

Species and genus richness and assemblage composition of stream caddisflies (Insecta: Trichoptera) vary with latitude in mountain rainforest of Argentina

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Abstract. Evidence found in results of studies of latitudinal gradients of benthic macroinvertebrate diversity is variable. This study analysed how species and genus richness and the composition of caddisfly assemblages (Insecta: Trichoptera) vary in Argentinean mountain forest through a latitudinal gradient from 22 to 28°S. Qualitative and quantitative data from 20 stream sites were compared. Assemblage richness and composition were analysed by comparing linear regressions, rank–abundance (RA) curves and non-metric multidimensional scaling (nMDS). Taxonomic richness increased from high to low latitude. RA curves showed changes in assemblage composition and structure across the latitudinal gradient. The nMDS revealed that the composition of the assemblages also changed along the latitudinal gradient. The patterns are similar to those observed in plants and vertebrates from the study region. The results are of particular note because a latitudinal gradient of aquatic insect diversity has rarely been observed in a narrow range.

Additional keywords: aquatic insects, protected areas, Yungas forest.

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Introduction

It is well known that the tropics contain more species of plants and animals than the high-latitude zones (Rohde 1999; Hawkins 2001; Willig *et al.* 2003). However, although diversity has been reported to be higher in the tropics for most groups of organisms, such as trees (Currie and Paquin 1987), mammals (Rosenzweig 1992; Kaufman and Willig 1998), birds (Gaston and Blackburn 2000) and fish (Oberdorff *et al.* 1995), a few groups exhibit a reversed latitudinal gradient of diversity (e.g. sawflies; Kouki *et al.* 1994) or no gradient at all (e.g. fig wasps; Hawkins and Compton 1992).

Freshwater habitats have received less attention than marine or terrestrial ecosystems, so we must not assume *a priori* that diversity patterns found in terrestrial or marine systems also apply to fresh waters (Boyero 2002). For example, diversity gradients for freshwater taxa may be weaker than those for marine and terrestrial taxa (Hillebrand 2004), and macroinvertebrate diversity data can show contradictory results (Vinson and Hawkins 2003; Boulton *et al.* 2008). As possible explanation for these weak patterns, Hillebrand (2004) proposed that, in contrast with both the marine and terrestrial environment, the freshwater realm is geographically isolated in small ‘freshwater islands’. Although some studies have suggested that tropical regions have higher species richness than temperate regions (Bishop 1973; Stout and Vandermeer 1975; Pearson *et al.* 1986),

others have suggested the opposite (Patrick 1964; Arthington 1990). In addition, most studies have analysed data from historical records, lack abundance data and have not quantified abundance or presence–absence using standardised methods (Boulton *et al.* 2008). However, the study of Lake *et al.* (1994) had a clear design and identical sampling method for the surveys conducted in Australian temperate and tropical streams, with the authors finding that the invertebrate fauna of cobbles was more diverse in tropical than in temperate streams. Other studies have used more comprehensive data, compensating for different sampling approaches. For example, Vinson and Hawkins (2003) collected results from many site-based surveys from around the world and showed distinct patterns of diversity among insects groups (Ephemeroptera, Plecoptera and Trichoptera). Vinson and Hawkins (2003) found that Trichoptera richness showed less latitudinal variation than that of the other taxa, but was slightly higher near the equator and at latitudes of 40°N and 40°S than at other latitudes. Conversely, Pearson and Boyero (2009) used a regional approach and examined extensive datasets from a range of latitudes and continents. Among the invertebrates, Ephemeroptera and Plecoptera were more diverse at higher latitudes, whereas Odonata were more diverse at lower latitudes; for the Trichoptera, no latitudinal gradient was apparent (Pearson and Boyero 2009). Heino *et al.* (2018) found that subtropical streams from Brazil harbour higher genus

richness of insects than boreal streams of Finland, but Trichoptera were regionally more diverse in the Nordic region. Thus, it is important to investigate latitudinal patterns in discrete taxonomic groups and in particular environments, because freshwater assemblages comprise a diverse mix of taxa that have invaded fresh waters independently, following different biogeographical patterns, which may explain why overall latitudinal diversity gradients are unclear (Heino *et al.* 2002).

