperla	-	0.81818182	3059.16519	0.59898187	0.18181818	24
Contulma	-	1.09677419	2999.05085	0.48085133	-0.0967742	5
Diamesinae	25.00	0.9047619	4739.9666	0.59577014	0.0952381	49
Geranomyia	-	1.14563107	2833.48431	0.49144964	-0.1456311	7
Helichopsychidae	-	1.01398601	2524.89892	0.437718	-0.013986	4
Hydroscaphidae	-	0.5	2368.58713	0.69011	0.5	2
Molophilus	101.73	1.12	4339.72815	0.62903164	-0.12	49
Mortoniella	-	1.09375	3074.35313	0.66006498	-0.09375	22
Nectopsyche	-	1.06976744	3010.99234	0.42459286	-0.0697674	7
Neotrichia	11.81	1.17241379	3825.95636	0.66414993	-0.1724138	16
Ochrotrichia	-	1.11111111	2828.84418	0.59834754	-0.1111111	18
Orthocladinae	9.85	0.85	4276.43536	0.55355456	0.15	50
Prionocyphon	81.87	1.05882353	4061.3257	0.64916095	-0.0588235	33
Simulium	-	1.29411765	4293.89242	0.56365828	-0.2941176	50
Synclita	-	0.97560976	1210.54275	0.42912267	0.02439024	5
Tanypodinae	34.78	0.91666667	4461.63517	0.6379309	0.08333333	28

7. APENDIXES

Appendix 1: Larvae abundance found in previous studies in the 51 sites.

STREAM	1	2	3	4	5	6	7	8	9	10	11	12
UTMX	814618	815612	817040	815010	816356	811651	812259	814760	816437	807111	809653	809920
UTMY	9949706	9948458	9947921	9947128	9947098	9945306	9945238	9945508	9945235	9944074	9944010	9943440
Altitude	4335	4521	4835	4535	4789	4196	4225	4496	4728	3988	4092	4050
Alluaudomyia	28	0	0	0	0	224	44	0	0	0	0	0
Atopsyche	4	4	0	0	0	32	16	0	0	8	0	80
Blepharicera	0	0	0	0	0	0	4	0	0	0	0	0
Cailloma	12	8	0	12	0	4	32	24	0	0	0	8
Chelifera	12	4	0	8	0	8	36	0	0	36	0	96
Chironominae	4	0	0	0	0	16	0	0	0	64	0	24
Claudioperla	0	0	0	0	0	8	0	0	0	0	0	12
Contulma	0	0	0	0	0	0	0	0	0	0	0	0
Diamesinae	0	4	0	12	0	0	0	0	4	0	12	0
Geranomyia	0	0	0	0	0	0	0	0	0	0	0	0
Helichopsychidae	0	0	0	0	0	0	0	0	0	4	0	0
Hydroscaphidae	0	0	0	0	0	0	0	0	0	0	0	0
Molophilus	4	4	0	0	0	0	0	4	0	8	0	0
Mortoniella	0	0	0	0	0	0	0	0	0	120	0	0
Nectopsyche	0	0	0	0	0	0	0	0	0	0	0	0
Neotrichia	0	0	0	0	0	0	0	0	0	0	0	0
Ochrotrichia	0	0	0	0	0	76	16	0	0	0	0	28
Orthocladinae	436	288	0	340	28	1656	444	172	8	756	3392	2160
Prionocyphon	0	0	0	0	0	16	8	0	0	0	0	0
Simulium	36	496	0	72	0	44	84	12	0	124	0	0
Synclita	0	0	0	0	0	0	0	0	0	0	0	0
Tanypodinae	0	0	0	0	0	4	0	0	0	28	4	0

Appendix 1: *Continued*

13	14	15	16	17	18	19	20	21	22	23	24	25	26
809919	809888	807788	808727	809103	808072	808184	813487	811943	806750	806952	813521	814168	814744
9943238	9943190	9940158	9940728	9941030	9947364	9947282	9947876	9946616	9943866	9943812	9943670	9942874	9942256
4045	4042	3917	3975	3950	4090	4090	4368	4262	3988	4006	4246	4268	4218
12	28	0	12	0	1192	116	28	0	0	0	340	484	208
4	20	8	0	0	0	60	68	0	4	4	24	0	4
0	44	0	0	0	0	0	0	0	0	0	0	0	0
4	60	0	0	0	48	4	0	0	40	104	28	0	8
20	136	36	68	20	468	76	0	8	12	8	0	0	0
12	80	8	76	68	248	16	728	0	196	8	16	4	0
4	4	0	16	8	36	0	0	0	0	28	24	0	4
0	0	0	0	0	60	0	0	0	0	4	0	0	0
8	136	148	176	4	836	4	4	4	32	12	8	0	0
4	0	0	0	0	0	0	4	0	0	0	0	4	0
0	0	0	44	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	28	40	80	96	32	76	0	0	16	44	44	0	28
56	1108	0	0	0	4	0	0	0	8	380	4	0	0
0	4	0	0	0	0	0	0	0	4	0	8	0	0
0	0	0	0	0	436	0	0	0	0	0	0	0	0
72	12	124	320	4	12	0	0	0	4	0	0	0	4
2816	2420	2516	6472	1864	11688	2504	2012	196	1352	2080	144	2124	728
4	20	12	32	0	680	272	4	0	88	40	276	4	156
304	80	48	88	104	84	672	668	0	92	20	268	592	508
8	4	0	0	0	0	0	0	0	0	0	0	0	0
20	88	64	64	8	28	8	520	0	0	0	0	0	12

