




Cold/Warm stenothermic freshwater macroinvertebrates along altitudinal and latitudinal gradients in Western South America: A modern approach to an old hypothesis with updated data

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Abstract

Aim: Traditionally, South American aquatic insects have been divided into cold and warm adapted forms. Cold-adapted forms inhabit freshwater systems from higher latitudes, or higher altitudes even around the Equator. Warm-adapted groups are defined as those found in lower latitudes and altitudes. This work aims to answer the questions: Are mayfly assemblages geographically segregated according to geographical (latitude) and topographical (altitude) surrogates of temperature? If so, where is this transition located?

Location: South America.

Methods: We compiled a data set about the relative incidence of 52 mayfly genera in 326 sampled communities. They span from 0 to 4,320 m and from 47.77° S to 5.74° N latitude. By virtue of the compositional nature of the data set, we applied the statistical procedures behind the Aitchison compositional data analysis. We delimited groups of assemblages based on their Aitchison distances and projected the data points onto a biplot obtained through Principal Component Analysis adjusted to compositions (Aitchison PCA).



Results: A strong correspondence among biological and geographical information was detected, with mayfly assemblages clearly segregated in space. *Andesiops* and *Meridialaris* are typical cold-adapted forms; *Baetodes*, *Leptohyphes* and *Thraulodes* represent the warm group. Thermal groups can be separated by a curved line of altitude in function of latitude expressed in terms of a superellipse arc.

Main conclusions: The classical ecological bipartition of mayflies into warm and cold freshwater groups is formalized quantitatively. The dividing line between warm and cold assemblages levels off at high altitudes (c. 3,300 m) around the Equator and falls to sea level at southern latitudes. The community bipartition line is useful for tracking global change through records of altitudinal displacement below and above of the warm/cold line of involved ecological groups.

KEYWORDS

altitude, cold adapted, Ephemeroptera, freshwater, latitude, oligostenothermal, polystenothermal, thermal limits, warm adapted

1 | INTRODUCTION

Since early studies on animal and plant diversity, the distributional patterns of organisms have attracted the attention of naturalists. Taxonomic resolution and poor georeferencing of the data impaired the formulation of hypotheses about the purported patterns. The advent of geopositioning technology has allowed to accurately pinpoint sampling locations within negligible ranges of uncertainty. In this sense, presently there are more accurate data points than ever before. This opens a unique opportunity to analyse the available data from different perspectives and to test previously stated hypotheses. For example, after the pioneering work of Ross (1956) on freshwater insects, the terms “warm-adapted” and “cold-adapted” have been widely used in limnology. Nevertheless, Ross (1956:19) states “On the basis of *unfortunately few recordings*, there seems to be a significant change in caddisfly fauna in the neighbourhood of maximum water temperature of 65° to 68°F [18–20°C]” (*italics are ours*). This dichotomy had a great impact on subsequent works not only on aquatic insect ecology but also in systematics and biogeography (Illies, 1969; Malicky & Chantaramongkol, 1993; Vannote & Sweeney, 1980; Ward & Stanford, 1982). For example, Pescador and Peters (1980) used this concept as a criterion to select the leptophlebiid mayfly genera for their systematics and biogeographic study. Savage (1987) explored the broad correspondence between these ecological groups and the South American regionalization based on leptophlebiid mayflies. Working in North America with mayfly assemblages and their response to temperature, Ide (1935:61) reached this interesting conclusion: “It is probably safe to say that a spring stream in its fauna, taken from the warmer reaches to the source, recapitulates south to north distribution, in the way that a mountain in the torrid zone gives in its fauna and flora, taken from the foot to the top, roughly a vertical section of geographical distribution from torrid to frigid zones”.

The Andes Mountains constitute the most striking topographical feature of Western South America. They extend along the entire western continental margin of South America and represent a formidable natural experiment to assess latitudinal patterns of biological associations at varying elevations. In the South American geographical context, the cold-adapted groups are expected to occur in both high altitude and latitude such as the Andes and Patagonia. On the other hand, the warm-adapted groups would occupy all tropical lowlands where a stable higher water temperature is maintained. Illies (1969) proposed an alternative terminology for these groups, namely “Oligostenothermal mountain fauna” and “Polystenothermal lowland fauna”. The availability of georeferenced community data provides us the opportunity to test if the previously proposed bipartition is meaningful for the Ephemeroptera of South America.

Ephemeroptera are among the major elements of freshwater benthos worldwide. They parallel changes operating at the community level as a whole. Consequently, their assemblages can be used as indicators of anthropogenic global environmental change in the community structure including patterns of spatial variation (Brasil, Juen, & Cabette, 2014; Firmiano et al., 2017; Jackson & Blois, 2015; Souza, Cabette, & Juen, 2011). Importantly, it is necessary to assess quantitatively the relevance of such changes, differentiating minor/random signals from critical, meaningful changes. In the case of the mayfly assemblages, understanding this difference would allow us to monitor and measure the community structure changes in altitude and latitude that can happen due to climate change. Furthermore, this understanding would allow the improvement of the distribution models for threatened species or indicators of environmental quality under different future scenarios. This work aims to answer the questions: Are there mayfly assemblages geographically segregated according to the global proxies of temperature (altitude and latitude)? And if so, where does the change take place?



2 | MATERIALS AND METHODS

The compositional nature of community data calls for specific statistical procedures that conventional techniques do not account for. Among others, compositions have the following properties: (1) they are always positive; (2) the amount of each part is relative to the whole; (3) the grand total is non-informative, since it is typically subject of artifacts in the measurement procedure (consequently, only relative changes are relevant); (4) the lack of independence among the parts of the composition (if the relative amount of one part increases, the others decrease) introduces spurious correlations (Chayes, 1960). These constraints were tackled by Aitchison (1986), who proposed some fundamental principles of data analysis. From these properties, Aitchison showed that the analysis should be based on ratios or log-ratios only. He introduced transformations (e.g. centred log-ratio and isometric log-ratio), operations (e.g. perturbation analogue to the addition operation in the geometry of the simplex) and a distance, all compatible with the above-mentioned properties. We analysed our Ephemeroptera compositional data within this theoretical framework.