Considering the much smaller research effort in tropical and southern regions than in northern temperate regions, it is necessary to produce more data on freshwater macroinvertebrate biodiversity at regional and local scales to properly examine latitudinal gradients (Boyero 2002). Few studies have recognised diversity gradients of macroinvertebrates along narrow latitudinal ranges. For example, Kay *et al.* (1999) detected that family richness of macroinvertebrates decreased with increasing latitude, along an $\sim 11^\circ$ gradient in north-western Australia. Bush *et al.* (2012) revealed that the taxa turnover of riffles habitat samples was negatively related to latitude, falling by 15% from north to south ($\sim 9^\circ$) in New South Wales, Australia. In addition, Al-Shami *et al.* (2013) observed that within-stream β -diversity was significantly related to latitude over a range of $\sim 3^\circ$ in the Malaysian Peninsula. Nevertheless, Pearson *et al.* (2017) did not find a relationship between richness and latitude along a gradient of $\sim 4^\circ$ in the Australian Wet Tropics. There are few studies of latitudinal diversity gradients of aquatic insects in South America. At a local scale, Jacobsen *et al.* (1997) found that the number of insect orders and families increased linearly with maximum stream temperature, and therefore decreased with latitude, among three groups of streams from the Equator (lowland, central valley and páramo). At a regional level, only Odonata and Ephemeroptera have been studied (Boyero 2002), but without reference to particular ecoregions. Although studies over a broad latitudinal range are needed to understand global patterns, it is also of interest to investigate latitudinal gradients within ecoregions to reduce the number of environmental variables. The focus of the present study, the Yungas forest of north-western Argentina, is part of a discrete ecoregion comprising a belt of montane forest that has a wide latitudinal distribution in South America from $\sim 10^\circ\text{N}$ to 29°S .

Although studies of macroinvertebrate communities in rivers of the Yungas forest have been undertaken (e.g. Fernández *et al.* 2001, 2002, 2006), only Von Ellenrieder (2007) suggests latitude to be a significant variable, and no study has investigated latitudinal patterns within particular taxa. Here we concentrate on Trichoptera larvae, which are important contributors to energy flow and nutrient dynamics in the aquatic environment because they provide a food source for a variety of aquatic predators, such as trout and other fish (Wiggins 2004), and are considered good indicators of water quality because of their low tolerance to changes in habitat conditions (Ward 1992). North-western Argentina includes many species that are widespread across central Argentina, as well as some local endemics (Dos Santos *et al.* 2015).

In this study we investigated the latitudinal distribution of trichopteran assemblages associated with streams in the Yungas forest. Analyses at the genus and species levels were made to

determine whether diversity and assemblage composition were related to the latitudinal gradient.

Materials and methods

Study area

The Yungas mountain forest is a narrow belt of mountain rain-forest that ranges in altitude from 300 to >3000 m above sea level (ASL), with an altitudinal stratification of the vegetation (Fig. 1). This highly diverse forest extends across Argentina between 22 and 28°S , covering $3\,900\,000$ ha from subtropical areas at the southern end to tropical areas in the northern end just at the border with Bolivia (Brown *et al.* 2001), but continues to Venezuela at the Equator (Kappelle and Brown 2001). The climate is warm and humid, with annual average temperatures ranging from 14 to 26°C . The Yungas forest is stratified into three vegetation floors or bands: (1) the high montane forest (1500 – 3000 m ASL), where rainfall reaches 1000 mm; (2) the low montane forest (700 – 1500 m ASL), which has the highest precipitation (2000 mm annual) and the least seasonal hydrological regime; and (3) the foothill forest (400 – 700 m ASL), with an annual rainfall that varies between 1000 and 1500 mm during the wet season, and a 6-month dry season (rainfall ≤ 50 mm) that extends from June to November (Brown *et al.* 2001). Pero *et al.* (in press) recorded slightly higher values of water temperature in streams located in the foothill forest compared with streams from the other floors. The Yungas has been included by UNESCO as a Biosphere Reserve and corresponds to the ‘hot spot’ known as the ‘Tropical Andes’ (Myers *et al.* 2000).

As shown in Fig. 1, there are four national parks in North-western Argentina included in this ecoregion (from south to north): Campo de los Alisos (Tucumán province; 170 km²), El Rey (Salta province; 441.62 km²), Calilegua (Jujuy province; 763.06 km²) and Baritu (North of Salta province; 724.39 km²).