Appendix 1. *Continued.*

27	28	29	30	31	32	33	34	35	36	37	38	39	40
814801	811104	808563	808548	808438	808325	806893	812471	812784	808062	811692	811078	811098	811025
9942182	9942040	9940791	9940528	9940298	9939596	9938980	9940326	9939636	9947152	9944864	9943872	9943836	9943792
4226	4009	3958	3930	3932	3921	3986	3944	3945	4077	4183	4109	4124	4116
324	28	0	12	4	0	4	776	32	496	0	24	0	32
8	12	16	8	12	0	0	36	4	60	8	0	12	28
0	260	76	12	40	0	0	16	0	0	0	0	0	4
12	48	20	36	32	0	4	12	52	84	0	4	0	0
8	700	108	92	104	4	24	36	72	156	0	0	0	0
4	28	8	576	108	0	12	0	20	96	0	0	0	4
0	220	0	12	8	0	0	4	0	28	4	0	0	0
0	1052	0	0	16	0	0	0	0	64	0	0	0	0
32	588	108	300	696	4	304	16	1528	316	0	8	0	0
8	8	0	0	0	0	0	0	0	0	0	0	0	0
0	20	0	0	0	0	0	0	4	0	0	0	0	0
0	4	0	0	0	0	0	0	0	0	0	0	0	0
64	88	8	80	36	4	60	56	12	44	0	4	4	4
0	352	216	32	16	0	16	180	20	0	0	0	0	4
0	40	0	0	0	0	0	0	0	0	0	0	0	0
0	576	0	8	16	0	4	4	12	32	0	0	0	16
0	40	12	0	0	0	0	0	0	0	0	4	0	0
912	3844	2316	7680	9488	84	9320	5768	28140	9328	12	4	28	20
64	64	0	8	4	0	4	48	60	332	0	0	12	20
44	52	20	12	12	4	16	80	44	524	16	60	0	12
0	4	0	0	0	0	0	0	12	0	0	0	0	0
44	964	12	52	16	0	4	56	11136	32	0	0	0	0

Appendix 1: *Continued*

41	42	43	44	45	46	47	48	49	50	51
811088	810941	809927	809890	809877	811710	811725	811707	809793	809783	809661
9943738	9943760	9944126	9944154	9944066	9945398	9945452	9945446	9943234	9943444	9943130
4120	4115	4093	4090	4095	4193	4195	4202	4050	4056	4039
32	16	644	0	104	1476	692	20	8	980	84
32	20	48	0	0	28	36	144	20	32	0
0	376	8	0	0	0	0	0	0	24	80
4	12	176	0	4	12	12	28	56	0	16
12	0	128	12	16	56	12	0	124	4	76
48	20	52	76	8	36	12	132	76	12	8
0	4	100	0	16	64	12	0	16	236	0
0	0	0	0	0	0	0	0	0	0	0
24	32	96	0	28	0	0	0	136	0	0
0	0	0	0	4	0	0	12	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	4	0	0	0	0	0	0
28	12	480	4	104	8	0	0	4	96	40
332	48	0	8	8	0	0	0	56	20	112
0	0	12	0	0	4	0	0	0	8	0
28	8	4	0	56	28	52	4	0	0	24
48	20	0	0	0	0	0	0	324	0	240
360	264	2984	920	1092	1224	388	2076	1412	760	2832
0	8	48	16	84	20	28	48	0	100	64
0	8	316	104	116	196	240	52	96	404	72
0	0	0	0	0	0	0	0	4	0	0
0	0	68	8	8	12	0	176	0	16	32

Appendix 2. Physico-chemical and hydromorphological variables of the 51 study sites

