Limnetica, 39(2): 677-691 (2020). DOI: 10.23818/limn.39.44
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Macroinvertebrate diversity patterns in tropical highland Andean rivers

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Received: 01/10/18 Accepted: 10/10/19

ABSTRACT

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We studied the macroinvertebrate diversity patterns at 44 sites in tropical highland streams (from 2600 to 4800 m a.s.l. and from northern Ecuador to southern Peru, South America) within six watersheds. The aquatic macroinvertebratealpha (α) diversity tended to decrease with increasing altitude and latitude. Moreover, a high variability existed in the local diversity, which was related to the local environment and habitat heterogeneity. A community composition analysis revealed changes associated with the transition from montane forest areas to páramo or puna areas (at altitudes close to 3500 m a.s.l.). The changes were related to the absence of vegetation in the basins and the absence of riparian areas above 3500 m a.s.l. Three areas could be clearly differentiated: The Northern Andes (Colombia and most of Ecuador), Central Andes (southern Ecuador and most of Peru up to the Altiplano area) and the Altiplano-Puna area. These differences are linked by the distance between basins, as well as biogeographic factors, such as the presence of the Huancabamba Depression between Ecuador and Peru. These three areas have distinct differences in composition, with some taxa more abundant in the south (some of them of Gondwanan origin) and others more prevalent in the north.

Key words: latitude, altitude, biodiversity patterns, tropical highland Andean rivers, aquatic macroinvertebrates, Huancabamba Depression

RESUMEN

Patrones de diversidad de los macroinvertebrados acuáticos en ríos altoandinos tropicales

Los ríos altoandinos tienen varios factores ambientales, climáticos y biogeográficos que inciden sobre las comunidades que los habitan. Por esto se estudiaron los patrones de diversidad de los macroinvertebrados acuáticos en 44 ríos altoandinos de referencia (desde los 2600 a los 4800 msnm, y desde el norte del Ecuador al sur del Perú, en Sudamérica) dentro de seis cuencas en estos países. La diversidad alfa (α) de los macroinvertebrados acuáticos tiende a decrecer cuando incrementan la altitud y la latitud. Se registró una alta variabilidad en la diversidad local, explicada por las características ambientales y la heterogeneidad de hábitats a nivel local. La composición de la comunidad de los macroinvertebrados acuáticos revela cambios asociados con los biomas en los que se encuentran los ríos. Tres áreas fueron claramente diferenciadas: los Andes Norte (norte y centro del Ecuador), Andes Centrales (sur del Ecuador y gran parte de Perú) y las áreas Altiplano-Puna (sur del Perú). Estas diferencias están vinculadas a la distancia entre las cuencas estudiadas, así como a los factores biogeográficos; como la presencia de la depresión de Huancabamba entre Ecuador y Perú. Estas tres áreas tienen diferencias en composición, con algunos géneros más abundantes en el sur (algunos de origen Gondwánico) y otros mayoritariamente prevalentes en el norte del área de estudio.

Palabras clave: *latitud, altitud, patrones de diversidad, ríos tropicales altoandinos, macroinvertebrados acuáticos, depresión de Huancabamba*

INTRODUCTION

Latitudinal and altitudinal gradients have been demonstrated to explain biodiversity patterns. For example, species richness tends to increase from the poles to the equator (Whittaker *et al.*, 2001; Willig *et al.*, 2003), and the reduction in species richness along the altitudinal gradient is a clear trend in many species' groups. In both cases, the patterns have been explained in terms of reductions of ecosystem productivity (Crespo-Pérez *et al.*, 2016; Madsen *et al.*, 2015), temperature and available oxygen (Crespo-Pérez *et al.*, 2016; Jacobsen, 2003; Jacobsen, 2008; Jacobsen & Marín, 2007; Jacobsen *et al.*, 2003; Madsen *et al.*, 2015) and/or the physiological stress imposed by the climatic harshness (Jacobsen, 2008; Jacobsen & Brodersen, 2008; Jacobsen & Marín, 2007). These patterns have been identified in both vegetal and animal groups. In the Neotropics, Anthelme *et al.* (2014) studied diversity patterns and insularity in the high Andes in different animal and vegetal groups and determined the importance of the geographical barriers and the spatial scale examined. They mentioned the importance of altitudinal variability in organism's dispersion and distribution as key factors in understanding species' distributions.

Recent biogeographical studies using geological (Argollo, 2006) and vegetal (Emck *et al.*, 2006) features have divided the Andes into three sections: the North Andes, Central Andes and South Andes. One of the most important biogeographical barriers in the Andes is the Huancabamba Depression, which is located from 4 to 6° S (Prat *et al.*, 2013; Weigend, 2002). It divides the North and Central Andes, where our study area is located. The Huancabamba Depression's importance has been studied for terrestrial ecosystems and fishes, but its importance for the dispersal of aquatic invertebrates remains unknown. Previous studies conducted in the Huancabamba Depression have concluded that the considerable reduction in altitude and the changes in geology, geography and climate that occur in this narrow section of the Andes can limit the presence of some species (Prat *et al.*, 2013; Weigend, 2004). With the use of the ichthyofauna, a map of freshwater ecoregions was created for this area (Abell *et al.*, 2008). The results of that study indicated large differences in fish biodiversity between the ecoregions of the North Andes and Central Andes, coinciding with the Huancabamba Depression. However, due to the dispersal ability of some insects, the characteristics of the aquatic macroinvertebrate community may not change between the North and Central Andes. Recent studies have shown the importance of the Huancabamba Depression for some midges of Gondwanan origin (Prat *et al.*, 2013), which have been unable to cross the depression coming from the south.