Survey design and methods

Sampling work was divided into discrete latitudinal ranges (A–F) as follows: A, 22 – 23°S ; B, 23 – 24°S ; C, 24 – 25°S ; D, 25 – 26°S ; E, 26 – 27°S ; F, 27 – 28°S (Fig. 1). Each latitudinal range, except D, included four sampling sites, each comprising a 100 -m stream reach. Range D only had one sampling site. Qualitative samples of adults were gathered in Ranges A, B, C and F, which were located in different national parks. Quantitative samples of larvae were gathered in all ranges.

Qualitative samples of adults

Adult material of Trichoptera was collected using light traps at the edge of rivers and springs from the following national parks in north-western Argentina: Campo de los Alisos, El Rey, Baritu and Calilegua. The light trap used is a white sheet supported in a metallic rectangular arch. The illumination system was a mercury vapour light bulb. The light trap was operated for ~ 4 h beginning at sunset. The material collected was fixed in 75% ethyl alcohol. Adult males were separated and cleared in a 10% NaOH solution and then neutralised with phenol. The cleared abdomens of males of all collected species were mounted in glycerine for observation and identification. The material was preserved in 75% ethanol. Samples were identified to the species

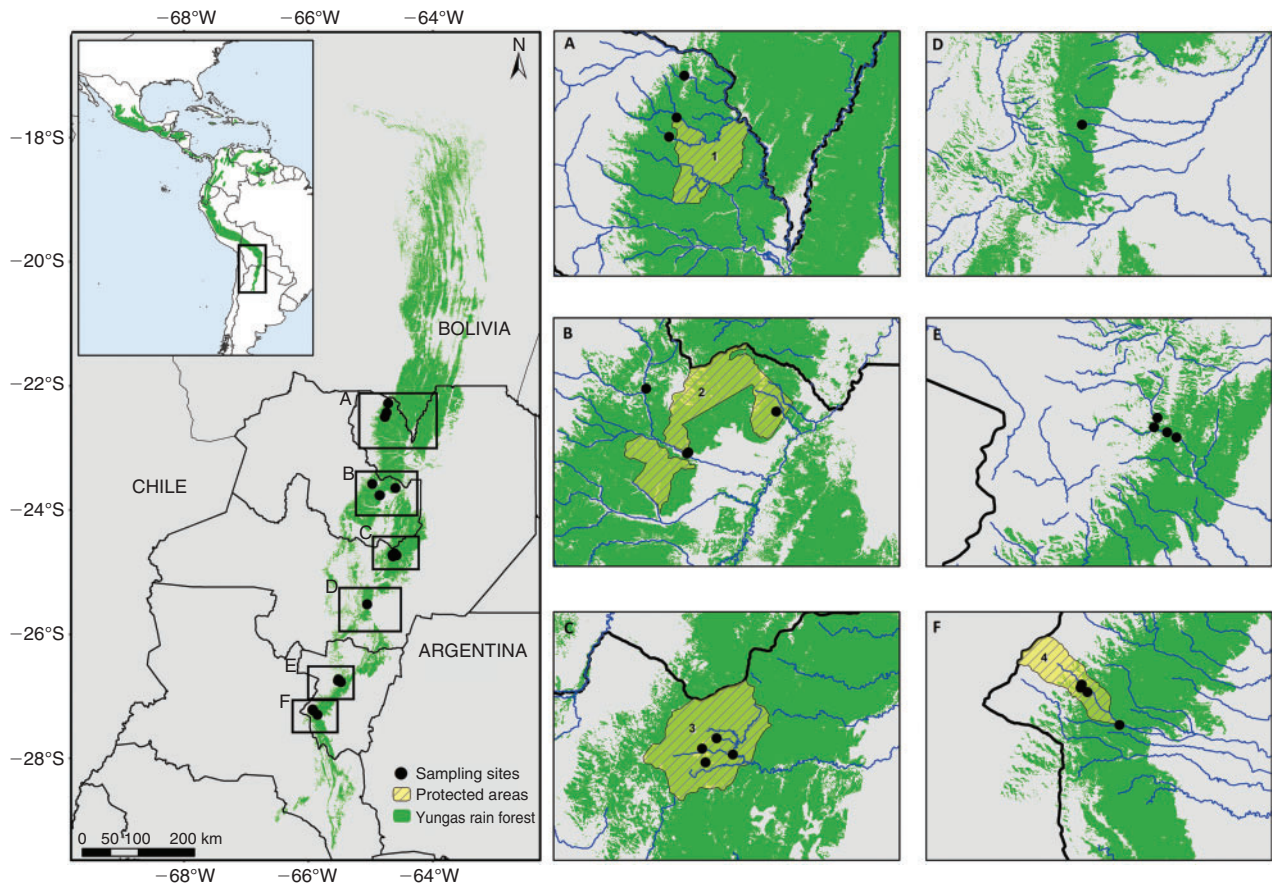


Fig. 1. Study area. The map on the left shows the location of each of the latitudinal ranges (A–F): A, 22–23°S; B, 23–24°S; C, 24–25°S; D, 25–26°S; E, 26–27°S; F, 27–28°S. Black circles indicate sampling points. 1, Baritú National Park; 2, Calilegua National Park; 3, El Rey National Park; 4, Campo de los Alisos National Park.

level by comparing them against type material and using specific bibliographical sources. Historical records of species from the same location were used to complete the species list.

Quantitative samples of larvae

Quantitative samples were collected using a Surber sampler (300- μm mesh, 0.09 m²), pooling three subsamples at each station from riffle habitat (Fig. 1). Samples were preserved in 4% formalin. The washed samples were conserved in 75% ethyl alcohol and later sorted in the laboratory under a stereoscopic microscope. Specimens were identified to the genus level, although the identification of some small specimens was possible only to the family level. All quantitative samples were collected in November, at the end of the dry season, in 2004, 2005 and 2006 (Appendix 1: Table A1).

Environmental variables