A data matrix composed of 326 sampling sites and 52 recorded genera (see Appendix S1) was compiled from original field data collection spanning from 2,000 to present, except a few data obtained from the literature (Ferru & Fierro, 2015; Gualdoni & Oberto, 2012; Gualdoni et al., 2009; Miserendino, 2007; Miserendino & Pizzolon, 2003, 2004; Romero et al., 2012). Data were gathered with the aim to cover as broad the altitudinal range as possible, at different latitudinal belts (Figure 1). Collections were made using Surber samples, kicknets and/or hand nets, representing mayfly diversity in all the available hydraulic conditions and microhabitats (riffles, pools, marginal vegetation, among others). All sites were sampled in a consistent way. Taxonomic resolution was at genus level (using keys in Domínguez & Fernández, 2009) and abundances of sampled communities were transformed into relative frequencies (percentages of genera), allowing us to perform a quantitative comparison of community compositions across a broad spatial extent.

Latitude, longitude and altitude were recorded at each site (Appendix S1). Each row of the table corresponds to the compositional profile of an assemblage at a specific site, each entry reflecting the relative abundance of a genus in a particular site. So, each row is a compositional vector consisting of D components which are proportions. The overall sum of their elements yields a constant c (here equals to 1). As composition vectors are strictly positive entries, the respective sample space is given by the simplex S^D defined as follows:

$$S^D = \{[x_1, x_2, \dots, x_D]^T : x_i > 0; \sum_i x_i = c\}$$

We transformed compositional data containing zero (i.e., absence of a given genus in a sample point) before data processing, following the procedure proposed by Smithson and Verkuilen (2006). Zero transformation resulted in a tiny positive number close to zero. Particularly, given n observations and d parts or dimensions, each component y of the vector Y is transformed through $y' = [y(n-1) + 1/d]/n$.

We have performed a particular variant of classical Principal Component Analysis (PCA) on the complete dataset to reduce its complexity and get a better understanding of the underlying structure. Conceptually, the goal of PCA is to reduce the number of variables of interest into a smaller set of components. PCA redistributes all variance into orthogonal components. Extraction is the process of forming principal components as linear combinations of the measured variables. By successfully reducing the dimensionality, PCA can thus help to identify new meaningful underlying variables and to understand better the correlation structure among the original variables (Jolliffe, 2002). Standard PCA should not be applied in an unmodified way to compositional data (Aitchison, 1986), because it relies on an underlined assumption of multivariate normality. We used an adapted version of PCA (Aitchison & Greenacre, 2002) known as Aitchison PCA. Analyses were performed with the R Statistical Platform and PCA adjusted to compositions was done with the package *compositions*. Readers interested in practical aspects of Aitchison PCA, as well as the interpretation of respective biplots, are referred to Gloor and Reid (2016).

Many analyses, such as those coming from clustering recognition, require calculating previously the distance between pairs of items to be clustered. Aitchison (1992) developed a distance measure between two compositional profiles. This distance complies the properties of subcompositional dominance and invariance for scale, permutation and perturbation. Formally, the Aitchison distance for any two compositions $\mathbf{x}, \mathbf{x}^* \in S^{D-1}$ is given by the following:

$$\Delta(\mathbf{x}, \mathbf{x}^*) = \left[D^{-1} \sum_{j < k} \left\{ \log \left(\frac{x_j}{x_k} \right) - \log \left(\frac{x_j^*}{x_k^*} \right) \right\}^2 \right]^{\frac{1}{2}}$$

The centred log-ratio transformation (clr) from S^{D-1} to \mathfrak{R}^D is obtained as follows:

$$\text{clr}(\mathbf{x}) = \log(\mathbf{x}) - \overline{\log(\mathbf{x})}$$

where $\overline{\log(\mathbf{x})}$ is the geometric mean of the composition \mathbf{x} . Therefore,

$$\Delta(\mathbf{x}, \mathbf{x}') = d_{eu}(\text{clr}(\mathbf{x}), \text{clr}(\mathbf{x}'))$$

where d_{eu} represents the Euclidean distance.

Bipartition of data points was obtained through a K -means algorithm implemented on the matrix of Aitchison distances between samples. The objective function of the standard K -means method is to minimize the sum of squared distances of each item to the centroid of its respective cluster (Ball and Hall, 1967; MacQueen, 1967; Anderberg, 1973; Jain and Dubes, 1988). Detected clusters were colored in the biplot form of the Aitchison PCA ordination diagram. Posteriorly, we drew contour lines for altitude and latitude. A logistic regression model was constructed to predict the membership of single points to a determined assemblage cluster. Since this analysis deals with binary dependent variables, the response variable was code 1 for data points previously classified and interpreted as cold-type, 0 otherwise. Altitude, latitude and their interaction were included as predictors. The contour lines of a