In this study, we explore the macroinvertebrate diversity patterns in tropical highland Andean streams (from 2000 to 4800 m a.s.l.) distributed throughout a wide area across the

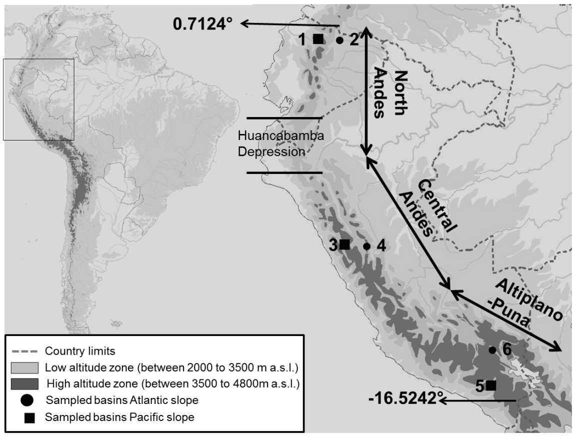

Figure 1. Geographical locations of the basins studied in Ecuador: 1) Mira and 2) Aguarico; and in Peru: 3) Santa, 4) Mosna, 5) Colca, and 6) Urubamba. The map shows the latitudinal gradient from the north of Ecuador to the south of Peru and the altitudinal gradient, for which light gray indicates the montane forest (between 2000 m and 3500 m a.s.l.) and dark gray indicates the páramo-puna (between 3500 m and 4800 m a.s.l.). Bains1, 3 and 5 belong to the Pacific slope (■), while basins 2, 4 and 6 belong to the Atlantic slope. *Localización geográfica de las cuencas estudiadas en Ecuador: 1) Mira and 2) Aguarico; y en Perú: 3) Santa, 4) Mosna, 5) Colca, and 6) Urubamba. En el mapa, se puede observar el gradiente latitudinal desde el norte del Ecuador al sur del Perú y el gradiente altitudinal, la coloración gris clara indica la formación vegetal de bosque montano (entre los 2000 m y 3500 msnm) y la coloración gris obscura indica el límite del páramo-puna (entre los 3500 m y 4800 msnm). Las cuencas 1, 3 y 5 pertenecen a la cuenca del Pacífico (■), mientras que las cuencas 2, 4 y 6 pertenecen a la cuenca del Atlántico (●).*

North and Central Andes (from northern Ecuador to southern Peru, South America). First, we hypothesized that there should be differences in the α diversity between basins according to their latitudinal situation, with relatively high α diversity occurring at relatively low latitudes. Second, we hypothesized that the distance between watersheds is the most important factor for explaining the difference in macroinvertebrate diversity. If we compare the diversity between the north and south basins, the Huancabamba Depression could act as an important geographical barrier, causing changes in the aquatic macroinvertebrate community along the latitudinal gradient. In the same way, the Andes could act as a geographical barrier to the Atlantic or Pacific slope, so we expect important differences in the community composition both along the latitudinal gradient and by slope. Our last hypothesis is that there should be significant differences in the aquatic macroinvertebrate communities with altitude, with an important breaking point in the area where the riparian and basin vegetation disappear (the limit between the forest and the páramo-puna areas).

METHODOLOGY

The study area: altitudinal and latitudinal gradients

Samples were collected from northern Ecuador (0.7124° N at the northernmost site) to southern Peru (16.5242° S at the southernmost site) between October 2007 and October 2008, coinciding with the dry season of each country. Forty-four sites were sampled at a range of different altitudes (from 2000 to 4800 m a.s.l.) and in 6 basins located at different latitudes (two basins in Ecuador—Mira and Aguarico; and four basins in Peru—Santa, Mosna, Colca and Urubamba) (Fig. 1, Table 1). All of these sampling sites were in rivers (with a minimum or lack of anthropogenic influence); thus, we eliminated the variability in the diversity patterns caused by pollution.

The selected altitudinal gradient included two large terrestrial biomes: montane forest and páramo-puna (Prat *et al.*, 2013). The montane forest was distributed in the relatively low elevation zone (from 2000 up to ~ 3500 m a.s.l.) and was characterized by significant forest cover (in the absence of human activity) and the presence of riparian vegetation along streams (Emck *et al.*, 2006). This area contrasts with what was found in the higher elevation zones (from ~ 3500 to 4800 m a.s.l.), where the basin was sparsely covered by steppe-type vegetation with scattered, small trees (e.g., *Polylepis*) or shrubs (Emck *et al.*, 2006; Mena & Hofstede, 2006), which are sometimes found close to the rivers.

The six basins of our study site from northern Ecuador to southern Peru cover a latitudinal gradient. Due to the differences in the hydromorphological and physicochemical features among these areas (Abell *et al.*, 2008), some authors have divided the Andes into three sections: the North Andes, Central Andes and South Andes (Villamarín *et al.*, 2013). In our study, we focused on the basins in the North and Central Andes. The Central Andes can also be divided into two groups, the Central Andes and Altiplano-Puna, from the north to the south of Peru, respectively (Argollo, 2006; Emck *et al.*, 2006). Using these already recognized regions, we can analyze the latitudinal changes among our basins. On the basis of this division, two basins with a similar number of sampling stations were included in each of the three regions considered, with one basin on the Pacific slope (Mira, Santa and Colca) and one on the Atlantic slope (Aguarico, Mosna and Urubamba) in each region (see Fig. 1).

Sampling of the aquatic macroinvertebrate community

The aquatic macroinvertebrate community was sampled following a multihabitat quantitative method called MIQU (‘MacroInvertebratsQUantitatiu’) (Villamarín *et al.*, 2013) using a Surber net with a sampling area of 0.1023 m^2 and a 250 µm mesh size. At each site, 11 microhabitats were identified and separated into dominant microhabitats (each covering > 5 % of the sampling site) and marginal microhabitats (covering ≤ 5 % of the sampling site) (Villamarín *et al.*, 2013).

In the laboratory, the macroinvertebrates were separated, identified, counted and preserved in 70 % ethanol. Literature suitable for each group was used to identify the macroinvertebrates at the

Table 1. Information about each sample site: code, river name, location, altitude, basin, Andes section, slope and vegetation type. *Información de cada sitio muestreado: código, nombre del río, coordenadas, altitud, cuenca, sección de los Andes, vertiente y tipo de vegetación.*