Altitude (m ASL), discharge (m³ s⁻¹), channel width (m) and water temperature (°C) were measured at all sampling sites. Altitude was registered using a global positioning system (GPS; eTrex 20; Garmin; Olathe, KS, USA). Discharge was estimated by measuring cross-sectional area, taking depth measurements every 25 cm (for streams ≤ 11 m wide) or every 1 m (for rivers

≥ 11 m wide) along one cross-sectional transect across the channel, and velocity was measured using a velocity meter at two-thirds depth at each point (Global Water Flow Probe FP111, Xylem Inc., College Station, TX, USA).

Statistical analysis

Data were analysed at two taxonomic levels: species and genus. The species-level analysis was performed using data from national parks and included both qualitative samples of adults and historical records. Historical records from national parks were obtained from the Instituto de Biodiversidad Neotropical (Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Tucumán) database and from the literature (Angrisano 1984, 1995; Rueda Martín 2006a, 2006b, 2008, 2011; Valverde and Abelando 2006; Rueda Martín and Sganga 2011; Rueda Martín 2011). Genus-level analyses were performed on quantitative samples collected using the Surber net. The relationship between taxonomic richness (species and genus) and latitude was evaluated through linear regressions.

We used rank–abundance (RA) curves (also known as dominance–diversity curves) to compare how assemblage structure varied across the latitudinal ranges. To create the curves, the

abundance data of the sampling sites within each range were summed. RA curves, in combination with species identity, can provide insights into specific patterns of species diversity, dominance, rarity and composition (e.g. Andresen 2005; Vidaurre *et al.* 2006; Cultid-Medina and Escobar 2016). These analyses were used to complement the multivariate analyses and allow more detailed observations of compositional and structural differences among assemblages (Feinsinger 2001).

Pairwise correlations between dependent variables were evaluated. Then, a multiple linear model was constructed to predict taxonomic richness according to environmental variables, and multicollinearity was assessed in each of the final models using a variance inflation factor (VIF), which is a more precise measure of multicollinearity. The VIF was calculated as the diagonal element of the inverse of the correlation matrix. The VIF equates the quotient of the variance of a regression coefficient in the multiple regression models to the variance of the coefficient in the hypothetically simplified model using only the particular coefficient. The smallest possible value of VIF is 1 (absence of multicollinearity). As a rule of thumb, a VIF value that exceeds 5 or 10 indicates a problematic amount of collinearity (James *et al.* 2014).