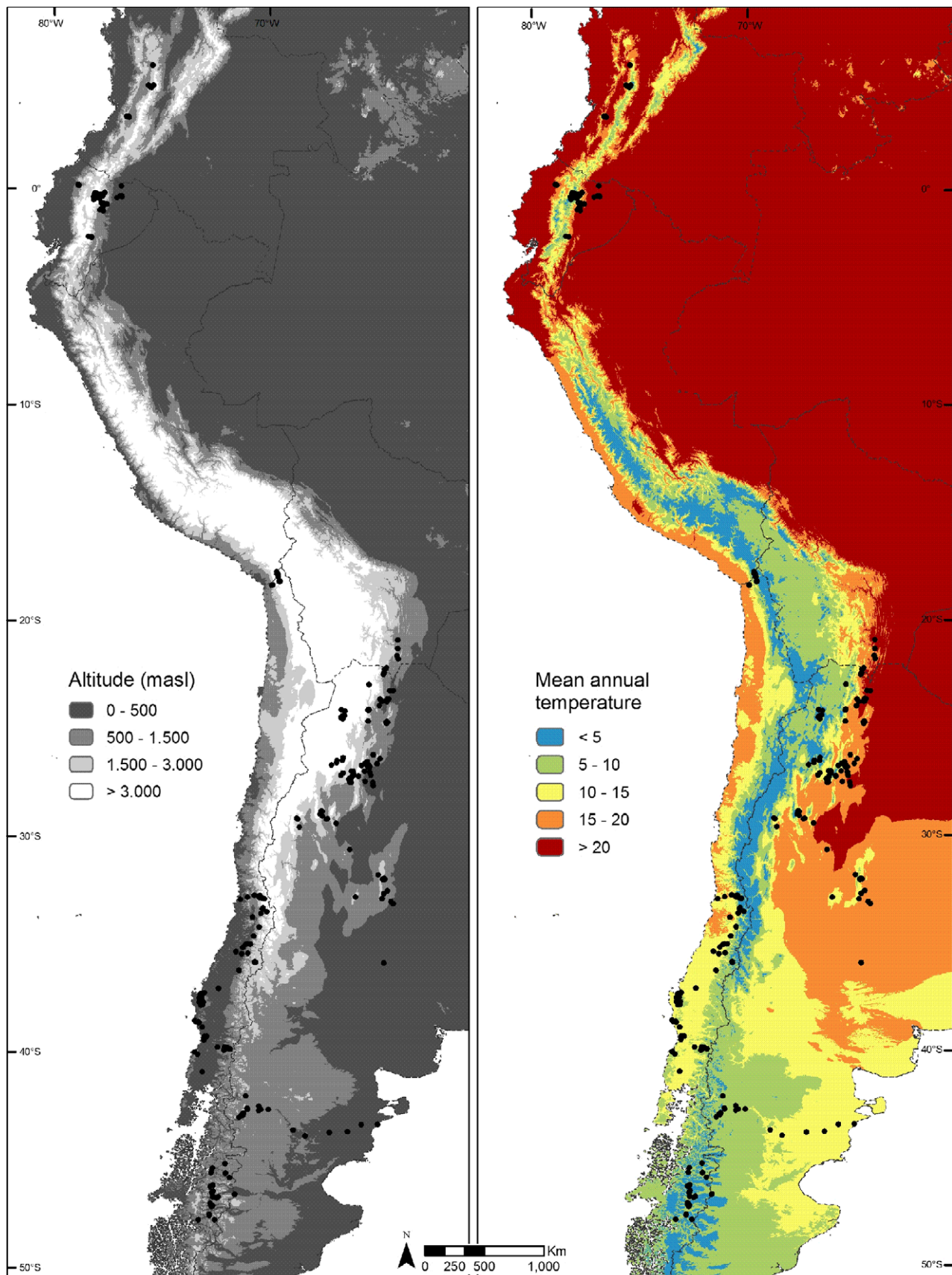


FIGURE 1 Sampling point localities projected on the same geographical extent of Western South America. Maps have been classified according to topographic elevations (to the left side) and annual mean temperature (to the right side) [Colour figure can be viewed at wileyonlinelibrary.com]



posteriori probabilities were drawn in a two-dimensional graphic of altitude by latitude. We selected as classifiers those values of a posteriori probabilities with the best performance in both specificity and sensitivity as pursued in the calculation of the area under curve (AUC) in a roc curve analysis. A simple equation of altitude in function of latitude as an assemblage composition change predictor is proposed. This procedure enables to establish the community bipartition band (CBB) that segregates the two main clusters of communities.

3 | RESULTS

Mayfly assemblages ordered after the multivariate analysis of their compositions are shown in the form biplot (Figure 2), the first two components explaining 48% of the entire variance. The genera with the highest loadings were: *Andesiops* Lugo-Ortiz & McCafferty, *Meridalaris* Peters & Edmunds, *Penaphlebia* Peters & Edmunds and *Nousia* Navas for the negative side; while *Baetodes* Needham & Murphy, *Leptohyphes* Eaton, *Thraulodes* Ulmer, *Americabaetis* Kluge and *Camelobaetidius* Demoulin for the positive side. After performing the bipartition of data points using K-means algorithm on the Aitchison distance matrix, two groups are segregated on both sides of the first biplot axis (Figure 3). Note that latitudinal isolines run almost parallel throughout the domain of analysis, suggesting a single gradient

vector, while altitude isolines show a more complex behaviour (Figure 3). Notwithstanding, focusing on the vertical axis separating both clusters (vertical line passing through zero), altitude and latitude isolines are correlated (i.e. higher altitudes intersect tropical latitudes and lower altitudes intersect austral latitudes). Nevertheless, it is important to underscore that the austral (-40°) latitude isoline is restricted to the negative side of the first component axis; in this section, the altitude does not play a critical role to distinguish one cluster from the other.

The resulting logistic regression model fit is shown in Table 1, where we list the regression coefficients that describe the relationships between predictors and natural logarithms of the odds of the target variable (here, the odds of observing a cold-type assemblage against a warm-type). A posteriori probabilities of class membership (when latitude and altitude are known) between 0.6 and 0.7 (Figure 4) perform very well as classifiers (i.e. observed bipartition and predicted bipartition agree greatly). In other words, a maximum for combined sensitivity and specificity is achieved when these values of a posteriori probabilities are used as thresholds for the data point bipartition. So, a Community Bipartition Band (CBB) can be recognized (marked with grey in Figure 4).