Code	Name	Latitud	Longitud	Altitud (m a.s.l.)	Basin	Andes Section	Slope	Biome
AG-07	Quebrada Tungurahua	18N0218139	0071130	2652	Aguarico	North Andes	Athlantic	Montaneforest
AG-08	S/N	18N0218781	0071024	2644	Aguarico	North Andes	Athlantic	Montaneforest
AG-09	La Chorrera	18N0216663	0070760	2612	Aguarico	North Andes	Athlantic	Montaneforest
AG-10	S/N	18N0216217	0070891	2602	Aguarico	North Andes	Athlantic	Montaneforest
AG-11	S/N	18N0213980	0069641	2793	Aguarico	North Andes	Athlantic	Montaneforest
AG-13	S/N	18N0201665	0070718	2871	Aguarico	North Andes	Athlantic	Montaneforest
AG-14	S/N	18N0200720	0068547	3387	Aguarico	North Andes	Athlantic	Montaneforest
CO-01	Chilli	19K0248766	8202119	3735	Colca	Altiplano-Puna	Pacific	Paramo/Puna
CO-05	Patapampa	19L0245931	8236954	4339	Colca	Altiplano-Puna	Pacific	Paramo/Puna
CO-06	Capellane	19L2354171	8247668	4392	Colca	Altiplano-Puna	Pacific	Paramo/Puna
CO-07	S/N	19L0225376	8256795	4800	Colca	Altiplano-Puna	Pacific	Paramo/Puna
CO-08	Pacocoporague	19L0222045	8262304	4431	Colca	Altiplano-Puna	Pacific	Paramo/Puna
CO-10	Escalera	19L0222397	8268917	3778	Colca	Altiplano-Puna	Pacific	Paramo/Puna
CO-15	S/N	19L0200560	8270024	3150	Colca	Altiplano-Puna	Pacific	Montaneforest
MI-01	Itambi	17N0815308	0018715	2799	Mira	North Andes	Pacific	Montaneforest
MI-03	Taxopamba 1	17N0801504	0020591	3078	Mira	North Andes	Pacific	Montaneforest
MI-04	Taxopamba 2	17N0801018	0022072	2821	Mira	North Andes	Pacific	Montaneforest
MI-09	San Vicente alto	18N0177947	0071489	3427	Mira	North Andes	Pacific	Paramo/Puna
MI-10	San Vicente	18N0179745	0074939	3735	Mira	North Andes	Pacific	Paramo/Puna
MI-11	La Rabija	18N0178407	0071712	3458	Mira	North Andes	Pacific	Montaneforest
MI-13	S/N	17N0832652	0078404	3578	Mira	North Andes	Pacific	Paramo/Puna
MI-14	Polilepys	18N0168150	0078312	3592	Mira	North Andes	Pacific	Montaneforest
MO-01	Pucavado	18L0255743	8928880	4446	Mosna	Central Andes	Athlantic	Paramo/Puna
MO-07	Shashal	18L0259659	8967866	3106	Mosna	Central Andes	Athlantic	Montaneforest
MO-08	Purhuay	18L0259242	8968808	3192	Mosna	Central Andes	Athlantic	Montaneforest
MO-09	Tambillo	18L0253790	8984870	4283	Mosna	Central Andes	Athlantic	Paramo/Puna
MO-10	Garguanga	18L0233421	8984188	3485	Mosna	Central Andes	Athlantic	Montaneforest
MO-12	Bajo San Luis	18L0244758	8994226	3517	Mosna	Central Andes	Athlantic	Montaneforest
MO-13	Quebrada pequeña	18L0239636	9008900	3353	Mosna	Central Andes	Athlantic	Montaneforest
MO-14	Lucma	18L0239431	9011426	3327	Mosna	Central Andes	Athlantic	Montaneforest
MO-16	Vaquería	18L0218952	8999312	4010	Mosna	Central Andes	Athlantic	Paramo/Puna
SA-01	Quellcayhuanca	18L0227950	8946656	3324	Santa	Central Andes	Pacific	Montaneforest
SA-03	Tinco	18L0210686	8946236	4039	Santa	Central Andes	Pacific	Paramo/Puna
SA-05	Ishinca	18L0223023	8961880	3364	Santa	Central Andes	Pacific	Montaneforest
SA-06	Bajo Collón	18L0222641	8960518	3316	Santa	Central Andes	Pacific	Montaneforest
SA-09	Llanganuco	18L0212272	8998446	3859	Santa	Central Andes	Pacific	Paramo/Puna
SA-10	Llanganuco bajo	18L0208499	8995420	3846	Santa	Central Andes	Pacific	Montaneforest
SA-11	Parón	18L0203480	9002796	4004	Santa	Central Andes	Pacific	Paramo/Puna
SA-16	Querococha	18L0244043	8923920	4026	Santa	Central Andes	Pacific	Paramo/Puna
VS-08	Huarocondo	18L0800434	8529536	2943	Urubamba	Altiplano-	Athlantic	Montaneforest
VS-09	Patacancha	18L0798717	8533742	2955	Urubamba	Altiplano-Puna	Athlantic	Montaneforest
VS-10	S/N	18L0792674	8537166	2954	Urubamba	Altiplano-Puna	Athlantic	Montaneforest
VS-14	Samboriochaujio	18L0792360	8507058	3529	Urubamba	Altiplano-Puna	Athlantic	Montaneforest
VS-15	S/N	18L0778948	8510664	2804	Urubamba	Altiplano-Puna	Athlantic	Montaneforest

genus level (Domínguez & Fernández, 2009; Holzenthal, 1988; Merrit & Cummins, 1996), including the chironomids (Prat *et al.*, 2011).

Data analysis

The diversity patterns of the aquatic macroinvertebrates along both the altitudinal and latitudinal gradients were analyzed first by considering the latitudinal order and the distance between the sites and second by considering the order of the sites along the altitudinal gradient regardless of the latitude. On the other hand, the sites were grouped according to the categories that may hypothetically be important for the changes in biodiversity at the regional scale. Four biodiversity patterns were explored: 1) the location of the site in one or another basin, 2) the draining range (Pacific vs. Atlantic slope), 3) the Andes section where the site was located (North, Central or Altiplano-Puna), and 4) the biome (montane forest or páramo-puna). The analysis of macroinvertebrate diversity was conducted independently for each surveyed group to evaluate our hypotheses.

Because the number of individuals in each group may be very different, before any analysis, rarefaction taxa and accumulation curves were constructed. The rarefaction values were calculated with Primer 6.0 software (Clarke & Warwick, 1994) using the fewest number of individuals found in any of the established groups (basin, vegetation type, latitude or slope).