Non-metric multidimensional scaling (nMDS) was used to determine the arrangement of the assemblages according to dissimilarity values based on our abundance data (for each site, data from the three subsamples was summed). Dissimilarity between assemblages was calculated with Dissim index (Nieto *et al.* 2017). Euclidean and Bray–Curtis distances are two dissimilarity indices that are frequently used in ecological analyses (Nollet and De Gelder 2014). However, both these indices are strongly influenced by dominant species and are only weakly affected by rare species (Valentin 2012) and are therefore not as useful when there are gradual changes in composition along a gradient. The Dissim index can be used when the observed taxa are assumed to have been sampled from a common regional pool of species. The Dissim index assesses whether assemblages are similar based on both the taxa present and their abundance. Thus, two sites would be very similar if they were consistently near each other after different orderings of sites by increasing values of taxa abundance (Nieto *et al.* 2017).

A vector adjustment procedure was applied to the ordination diagram obtained from nMDS analyses to test the effects of stream environmental variables and latitude on the ordination of the assemblages. The environmental variables were projected using fitted vectors in ordination (*vegan*, R ver. 2.5–2; J. R. Oksanen, see <https://cran.r-project.org/>). All analyses were performed using R Software version 3.3.0 (R Foundation for Statistical Computing, Vienna, Austria, see <http://www.R-project.org/>, accessed 3 October 2018).

Results

Latitudinal patterns of Trichoptera diversity

In all, 45 species were recorded in national parks of the Yungas forest, distributed across 25 genera. The data from historical records of Trichoptera species showed a noticeable tendency to a diminution of the number of species with increasing latitudinal gradient (Fig. 2; Table A2). The genus richness from individual

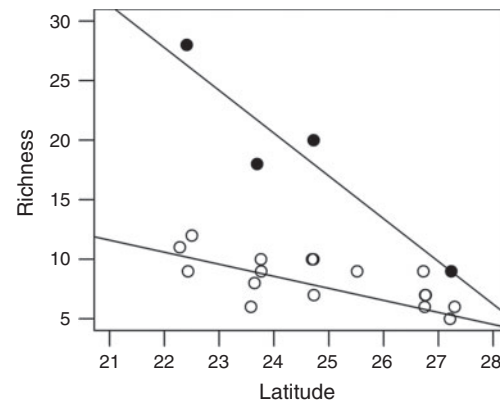


Fig. 2. Linear regressions of taxonomic richness (black circles, species; white circles, genus) plotted against latitude in decimal degrees. For species, $F_{1,2} = 15.78$, $P = 0.05$ and $r^2 = 0.88$; for genus, $F_{1,18} = 13.09$, $P = 0.001$ and $r^2 = 0.42$.

sites also showed a decreasing tendency with increasing latitudinal gradient (Fig. 2). Across latitudinal ranges (A–F), the maximum number of genera was collected in the northern range (A, 15; B, 13; C, 12; D–F, 9).

Baritú National Park, located at the lower latitude range (A), contained 28 registered species; Calilegua National Park (Range B) and El Rey National Park (Range C) had 18 and 20 species records respectively, whereas Campo de los Alisos National Park (Range F) had only 9 species records (Table A2).

Community structure: composition and abundance

RA curves showed the structure of Trichoptera assemblages in the different latitudinal ranges (Fig. 3). Exclusive taxa were found in some ranges, and included *Grumichella* (Range A), *Alisotrichia* and *Protoptila* (Range B), *Ithytrichia* (Ranges A and B), *Cailloma* (Ranges E and F) and *Leucotrichia* (Range F). In Range A, *Grumichella* was the dominant taxa, followed by *Smicridea* and *Mortoniella*. In Range B, taxa from the family Hydroptilidae were dominant, and *Alisotrichia* and *Smicridea* were very abundant. *Smicridea* was the most abundant taxa along Ranges C–F.

Environmental variables from each sampling site are presented in Table 1. Water temperature and channel width were strongly correlated with altitude ($r = -0.87$) and discharge ($r = 0.72$) respectively; thus, we excluded these variables from the following analyses. A multiple linear model was constructed to predict taxonomic richness according to the topographic (latitude and altitude) and hydraulic (discharge) predictors. Table 2 provides information about the estimated coefficients, with the effect of latitude the only significant one. The very low values of the calculated VIFs exclude the occurrence of multicollinearity among explanatory variables, thus providing support to the model as a whole.