In searching an easy formulation for a curve embedded into the CBB, the parametric equation behind superellipses was adopted as mathematical expression. Thus, the formulation for the arc of

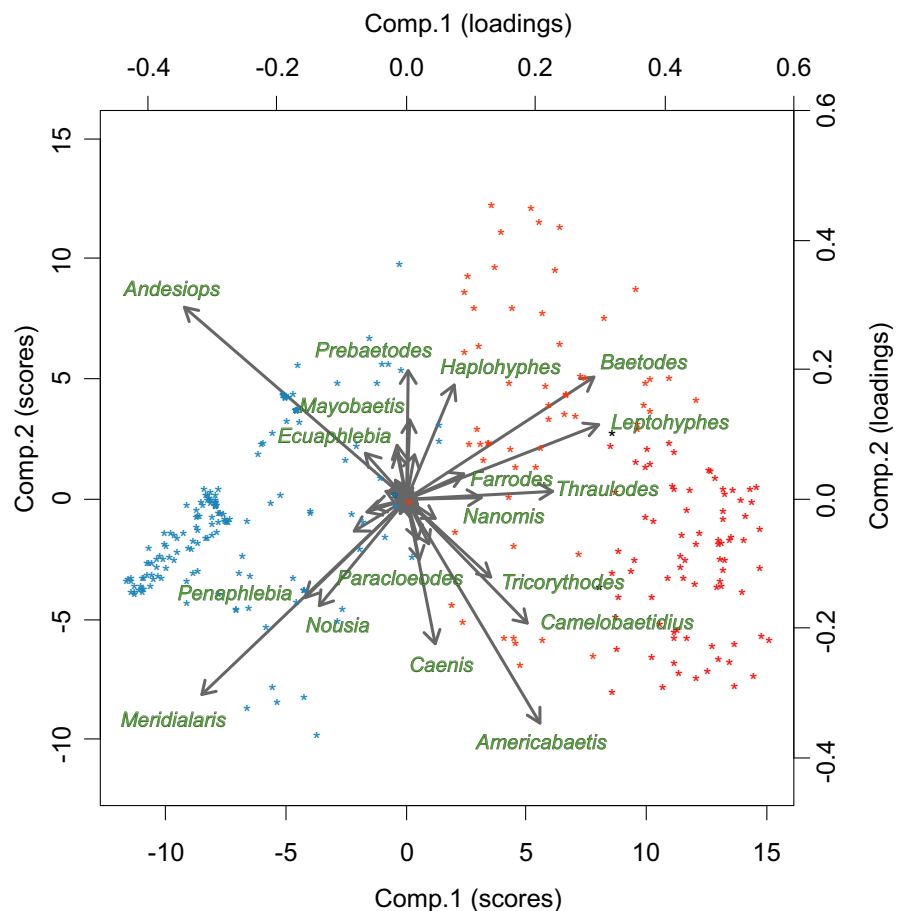


FIGURE 2 Form biplot of genera by sampled communities. The set of points located at the positive domain of the first component are characterized by larger proportions of warm-adapted taxa (e.g. *Baetodes*, *Leptohyphes*, *Thraulodes*). The negative domain of the first component is characterized by higher incidences of cold-adapted taxa (e.g. *Andesiops*, *Meridalaris*). Sites are coloured in concordance with Figure 3, reflecting the two main groups of samples obtained after clustering in function of their mayfly compositions [Colour figure can be viewed at wileyonlinelibrary.com]

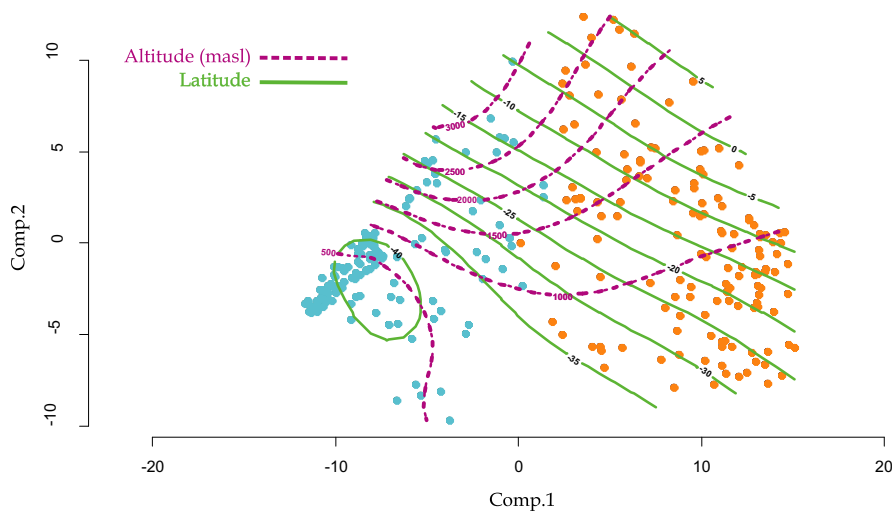


FIGURE 3 Bipartition of mayfly assemblages and their relationship with altitude and latitude. Data points (assemblages) are mapped onto the first two dimensions of PCA. Points are colored by their membership to one of two clusters determined by K-means analysis. Blue and red points correspond to the cold- and warm-type of communities. Contour lines for latitude and altitude are superimposed [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Statistical summary of logistic model oriented to predict the occurrence of the cold-type community in function of altitude, latitude and their interaction

Coefficients	Estimate	Standard error	$p(> z)$
Intercept	-3.654	1.738	<.001
Latitude	-0.422	0.051	<.001
Altitude	4.25E-02	5.90E-04	<.001
Latitude: Altitude	1.14E-04	1.81E-05	<.001