To determine the α diversity patterns, Fisher's index was calculated for each site and later analyz-

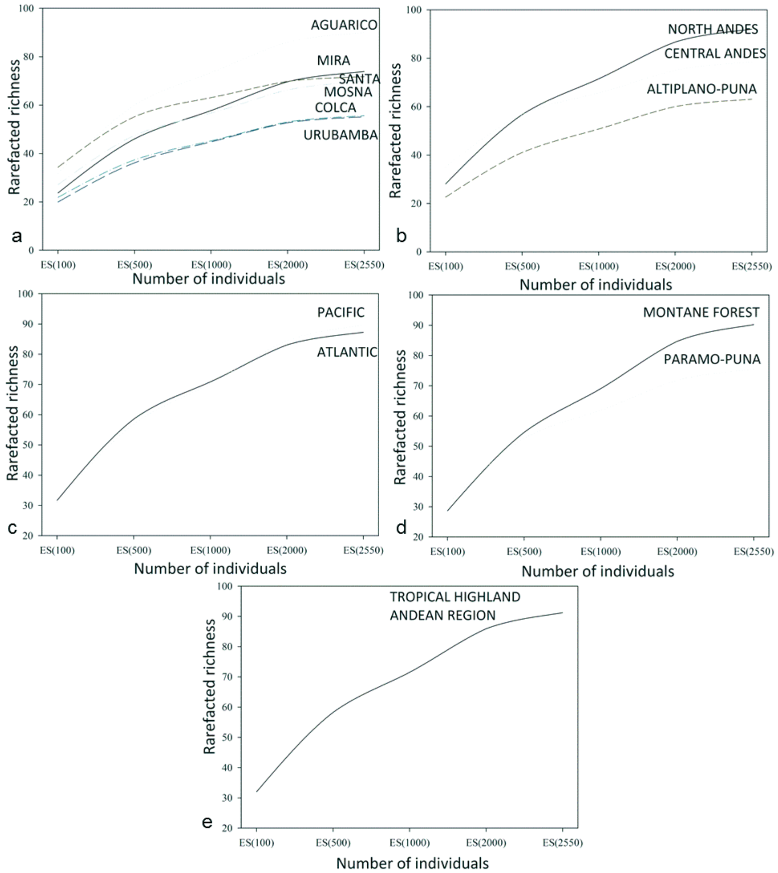

Figure 2. Potential richness of each study level: basin (a), Andes sections (b), slope (c) vegetation type (d), and tropical highland Andean region (e). *Riqueza potencial de cada nivel de estudio: Cuenca (a), Sección de los Andes (b), Vertiente (c) y Tipo de vegetación (d), Región altoandina tropical (e).*

ed by grouping the data according to the selected categories, the Fisher's index attempt to describe the relationship between the number of species and the number of individuals in those species. To determine the differences between the α diversity of each category, an ANOVA was conducted.

Subsequently, the community composition was defined with the Bray-Curtis matrix, which was transformed to dissimilarity resemblance (Anderson *et al.*, 2006). Nonmetric multidimensional scaling (NMDS) was performed to represent the sites in a bidimensional area, and then an analysis of similarity (ANOSIM) was executed to determine the differences between the groups.

To identify the main taxa (at the genus level) that contribute to establishing the differences in the community composition along both the latitudinal and altitudinal gradients, an indicator value analysis (INDVAL) was conducted using the statistical software PCORD4 (McCune & Mefford, 1999). To establish the characteristic genera ($p > 0.005$), the sites were assigned to one of the biomes (montane forest and páramo-puna) considered in the INDVAL analysis. On the other hand, the sites were assigned to one of the three established sections of the Andes (North Andes, Central Andes and Altiplano-Puna) to determine the characteristic genera of each section.

RESULTS

Local and regional diversity

The total richness of aquatic macroinvertebrates in the streams of the Andean tropical region of Ecuador and Peru on both the Pacific and Atlantic slopes and from 2000 m a.s.l. to 4800 m a.s.l. comprised 178 taxa.

Note that the taxon accumulation curves (Fig. 2) did not reach total saturation, which reflects

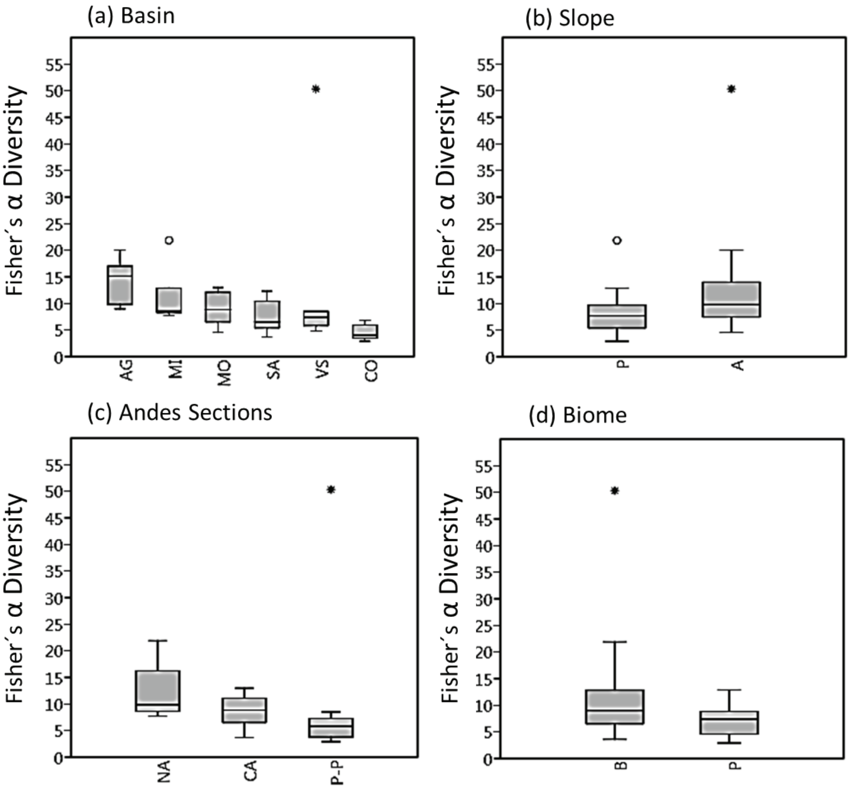

Figure 3. Fisher's α diversity box plot of each category (basin, slope, biome, Andes section). *Gráfico de cajas de la diversidad α de Fisher registrada en cada categoría (Cuenca, Vertiente, Sección de los Andes y Bioma).*

Table 2. ANOVA results of the α diversity between the categories (basin, slope, biome, Andes section). *Resultados del análisis ANOVA de la diversidad α entre las categorías (Cuenca, Vertiente, Bioma y Sección de los Andes).*

Category	F	df	*p*
Basins	8.284	15.73	0.0005325**
Slope	3.238	26.82	0.08319
Andes secction	3.655	19.45	0.04492*
Biome	4.549	38.8	0.03933*

the heterogeneity of the tropical highland Andean aquatic macroinvertebrate community. Nevertheless, when approximately 500 individuals were accumulated, the accumulation curve exhibited some smoothing in all studied groups (Fig. 2). This smoothing was more evident once 2000 individuals had been accumulated in a group. The taxon accumulation curves exhibited differences at three of the analyzed levels and followed the same trend obtained for the α diversity values. The northern basins (Mira, Aguarico) accumulated more taxa with a similar number of individuals compared to that of the southern basins (Fig. 2a). The northernsection of the Andes is more diverse than the southern section beyond the Huancabamba Depression (Fig. 2b), and the montane forest sites support more taxa per accumulated individual than the páramo-puna sites (Fig. 2d), whereas no differences were detected between the two Andean slopes (Fig. 2c).