The nMDS analyses ordered the sites following a latitudinal gradient arrangement both with abundance (Fig. 4) and presence–absence data. Although the arrangement did not exhibit an exact sites order following the latitudinal gradient, the sites were grouped into two clear sets. One set included the northern sites located between 22 and 24°S (Ranges A, B and C), and the other

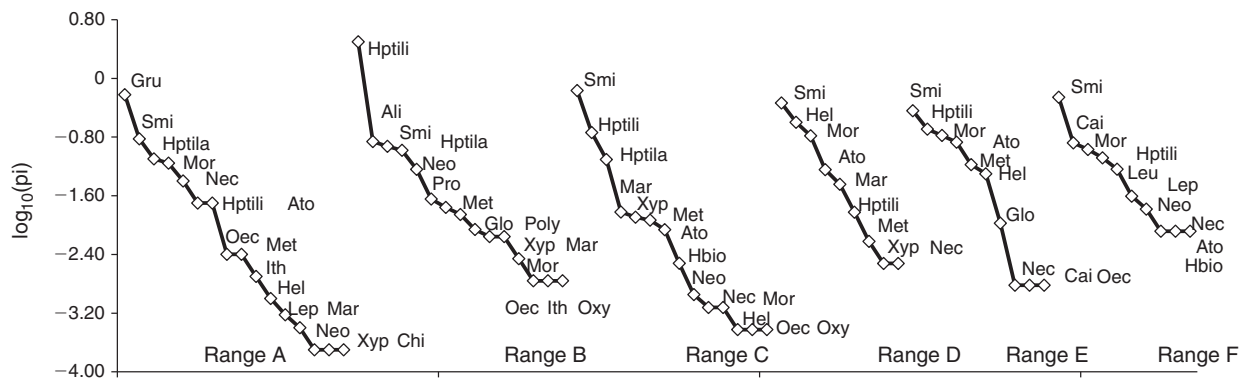


Fig. 3. Rank–abundance curves of Trichoptera assemblages at different latitudinal ranges (A–F). Abundance is expressed as $\log_{10}(pi)$ ($pi = ni/N$, where ni , number of individuals of the taxa, and N , total number of individuals found in the assemblage). The x-axis represents the taxa in decreasing order of abundance. Ali, *Alisotrichia*; Ato, *Atopsyche*; Cai, *Cailloma*; Chi, *Chimarra*; Glo, *Glossosomatidae*; Gru, *Grumichella*; Hbio, *Hydrobiosidae*; Hel, *Helicopsyche*; Hptila, *Hydroptila*; Hptili, *Hydroptilidae*; Ith, *Ithytrichia*; Lep, *Leptonema*; Leu, *Leucotrichia*; Mar, *Marilia*; Met, *Metrichia*; Mor, *Mortoniella*; Nec, *Nectopsyche*; Neo, *Neotrichia*; Oec, *Oecetis*; Oxy, *Oxyethyra*; Poly, *Polycentropus*; Pro, *Protoptila*; Smi, *Smicridea*; Xyp, *Xyphocentron*.

Table 1. Environmental variables of sampling sites
A°, arroyo (stream)

Sampling sites	Latitude (decimal degrees)	Altitude (m ASL)	Discharge ($m^3 s^{-1}$)	Channel width (m)	Water temperature ($^{\circ}C$)
Huaico Grande	-22.27889	1645	0.848	15.3	15.0
Los Naranjos	-22.42972	1109	0.209	3.30	18.0
Baritú	-22.49944	1481	0.384	10.2	18.5
San Lorenzo	-23.76444	589	0.818	12.0	27.0
A° Aguas Negras	-23.76056	650	0.073	2.40	24.5
El Sunchal	-23.57917	1240	0.320	3.30	16.0
A° Yuto	-23.64444	505	0.043	1.80	23.5
San Roberto	-24.71611	935	0.017	1.00	22.0
Los Noques	-24.74556	905	0.361	3.00	27.0
Río Popayán	-24.72889	760	0.287	15.4	25.0
Río Aguas Negras	-24.69417	905	0.018	2.40	23.0
Río Palo Largo	-25.51778	1030	0.177	3.19	19.0
Garabatal	-26.72750	1278	0.501	6.40	15.0
Anfama	-26.74778	1105	1.000	7.40	20.0
Las Juntas 1	-26.75833	1069	3.000	10.8	18.0
Las Juntas 2	-26.76917	960	4.000	21.0	21.0
Jaya	-27.29556	827	0.017	5.10	19.0
Pavas	-27.21083	1655	0.391	9.50	9.00
A° Grande	-27.22667	1530	0.048	3.00	14.0
Tributary of A° Grande	-27.21722	1625	0.037	2.00	9.00