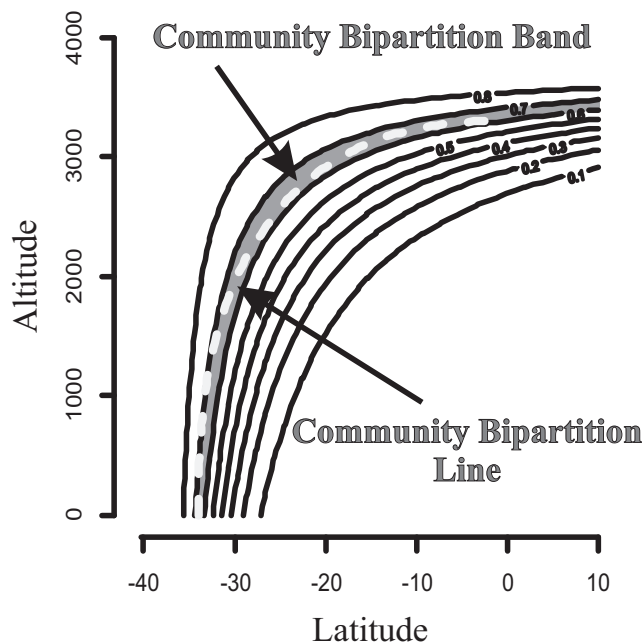


FIGURE 4 Contour lines for the a posteriori probabilities calculated from the logistic regression model. The higher the values of a posteriori probability, the higher the chance of occurrence of communities interpreted as cold-type. Any line located within the solid band between 0.6 and 0.7 values performs accurately to segregate both classes of communities. A white dashed line has been drawn within the limits of the band, and corresponds to the Community Bipartition Line (CBL)

superellipse running across the CBB, and named henceforth as Community Bipartition Line (CBL), remains as follows:

$$\text{CBL Altitude} = 3300 \cdot \sin^t(x)$$

$$\text{CBL Latitude} = -34 \cdot \cos^t(x)$$

where x concerns to the angular parameter and ranges from 0 to $\pi/2$. The exponent t denotes the curvature of the superellipse. We found $t = 0.8$ for our CBL. This single parameter can be used to perform comparisons between different patterns (e.g. other insect orders) of altitudinal variations in relation to latitude. For example, Table 2 shows that altitude is meaningless from 34° S latitude to the South, but around 33° S and 27° S larger changes in altitude occur with latitudinal changes, and from 9° S to the Equator the predicted altitude separating cold-warm assemblages almost does not vary (3,252 m).

Overall, CBL yields an accuracy of c. 97% when the classification guided by CBL is contrasted with the clustering guided by compositional distance. The coefficient 3,300 represents the critical altitude for equatorial CBL, whereas -34° represents the critical latitude of CBL where cold groups became dominant irrespective of altitude. Community subsumed into the categories of cold and warm are expected to lie above and below the CBL, as effectively happens with mayfly assemblages.

Andesiops, *Meridialaris* and *Baetodes* account largely for the trend in compositional variation. For the case of a three compositional vector, ternary diagrams (Figure 5a) are very useful to illustrate the overall dispersion of data points. The ternary diagram (Figure 5b) for the subcompositions induced by the three previous genera shows a co-variation between the fractions of *Andesiops* and *Baetodes* in one side and between *Andesiops* and *Meridialaris* on the other side. With the exception of the single point inward the ternary plot, *Baetodes* and *Meridialaris* hardly co-dominate. *Andesiops* does co-vary with the remaining involved genera. Even if *Andesiops* can be found from sea level in the most austral streams in South America up to 4,000 m in the tropics, the interaction of



TABLE 2 Examples of pairs of values for latitude and altitude extracted from the Community Bipartition Line (CBL) that predicts the transition zone between cold and warm mayfly communities. Given the symmetric nature of this relationship, we only inform Southern Hemisphere values

Latitude	Altitude	Latitude	Altitude	Latitude	Altitude
-34.00	0	-22.50	2,767	-11.00	3,220
-33.50	877	-22.00	2,800	-10.50	3,229
-33.00	1,151	-21.50	2,832	-10.00	3,237
-32.50	1,348	-21.00	2,862	-9.50	3,245
-32.00	1,506	-20.50	2,890	-9.00	3,252
-31.50	1,639	-20.00	2,917	-8.50	3,258
-31.00	1,755	-19.50	2,943	-8.00	3,264
-30.50	1,858	-19.00	2,967	-7.50	3,270
-30.00	1,951	-18.50	2,990	-7.00	3,274
-29.50	2,035	-18.00	3,012	-6.50	3,279
-29.00	2,113	-17.50	3,033	-6.00	3,283
-28.50	2,185	-17.00	3,053	-5.50	3,286
-28.00	2,252	-16.50	3,072	-5.00	3,289
-27.50	2,314	-16.00	3,090	-4.50	3,292
-27.00	2,372	-15.50	3,106	-4.00	3,294
-26.50	2,427	-15.00	3,122	-3.50	3,296
-26.00	2,478	-14.50	3,137	-3.00	3,297
-25.50	2,526	-14.00	3,151	-2.50	3,298
-25.00	2,572	-13.50	3,165	-2.00	3,299
-24.50	2,615	-13.00	3,177	-1.50	3,299
-24.00	2,656	-12.50	3,189	-1.00	3,300
-23.50	2,695	-12.00	3,200	-0.50	3,300
-23.00	2,732	-11.50	3,210	0.00	3,300

both altitude and latitude is of utmost importance here. There are particular places where all three genera could coexist evenly, although these are rather exceptional.