The α diversity values indicate a high variability within each of the levels at which we grouped our stations in this study (basin, slope, Andes section or vegetation type, see Fig. 3).

Thus, the α diversity at the basin level showed differences between basins (Fig. 3a, Table 2). At the slope level, the α diversity did not show differences between the Atlantic and Pacific slopes (Fig. 3b, Table 2). Nevertheless, the α diversity analysis showed significant differences between the basin of the North Andes and that of the Central Andes (Fig. 3c, Table 2) and between forested areas and paramo areas (Fig. 3d, Table 2).

Therefore, the α diversity exhibited a decreasing trend as the latitude increased (Fig. 3a, 3c), and there is a breaking point between the α diversity of the North and Central Andes (Fig. 4a). However, the α diversity decreased, whereas the altitude increased (Fig. 4b) or the biome changed (Fig. 3d).

Changes in aquatic macroinvertebrate community composition in the North and Central Andes

The change in community structure or dissimilarity among sites shows differences in the category of Andes section. Thus, the analysis indicates a grouping of sites by the category of Andes sections that are in close proximity, with differences in the community composition between the basins (Fig. 5a, Basin). The slopes do not show differences in the community structure (Fig. 5b). The pattern

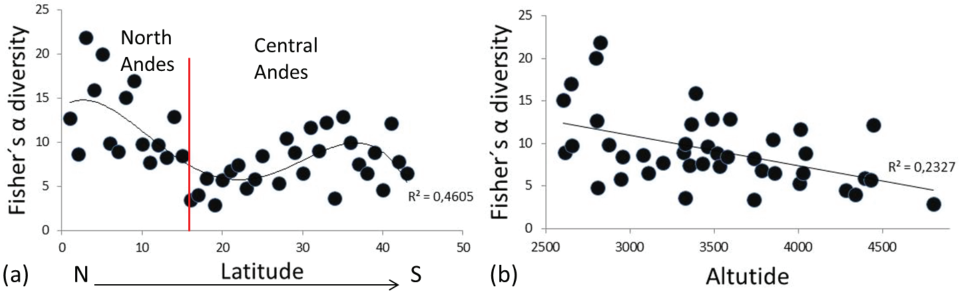

Figure 4. Fisher's α diversity (a) along the latitudinal gradient. The red line shows the break between the North and Central Andes in the Huancabamba Depression and (b) along the altitudinal gradient. *Diversidad alfa de Fisher (a) a lo largo del gradiente latitudinal, la línea roja muestra el quiebre entre los Andes Norte y Centrales en la depresión de Huamcabamba, y (b) a lo largo del gradiente altitudinal.*

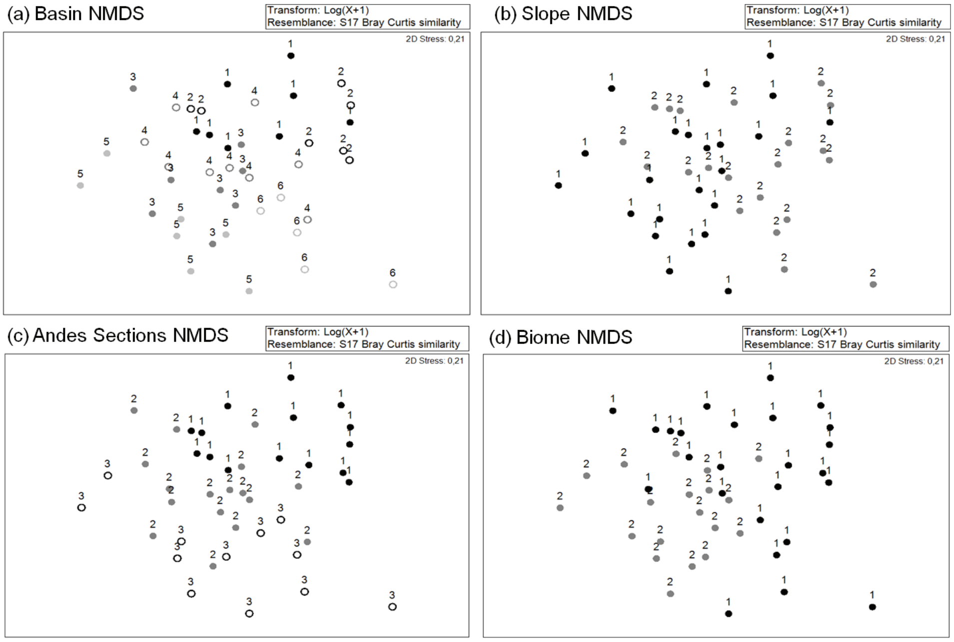

Figure 5. NMDS of the community composition based on the Bray-Curtis matrix. Basin (a: 1 Mira, 2 Aguarico, 3 Santa, 4 Mosna, 5 Colca, 6 Urubamba), Slope (b: 1 Atlantic, 2 Pacific), Biome (c: 1 Montane forest, 2 Páramo-Puna) and Andes Sections (d: 1 North Andes, 2 Central Andes, 3 Altiplano-Puna). *NMDS de la composición de la comunidad basada en la matriz de Bray-Curtis. Cuenca (a: 1 Mira, 2 Aguarico, 3 Santa, 4 Mosna, 5 Colca, 6 Urubamba), Vertiente (b: 1 Atlántico, 2 Pacífico), Tipo de vegetación (c: 1 Bosque montano, 2 Páramo-Puna) y Sección de los Andes (d: 1 Andes Norte, 2 Andes Central, 3 Altiplano-Puna).*