Stream	pH	Slope	Lenght	Width	chlA	CPOM	Conductivity	Temperature	Turbidity	Pfankuch
1	6.44	0.292	63.1	10.4	0.8095199	7.27488	6.6	7.2	290	43
2	6.86	0.388	59.1	5.8	1.1980164	0.66318	15	5.8	325	39
3	7.98	0.468	66.8	5.2	0.0472124	0.39912	3	4.1	1000	41
4	7.04	0.432	132.8	10.4	2.0363244	1.22802	8.2	4.2	511	32
5	6.31	0.96	71.9	6.3	0.1836061	0.46284	7.2	3.1	237	29
6	7.22	0.0733333	132.7	17.5	0.6034644	1.10216	87.9	9.9	58	31
7	7.04	0.36	158.4	18.7	0.3692656	2.41196	11.8	7.4	414	36
8	6.36	0.348	204.3	13.1	1.1268467	3.1294	4.3	4.9	774	39
9	7.47	0.0466667	38.5	3.1	0.1479428	0.43376	1.6	2.4	543	39
10	7.65	0.06	60.2	55.8	1.1342514	1.17586	164	7.9	4.97	32
11	8.04	0.068	531	19.1	6.8695951	4.04142	241	11.8	1.22	49
12	7.12	0.272	355.5	32.1	9.028101	2.90366	139.6	7.2	1.01	37
13	8.08	0.384	55.5	17.5	7.2940128	1.82576	154	7.9	1.75	34
14	8.38	0.092	145.6	32.8	3.4039636	1.20072	150.6	10.6	202	23
15	8.89	0.1066667	181.4	18.7	4.3326293	1.2612467	235	11.6	9.25	32
16	8.01	0.164	227.6	42.9	6.6802812	1.74286	275	10.6	6.37	42
17	8	0.16	223	65.8	6.6802812	1.8665	276	10.3	6.76	50
18	7.33	5	57	18.36	4.2237977	5.27855	121	7.3	9.09	28
19	7.33	8.8	68.6	8.53	7.2204206	3.09916	146.5	8.5	4.19	27
20	7.73	2.3	48.8	5.51	3.7111095	1.47205	14.9	16.9	4.31	29
21	8.68	3.92	80.4	6.8	0	5.52034	98.6	8.2	5.92	35
22	6.51	0.88	111	26	2.2277138	3.4144	201	14.1	4.71	27
23	7.74	0.7	212	14.72	2.330978	3.11152	230	13.4	4.6	30
24	7.36	4.8	50.6	18.47	0.1605281	3.86814	45.1	12.9	75.3	29
25	7.49	6.8	227	4.26	0	2.88358	94.1	16.9	5.2	46

Appendix 2. *Continued*

26	7.23	27	140	8.64	0.1805997	4.661125	79.4	13.1	20.5	31
27	6.6	15.411765	101	13.07	0.1505694	3.69948	100.4	10.1	7.32	30
28	8.08	4.6	195	23.37	1.9747952	6.63558	270	9.2	3.17	36
29	8.54	2.4	259	27.15	4.1064103	0.88896	149.9	11.8	66.6	30
30	7.54	1.2	408	30.32	2.2192573	4.06862	163.2	9.4	24.4	34
31	7.28	1.8333333	344	13.74	13.955036	2.42096	180.6	10.7	21	28
32	5.74	0.56	504	24.73	11.2872	0.51176	352	11.2	97	44
33	5.39	2.12	462	37.8	10.2648	0.97862	261	13.5	19.6	25
34	7.86	3.7368421	148.3	9.2	3.5413857	2.5553	183.2	14.8	30	32
35	7.68	8.15	136.7	16.9	3.7911717	1.05814	128.8	9.5	33.3	21
36	7.21	4.28	96.4	19.66	9.4425548	3.07598	124.4	8.6	8.49	39
37	7.9	2.5	199.04	6.794	3.6391097	0.43116	9.8	8.25	282	23
38	7.38	3.76	80.52	8.7628163	2.2939753	1.50775	38.8	9	284	23
39	7.85	4.28	109.98	13.346	3.2932985	2.61581	303	17	5	41
40	7.98	6.25	79.32	20.558	1.6234014	3.68807	184.4	16.2	111	23
41	7.66	3.08	80.2	24.47	2.6698768	4.007968	157.4	11.7	7	38
42	8.047	2	115	29.2	2.2939401	3.431625	167.2	13.4	44	23
43	7.08	3.3	74.6	19.13	2.1200639	7.11394	35.9	10.8	92	26
44	7.08	5.925	70.6	13.06	6.234253	4.07796	209	9.6	10	40
45	7.22	3	76	20.06	8.1492858	1.82636	165.3	9.8	32	25
46	7.8	5.2	91.44	15.168	2.4920518	1.37406	22	11.4	131	24
47	7.7	5.6	65.64	10.346	2.3925168	2.2736	20	11.8	133	25
48	8.47	38.75	55.54	7.01	3.7817927	5.04876	108	12.2	4	33
49	7.43	2.5208333	98.2	31.52	3.463563	1.52424	142	9.9	17	30
50	8.57	6.375	67.6	26.545	18.772202	1.57332	138	9.9	62	34
51	7.46	5.375	181.4	43.604796	2.330978	6.7507	102.2	10.8	60	37

DECLARACIÓN Y AUTORIZACIÓN

Yo, Ana Carolina León Cedeño, con CC. 1722371588, autora del trabajo de graduación intitulado: “Influencia de la dispersión de macroinvertebrados acuáticos sobre la composición de comunidades de ríos de páramo en la Reserva Ecológica Antisana”, previa a la obtención del grado académico de **LICENCIADA EN CIENCIAS BIOLÓGICAS** en la Facultad de Ciencias Exactas y Naturales.

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