When we study the faunal replacement from the lower left (*Baetodes*) to the lower right (*Meridialaris*) vertices in the ternary diagram (Figure 5b), we can find two instances of dominance inversion (Figure 6, middle panel). The two vertical bars, transversal to all the three plots, mark instances of inversion for the subcomposition dominance. The leftmost bar (red) pinpoints the reciprocal replacement between *Baetodes* and *Andesiops* (middle panel), occurring at northern latitudes (upper panel) and altitudes ranging from middle to high levels (lower panel). In a similar fashion, the rightmost bar (blue) pinpoints the reciprocal replacement between *Andesiops* and *Meridialaris* (middle panel), occurring at southern latitudes (upper panel) and a broad range of altitudes (lower panel).

4 | DISCUSSION

Multiple global patterns can be represented through a curved relationship of altitude in function of latitude. For example, the distribution of the alpine life zone, circumscribed between the tree line and the snow line follows this relationship (Körner, 1999). Also, at the global scale, isotherms follow a curved trajectory determined by latitude and atmospheric pressure dictated ultimately by the altitude (Körner, 1999; Mani, 1968). The curved nature of these relationships is also replicated in the community bipartition band here reported. In a given latitudinal isoline, the change from one type of community (cold) to the other (warm) takes place at a given altitude, the lower the latitude the higher the altitude where the shift occurs (Figure 3). The curvilinear nature of the altitudinal divider between both assemblages (instead of a simple rectilinear relationship of altitude against latitude) is a consequence of multiple constraints and not only temperature. At low latitudes (from 9° S to 0°) this limit remains rather constant: 2,252–3,300 m. Oxygen availability may act as an ecological limiting factor for the occurrence of taxa on these environments (Crespo-Pérez, Andino, Espinosa, Dangles, & Jacobsen, 2016; Jacobsen, 2008; Jacobsen, Rostgaard, & Vásquez, 2003; Madsen et al., 2015), but other not

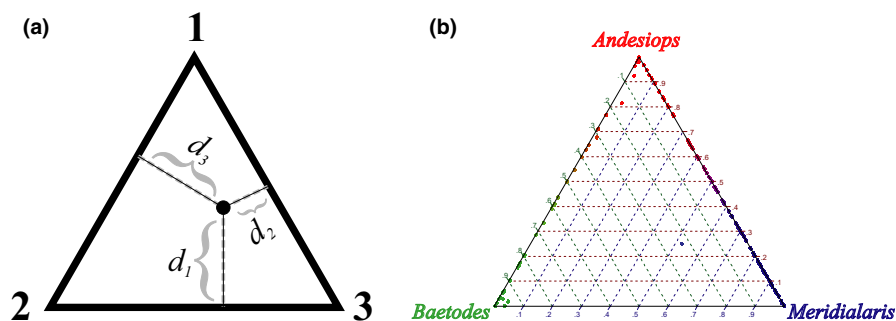


FIGURE 5 For the particular case of $D = 3$, the simplex S^3 can be graphically represented with a ternary plot. This plot is an equilateral triangle where tripartite compositional data are unequivocally represented on it through a point. A given compositional datum $\mathbf{x} = [x_1, x_2, x_3]^T$ corresponds with the point that is d_1, d_2 and d_3 from the opposite sides to the respective apices 1, 2 and 3, being d_1, d_2 and d_3 distances linearly proportional to x_1, x_2 and x_3 , respectively. (a) Ternary plot with a single composition datum (here $\mathbf{x} = [0.37, 0.21, 0.42]^T$) mapped on it. Distances between point and triangle sides are proportional to the components of composition vector. (b) Ternary diagram restricted to the subcompositions represented by the very informative taxa *Baetodes*, *Andesiops* and *Meridialaris*. A gradual and structured replacement in relative incidences can be seen [Colour figure can be viewed at wileyonlinelibrary.com]