Table 3. ANOSIM results of the differences in community composition between the groups (basin, slope, biome and Andes sections). Basingroups: 1 Mira, 2 Aguarico, 3 Santa, 4 Mosna, 5 Colca, 6 Urubamba. Andes Sections: 1 North Andes, 2 Central Andes, 3 Altiplano-Puna. *Resultados del ANOSIM de las diferencias de la composición de la comunidad entre grupos (Cuenca, Vertiente, Tipo de Vegetación y Sección de los Andes).*

Scales	R	*P*		R	*P*
Basin	**0.342**	**0.001****	**Basin**		
2, 5	**0.73**	**0.001****	5,6	**0.414**	**0.006****
2, 1	0.135	0.106	1,4	0.111	0.086
2, 4	0.286	0.014*	1,3	0.244	0.005**
2, 3	**0.44**	0.002**	1,6	**0.708**	**0.001****
2, 6	**0.49**	0.003**	4,3	-0.074	0.834
5, 1	**0.63**	**0.001****	4,6	0.267	0.032*
5, 4	**0.44**	**0.001****	3,6	**0.387**	**0.005****
5, 3	0.29	**0.009****			
Andes Section	**0.34**	**0.001****			
1, 3	**0.54**	**0.001****			
1, 2	0.25	**0.001****			
3, 2	0.29	**0.001****			
Slope	0.09	0.16			
Biome	0.147	**0.001****			

shown among the Andes section groups was clearer (Fig. 5c, Andes sections). Finally, the biomes showed differences (Fig. 5d, Table 2) independently of the basin, Andes section or distance between basins. The ANOSIM determined the differences between the Andes section groups to be the most important variable (Table 3).

In the study, the Aguarico and Colca basins, which had the highest distance between them, showed significant differences in community composition (Fig. 5a and Table 3). It is interesting to note the importance of the geographical distance, which acts as an organism's distribution barrier (Fig. 6). Thus, the increase in the distance between basins has a high correlation with community dissimilarity.

Aquatic macroinvertebrate genera representative of the North and Central Andes

The INDVAL analysis showed statistically characteristic genera ($p < 0.05$) for each Andes section

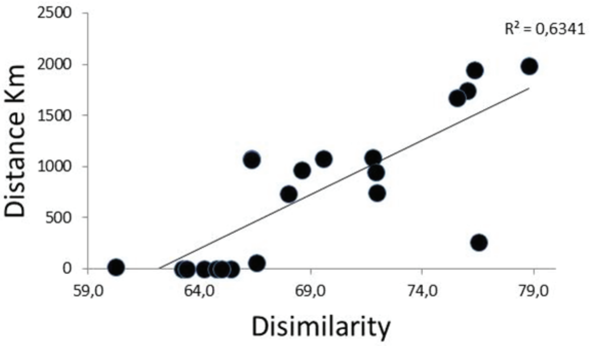

Figure 6. Correlation between the community composition dissimilarity and the geographic distance between basins. *Correlación entre la composición de la comunidad y la distancia geográfica entre las cuencas.*

over the studied latitudinal gradient. The North Andes included 6 statistically significant genera, of which 3 were Ephemeroptera, 2 were Coleoptera and 1 was Diptera. In the Central Andes, 12 genera occurred statistically more frequent, of which 1 belongs to Acari, 1 belongs to Ephemeroptera, 1 belongs to Coleoptera and 9 belong to Diptera. Finally, in the Altiplano-Puna section, 4 genera were selected as representative in the INDVAL analysis: 1 Crustacea, 1 Coleoptera and 2 Diptera (Table 4).

The community composition analysis for the changes in the biome type also showed clear results, where the most important ecotone present was marked with the vegetation type changes (from montane forest to páramo-puna) along the

Table 4. Genera of indicator aquatic macroinvertebrates of the different latitudinal zones according to the INDVAL analysis ($p > 0.05$). *Géneros de macroinvertebrados acuáticos representativos de las diferentes zonas latitudinales usando el análisis INDVAL (*p *> 0.05). *: significativo, **: altamente significativo.*

Family	Genus	Group	IndicatorValue	*p*	Sig
Chironomidae	*Genus 1*	North Andes	61.0	0.005	**
Elmidae	*Heterelmis*	North Andes	46.9	0.001	**
Baetidae	*Camelobaetidius*	North Andes	40.0	0.001	**
Baetidae	*Mayobaetis*	North Andes	33.3	0.001	**
Ptilodactylidae	*Anchytarsus*	North Andes	33.3	0.001	**
Leptohyphidae	*Leptohyphes*	North Andes	20.7	0.008	**
Chironomidae	*Limnophyes*	Central Andes	62.7	0.001	**
Chironomidae	*Hudsonimyia*	Central Andes	60.6	0.001	**
Simulidae	*Simulium*	Central Andes	59.7	0.008	**
Ceratopogonidae	*Ceratopogonidae sp1*	Central Andes	56.2	0.002	**
Tipulidae	*Tipula*	Central Andes	49.1	0.001	**
Acari	*Hydracarina*	Central Andes	43.4	0.007	**
Blepharoceridae	*Linomicola*	Central Andes	41.1	0.001	**
Chironomidae	*Cricotopus fl5*	Central Andes	40.8	0.007	**
Chironomidae	*Tanytarsus*	Central Andes	40.2	0.009	**
Chironomidae	*Thienemanniella*	Central Andes	35.4	0.004	**
Elmidae	*Neoelmis*	Central Andes	34.1	0.008	**
Perlidae	*Anacroneuria*	Central Andes	29.5	0.001	**
Chironomidae	*Onconeura*	Altiplano-Puna	75.3	0.001	**
Elmidae	*Austrelmis*	Altiplano-Puna	67.4	0.001	**
Hyalellidae	*Hyalella*	Altiplano-Puna	65.1	0.001	**
Chironomidae	*Cricotopus (Isocladius)*	Altiplano-Puna	60.5	0.001	**

sections of the Andes studied. These results indicate the importance of the vegetation cover of the basin and the presence of a riparian forest to the aquatic macroinvertebrate composition (Fig. 5d, Table 2 biome). When the INDVAL analysis was used as an indicator of the different altitude areas, 4 genera (1 Ephemeroptera, 1 Coleoptera, 1 Trichoptera and 1 Diptera) were identified in the montane area and 8 genera were identified in the páramo-puna (1 Plecoptera, 1 Trichoptera and 6 Diptera) (Table 5).