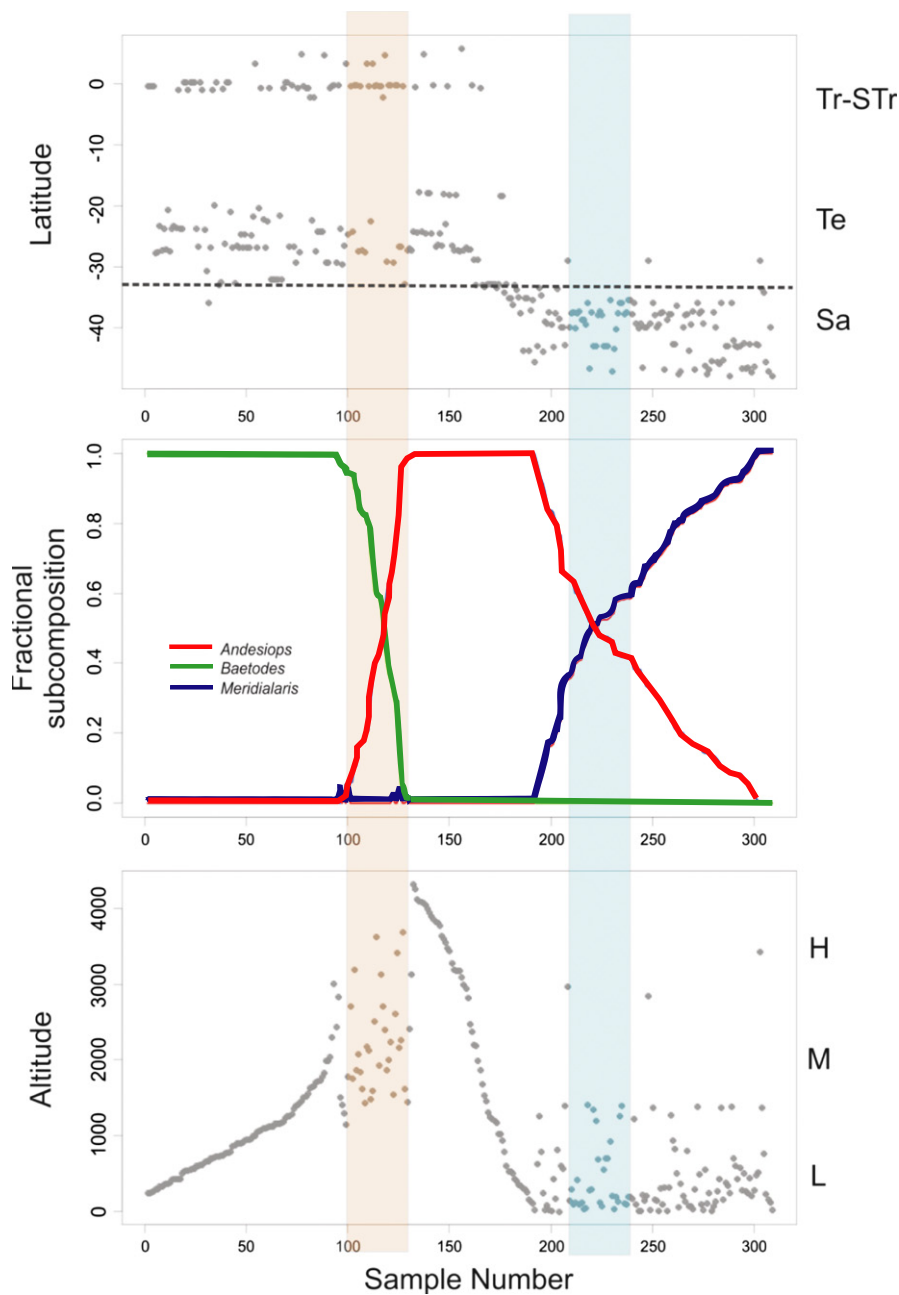


FIGURE 6 Faunal replacement visualized in a multilayered plot. The 326 samples (dots) are ordered from left to right in function of the gradual replacement recorded among the genera *Baetodes*, *Andesiops* and *Meridialis*. The two vertical bars, common to all the three plots, mark instances of inversion for the subcomposition dominance. Tr–STr: Tropical–Subtropical; Te: Temperate; Sa: Subantarctic. H: High altitude; M: Middle altitude; L: Low altitude [Colour figure can be viewed at wileyonlinelibrary.com]

altitude-specific environmental factors (e.g. slope, sun exposure, seasonality) surely influence this pattern at the local level (Körner, 2007). The large extent of our data overcomes the influence of these local variables reinforcing the idea of altitude as a proxy of temperature. In fact, Körner (2007) recognized four unambiguously atmospheric changes linked to altitude: (1) atmospheric pressure, (2) temperature, (3) radiation and (4) fraction of UV-B.

The study of Ide (1935) with Ephemeroptera in a North American stream reached conclusions that partially agree with our results. For example he found (Ide, 1935:72) that species "... at the source have a northern distribution on this continent, some being circumpolar" and "those which are confined to the lower parts of the stream have a more southerly distribution". Ide (1935) did not attempt to classify the specific assemblage studied into cold and warm stenothermic taxa, but realized that temperature of the water sets the limits to

their distribution. Despite being part of the standard terminology in papers on running water, the terms cool- and warm-adapted groups remain hypothetical (Malicky & Chantaramongkol, 1993). Classifications of the general compositional patterns of aquatic insect communities used low-resolution geographic data together with few biotic examples. Ross (1956) did not use specific data about composition and location of sampled communities to define cold and warm adapted groups in a geographical context, neither Illies (1969) worked with this kind of data, and none of them used quantitative compositional data of whole assemblages to characterize these groups. Following Illies (1969), cold-adapted aquatic insects (his oligostenothermal mountain fauna) exist in South American tropics only above 3,000 m, roughly coincident with our limit around the Equator (3,300 m). In his Figure 1, Illies (1969, p. 687) depicts a typical qualitative association of this fauna, including two mayflies:



Atalophlebia Eaton (now *Meridialaris*) and *Baetis* Leach (now *Andesiops*) (Dominguez, Molineri, Pescador, Hubbard, & Nieto, 2006; Lugo-Ortiz & McCafferty, 1999). In general, we found similar results, but we emphasize that co-dominance is not the rule for these cold exemplars and complex patterns of turnover involving both genera, with *Meridialaris* being restricted latitudinally. Illies (1969) also states that critical elevation of 3,000 m change towards the South, occurring “at medium elevations”, until Patagonia where it occurs at the “flat plains”. In this paper, we provide exact values (elevation for each latitude) that act as predictions refutable by possible future studies. On the other hand, Illies (1969) restricts the warm-adapted or “polystenothermal” fauna to the lowlands (and slopes of surrounding mountains) of the Amazon, Orinoco and La Plata river systems. In his typical warm-adapted association (in the foothills of Huallaga, Peru) the following mayflies were included: *Thraulodes*, *Baetodes*, *Leptohyphes* and *Dactylobaetis* Traver & Edmunds (now *Camelobaetidius*). This composition is coincident with our results, and we found additional groups that appear even in Patagonian lowlands (not strictly warm environments, but relatively warmer than mountainous counterparts at these latitudes), *Traverella* Edmunds and *Americabaetis*.

Cold-adapted genera of Ephemeroptera have been reported south to the Tropic of Capricorn in Andes (23.5° S), Patagonian plains, Tierra del Fuego, and the southern coastal mountains of Brazil (Edmunds, 1972; Hubbard & Peters, 1977; Pescador & Peters, 1980; Savage, 1987). This is coincident with our results, except that our northern limit is 7° further northward of the Tropic of Capricorn. The inclusion by the mentioned authors of the southern coastal mountains of Brazil is due to *Massartella* Lestage, a genus now reported to occur also up to the Venezuelan uplands (Derka, Nieto, & Svitok, 2012). The phylogeny and ecology of this genus is a promising research topic, since it is the only mayfly genus distributed in the Guiana and Brazilian Cratons and phylogenetically related with Notogeic taxa.

Since generic ranges are hypothesized here, our results can alert of the probable misidentifications of otherwise possible outliers. For example, Gutiérrez and Reinoso-Flórez (2010) list minimum and maximum altitudes for the occurrence (not dominance) of mayfly genera in Tolima, Colombia (c. 4° N latitude): *Andesiops* (1,318–3,533 m), *Baetodes* (290–2,847 m), and *Meridialaris* (290–1,386). We can predict that *Meridialaris* constitutes misidentification, since from our results, the altitudinal range reported is completely outside its continental pattern (i.e. the genus is not expected to be found at this latitude, and if present it would be found at elevations more similar to those reported for *Andesiops*).

In central Argentina (Córdoba, c. 32° S), *Andesiops* was not found at 1,100 m or below (Corigliano, Gualdoni, Oberto, & Raffaini, 2001; Márquez, Cibils, Principe, & Albariño, 2015; Principe, Raffaini, Gualdoni, Oberto, & Corigliano, 2007). This pattern (*Baetodes* present, *Andesiops* absent) is coincident with our prediction, since the change between both types of assemblages is expected to occur only above 1,500 m at this latitude.

The replacement instance involving *Andesiops* and *Meridialaris* takes place at high latitudes (i.e. Patagonia) and is correlated with neither altitude nor latitude. It is probably more related to other

ecological factors than to temperature per se, as happens at lower latitudes with other mayfly taxa (e.g. *Baetodes*, *Farrodos* Peters, *Leptohyphes*, *Thraulodes*, *Americabaetis*) (Dominguez & Ballesteros Valdez, 1992). Despite *Meridialaris* and *Andesiops* are scrapers (biofilm grazers), may well be the case of niche segregation. Both species present important morphological differences in mouthparts, grazing behaviour and digestibility (Diaz Villanueva & Albariño, 2003; Diaz Villanueva, Albariño, & Modenutti, 2004).

In relation to upper limits of mayfly genera, Crespo-Pérez et al. (2016) and Molineri, Zúñiga, Ramos, Giraldo, and Cardona (2016) found that *Leptohyphes* reaches 3,000 to 3,300 m in Ecuador and Colombia, respectively, in broad concordance with CBL prediction for a typical taxon from the warm group. Crespo-Pérez et al. (2016) found an abrupt decline of *Leptohyphes* along an altitudinal transect, hypothesizing that the upper altitudinal limit is conditioned by mean oxygen saturation, temperature and current velocity.

The results from this analysis, using taxonomic data at the genus level, should be understood as general rules for large or continental scale analyses. We are aware that temperature preferences and distribution patterns may vary within a genus to altitude and latitude. However, our results are not expected to change significantly since most of the widespread high altitude mayflies are monotypic. Additionally, experimental studies will be useful to test hypotheses about temperature effects on these aquatic insects.

Biological imprints of low temperatures are not equivalent between those coming from high altitude and high latitude conditions. Mani (1968) highlights that low temperatures at high altitudes counteract the injurious effects of these environments because it delays the rapid evaporation, favours the precipitation of atmospheric moisture and depresses the respiratory activity, among other reasons. He points out that the ecological significance of low temperature at high elevations is fundamentally different from that observed in open habitats near sea level at high latitudes. Mani (1968) postulates a paradoxical statement by which insects seem to exist *in spite of* the great atmospheric cold in lowland open habitats, whereas at high elevations they exist only *because of* the atmospheric cold. Ultimately, this implies that cold conditions are not comparable between high altitudes and high latitudes. This distinction also follows in the analysed data. *Andesiops* dominates the composition of subtropical and tropical high Andean assemblages, while notogeic or subantarctic lineages (*Meridialaris* among others) dominate the composition of assemblages at high latitude.

The probable presence of warm communities above the CBL can be indicative of global changes operating at a local scale. In this sense, long-term environmental changes could be reflected through changes in the trajectory of CBL. Given that our sampling time horizon involves the last two decades, it is possible that CBL has already been influenced by recent changes. Anyway, our results could be considered as a baseline to benchmark future research. Thus, monitoring of global change through the altitudinal displacement of the community bipartition line (CBL) is a promising tool. We expect a greater change (in the position of the CBL) in medium latitudes, since at high latitudes the altitudinal effect blurs out, whereas at

lower latitudes oxygen availability become a prime factor. Schmeller et al. (2017) proposed eight variables to track biodiversity changes at a global scale: allelic diversity, body mass, size at first reproduction, phenology, abundance, survival rates, range dynamics and ecosystem heterogeneity. From this suite of essential biodiversity variables, monitoring the shifts of CBL inscribes within the range dynamics and can be an important indicator of biospheric change.

5 | MAIN CONCLUSIONS

Since latitude and altitude are two drivers of temperature at global scale, we expect that groups characterized by opposed thermal preferences remain separated by a divider reflecting the combined effects of altitude and latitude. The two clusters of data points, established from mayfly assemblage compositions, can be arranged on either side of a curvilinear altitude-by-latitude relationship. This curve was modelled with the very versatile parametric equation associated with the arc of a superellipse. Results have implications for future monitoring of global change as well as for comparative purposes with other taxa and relevant ecological lines such as the tree line.

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BIOSKETCH

The research team works with the ecology of running waters in South America and some of the members of the group work with systematics of mayflies.

SUPPORTING INFORMATION

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