DISCUSSION

As we hypothesized, the α diversity of the aquatic macroinvertebrates of tropical highland Andean rivers tends to decrease as latitude and altitude increase. Nevertheless, the results showed the importance of local environmental variability. This pattern has previously been demonstrated in studies at different locations worldwide and for different animal (Barber-James *et al.*, 2008; Múrria *et al.*, 2013; Wiens *et al.*, 2011) and vegetal groups (Cuesta *et al.*, 2016), and the aquatic macroinvertebrates of the tropical highland Andean rivers, at the genus level, do not appear to be the exception. The α diversity pattern in both the altitudinal and latitudinal gradients showed statistical relevance. The α diversity between basins showed a significant difference, and in this case, the high environmental variability (Villamarín *et al.*, 2014; Villamarín *et al.*, 2013), the distance between basins and the geographical barriers explain this variation.

The community composition in the two studied gradients confirms the importance of both the transition from montane forest to páramo-puna (Villamarín *et al.*, 2013) and the biogeographic changes related to the geographical barriers and the distance between sites in the northern and southern Andes (Prat *et al.*, 2013).This could be explained by the scale size, where the importance of the local environmental changes is reduced in relation to the biomes, which are the dominant factor in the determination of the community assemblage determined in our study.

In the Neotropics, several studies have explained how changes in climate (Emck *et al.*, 2006) and geomorphology (Argollo, 2006) are responsible for latitudinal and altitudinal changes in vegetation (Cuesta *et al.*, 2016; García & Beck, 2006). This environmental variability is responsible for the diversity patterns in the tropical highland Andean rivers benthonic community (Crespo-Pérez *et al.*, 2016; Jacobsen, 2003; Jacobsen, 2008; Madsen *et al.*, 2015). On the other hand, the biomes present in the basin and in the riparian zone appear to be two of the most important factors for explaining the biodiversity patterns of the benthic communities of the tropical highland

Table 5. Genera of aquatic macroinvertebrate indicators of different altitudinal ranges based on the INDVAL analysis. ($p > 0.05$). *: significant, **: highly significant. *Géneros de macroinvertebrados acuáticos representativos de las diferentes zonas altitudinales usando el análisis INDVAL (*p *> 0.05). *: significativo, **: altamente significativo.*

Family	Genus	Group	IndicatorValue	*p*	Sig
Chironomidae	*Genus 1*	Montaneforest	59.9	0.05	*
Leptoceridae	*Nectopsyche*	Montaneforest	40.6	0.046	**
Baetidae	*Camelobaetidius*	Montaneforest	19.4	0.04	*
Ptilodactylidae	*Anchytarsus*	Montaneforest	16.1	0.049	**
Chironomidae	*Podonomus*	Paramo-Puna	60.6	0.001	**
Chironomidae	*Cricotopus fl5*	Paramo-Puna	58.3	0.001	**
Chironomidae	*Limnophyes*	Paramo-Puna	51.2	0.048	*
Chironomidae	*Alotanypus*	Paramo-Puna	47.1	0.004	**
Grypopterigidae	*Claudioperla*	Paramo-Puna	44.0	0.005	**
Limnephilidae	*Anomalocosmoecus*	Paramo-Puna	38.9	0.001	**
Chironomidae	*Hudsonimyia*	Paramo-Puna	38.5	0.003	**
Chironomidae	*Paracladius*	Paramo-Puna	37.2	0.005	**

Andean rivers, especially in terms of structure, composition and density (Cuesta *et al.*, 2016; Jacobsen, 2008; Lorion & Kennedy, 2009; Milner & Gloyne-Phillips, 2005). In our study, the α diversity decreased with altitude. Nevertheless, significant differences exist between the montane forest and the páramo-puna, which could be explained by various factors. Altitude adversely affects diversity in tropical highland rivers due to the reduced oxygen concentration, atmospheric pressure and temperature (Acosta & Prat, 2010; Crespo-Pérez *et al.*, 2016; Jacobsen & Brodersen, 2008; Madsen *et al.*, 2015), whereas the intensity of solar radiation and the rainfall are increased (Cuesta *et al.*, 2016). On the other hand, the local environmental factors showed differences in relation to scale (Villamarín *et al.*, 2014). In this study, the sites grouped by scale in the Andes showed notable differences from groups with relatively few sites, and the differences decreased for the groups with more sites. This could be explained by the environmental differences at different scales (Villamarín *et al.*, 2014) and the importance of microclimatic patterns along both altitudinal and latitudinal gradients. This causes not only a reduction in diversity but also a change in the composition of the aquatic macroinvertebrate community. *Hyalella*, *Claudioperla*, *Podonomopsis*, *Podonomus*, *Anomalocosmoecus* and *Limnophyes* were some of the genera that exhibited a preference for the high-altitude zone where the temperature and available oxygen are lower. Other genera prefer relatively lower-altitude areas where the temperature and available oxygen increase, including *Polypedilum*, *Rheotanytarsus*, *Cochliopsyche*, *Helicopsyche*, *Parametriocnemus*, *Camelobaetidius* and *Lachlania*. This finding agrees with previous works, such as the study by Jacobsen & Brodersen (2008), who noted that the trend of *Claudioperla*, *Anomalocosmoecus* and *Lachlania* genera was similar to that obtained in our study. Referring to chironomids, Acosta & Prat (2010) highlight *Podonomopsis*, *Podonomus* and *Limnophyes* as being more frequent and abundant in the highland parts of the Cañete basin (south of Peru), whereas *Rheotanytarsus* was more common to the relatively low zones. Adaptations of macroinvertebrates to life at high altitudes include an increased affinity for oxygen (Crespo-Pérez *et al.*, 2016; Jacobsen & Brodersen, 2008; Madsen *et al.*, 2015) and more melanin in their bodies (Loayza-Muro *et al.*, 2013).

The differences in the community composition from the montane forest to the páramo-puna appear clearly in the three altitudinal gradients studied in Ecuador and central and southern Peru; the community composition change occurs at ~ 3500 m a.s.l. in both slopes of the tropical highland Andes. The species turnover occurs preferentially at this altitude. Samples from the páramo on each slope were more similar than when we compared the two different slopes, confirming the importance of biome and the limiting factors linked to altitude (temperature, oxygen, and solar radiation), which were more important than the slope in tropical highland Andean rivers (Cuesta *et al.*, 2016). Some differences were found in the composition and structure of the macroinvertebrate community between the slopes of the Andes (Sites *et al.*, 2003); however, the altitudinal range evaluated in this study was larger than the altitudinal range in our study, so the dispersion capacity and the geographical barriers could act more intensively as key factors in these differences with respect to our results.

One of the most interesting distributions is that of the Gondwanan elements, which species are belonging to genera now living in Australia, New Zealand or South Africa and Patagonia (relics of Pangea). For midges, this type of distribution was studied by Brundin (1966) and recently revisited by Cranston & Krosch (2011). These Gondwanan taxa include many species in Chile and Argentina, whereas in tropical Andean rivers, there are few Gondwanan species, which are mostly confined at the highest elevation zones (Brundin, 1966). One of the best examples is the genus *Barbadocladius*, which is present at low altitudes in the Patagonian Andes but only at high altitudes in the southern part of the high-altitude rivers of the tropical Andes and is never present in the Northern Andes (Prat *et al.*, 2013). The reverse is true for several genera of Elmidae found only in Ecuador (*Notelmis*, *Cylloepus*, *Hexanchorus*, *Huleechius*, *Microcylloepus*, *Onychelmis*, *Phanocerus* and *Xenelmis*). Therefore, we expect that, independent of the lower α diversity found in the southern high-altitude tropical streams, there is an important change in composition from the north basins to the south basins, as is the case for other nonaquatic organisms (Buzas *et al.*, 2002; Cuesta *et al.*, 2016; Willig *et al.*, 2003).

Despite being a recognizable gradient, the interpretation of the controlling factors of diversity patterns across latitudes can be complex (Willig *et al.*, 2003), and it is difficult to establish cause and effect. Willig *et al.* (loc. cit.) noted some studies that analyzed latitudinal gradients and mentioned energy availability, temperature variability, climatology and the study area size as the relevant aspects responsible for changes in diversity. Nevertheless, in the highland Andes, the geomorphology and distance could act as influential factors in the insularity and distribution of the organisms (Anthelme *et al.*, 2014; Cuesta *et al.*, 2016), as shown in our study. In aquatic ecosystems, river zonation and biogeographical barriers play a key role in the distribution and speciation of macroinvertebrates (Múrria *et al.*, 2013), and tropical highland Andean rivers are no exception. In this context, the local environmental variables responsible for controlling the diversity patterns were better predictors of the community composition variability than spatial variables (Heino *et al.*, 2015).

The main differences between the sections of the Andes (i.e., the latitude) are related to biogeographic features and the limitations imposed by altitude (Cuesta *et al.*, 2016; Madsen *et al.*, 2015). In our study, one important feature appears to be the presence of the Huancabamba Depression, which acts as a biogeographical barrier to many vegetal and animal species (Cuesta *et al.*, 2016; Weigend *et al.*, 2010), including many midges at the genera (Prat *et al.*, 2013) or species level (Prat *et al.*, 2018), separating the lowest section of the Andes. Thus, species distributed south of the Huancabamba Depression that have not dispersed to the north and vice versa could help to explain the lower diversity in both the páramo-puna and tropical high-altitude Andean rivers of central and southern Peru. However, in our results, the discrimination among the groups between the sections of the Andes showed differences in local diversity or in community composition, which could be explained by the macroinvertebrate dispersion capacity, in contrast to populations of fish (Oberdorff *et al.*, 2011) or vegetation (Cuesta *et al.*, 2016; Weigend, 2002; Weigend, 2004), which present relatively strong differences among the frontiers of the three sections of the Andes.

Finally, the interaction between altitude and latitude deserves some attention. If there was a decrease in temperature along the latitudinal gradient, we would expect that the ecotone between the forest and the páramo-puna vegetation types would occur at lower altitudes rather than at higher latitudes. Nevertheless, this hypothesis was not clearly supported by our results, as the community composition in the altitudinal gradient was almost constant across the latitudinal gradient, occurring at approximately 3500 m a.s.l. This largely coincides with the conclusions of Argollo (2006), who grouped the highland zone of the North Andes, the Central Andes and the Altiplano-Puna as a single province: the "Páramos puneños". According to this author, despite small differences in environmental factors, especially humidity, the changes in the vegetation landscape with altitude are very similar across this province (Cuesta *et al.*, 2016). Hence, the differences in the community composition at different altitudes in the tropical highland Andean rivers are due to the strong changes in environmental factors, whereas the latitudinal changes are more related to the biogeographic factors such as the presence of the Huancabamba Depression or the cline existing in the distribution of Gondwanan taxa than to the environmental changes at the regional scale. Argollo (2006) mentioned that the landscape change (from montane forest to páramo-puna) in the studied latitudinal gradient varies very little between the North Andes and the Altiplano-Puna, and it occurs at a lower altitude only at the highest latitudes, corresponding to the southernmost Andes, which were not included in this study. Thus, the assemblage of macroinvertebrate communities of tropical highland Andean rivers occurring at similar altitudes in the three sections of the Andes has emerged as one of the most interesting findings of the present work together with the latitudinal gradient and the importance of the Huancabamba Depression as a barrier for some genera.

ACKNOWLEDGEMENTS

This study was developed in the framework of the project "*CERA: Evaluación del estado ecológico de cuencas altoandinas de Ecuador y Perú. Herramientas de gestión*" funded by the Ministerio de Educación y Ciencia de España (CGL2006-04333) and the project "*FUCARA: Funcionalidad y calidad ecológica de los ríos alto-andinos. Reforzamiento del laboratorio de ecología acuática de la USFQ (Universidad de San Francisco-Quito)*". *D/011294/07* (Acción Integrada-PCI Iberoamérica- AECI 2007- Ministerio de Asuntos Exteriores). We thank the government entities in both countries, including the Ministerio del Ambiente of Ecuador and the Instituto de Recursos Naturales of Perú, for the facilities provided. We thank to Clorinda Vergara from the Museo de Entomología - Universidad Nacional Agraria "La Molina" and Andrea Encalada from the Laboratorio de Ecología Acuática - Universidad San Francisco de Quito for the laboratory and field facilities. We thank Núria Sánchez-Millaruelo, Raúl Acosta, Manuel Andía, Carolina Arroyo, Fernanda Gonzáles and Karla Jiménez for laboratory and field support. Finally, we thank the FEM (*Freshwater Ecology and Management*) Research Group-Universitat de Barcelona for their support of this study.

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Con el patrocinio de:

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MINISTERIO PARA LA TRANSICIÓN ECOLÓGICA Y EL RETO DEMOGRÁFICO

Fundación Biodiversidad