set included the southern sites situated between the 25 and 28°S (Ranges D, E and F). There is one exception in the ordination, which corresponds to the site located in Los Noques stream from the latitudinal Range C.

Discussion

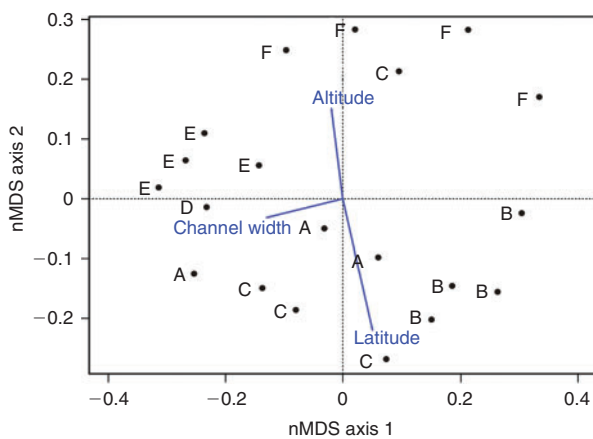
The results of this study revealed an increasing diversity gradient of Trichoptera from high to low latitudes. Accordingly, latitude was most strongly associated with assemblage distribution. This pattern is interesting given that most previous studies of both global assessment of richness and richness site by

site have not found such a gradient. Furthermore, the gradient revealed was remarkably observed over a narrow latitudinal range ($\sim 6^{\circ}$) from tropical to subtropical zones. In addition, two groups of assemblages were identified based on composition; one included the northern Yungas and the other included the southern Yungas.

Our findings provide information to help elucidate whether the patterns of latitudinal diversity commonly observed in terrestrial and marine taxa also occur in freshwater organisms. Previous studies that evaluated the latitudinal distribution of freshwater communities showed results that varied from weak

Table 2. Multiple regression model with variance inflation factor (VIF) statisticsProbabilities are significant at: *, $P < 0.1$; **, $P < 0.05$; ***, $P < 0.01$

	Dependent variable: taxonomic richness (s.e.)	VIF
Latitude	1.079*** (-0.312)	1.12
Discharge	0.496 (-0.524)	1.079
Altitude	-0.0001 (-0.002)	1.045
Intercept	34.339*** (-7.606)	
Observations	20	
R^2	0.441	
Adjusted R^2	0.337	
Residual s.e.	2.279 (d.f. = 16)	
F statistic	4.213** (d.f. = 3,16)	

**Fig. 4.** Assemblage ordination obtained from non-metric multidimensional scaling (nMDS) analysis according to dissimilarity values. Stress value: 19.0898. Letters indicate latitudinal ranges (A–F).

patterns (Hillebrand 2004), to contradictory among different orders of insects (Vinson and Hawkins 2003; Boulton *et al.* 2008), to positive (Patrick 1964; Arthington 1990) or negative (Bishop 1973; Stout and Vandermeer 1975; Pearson *et al.* 1986) associations between latitude and diversity. Our results support this last possibility. Among previous studies of aquatic insects, Pearson and Boyero (2009) did not find an apparent diversity gradient for Trichoptera. However, others found higher (Vinson and Hawkins 2003; Boulton *et al.* 2008) or lower (Heino *et al.* 2018) diversity of Trichoptera in tropical than temperate regions. Within narrow latitudinal ranges, Pearson *et al.* (2017) did not find an apparent association between diversity and latitude. In contrast, other studies (Kay *et al.* 1999; Bush *et al.* 2012; Al-Shami *et al.* 2013) found similar patterns to those observed in the present study.

Different levels of taxonomic resolution could affect relationships between diversity and latitude, but generally in terms

of degree more than shape. The less noticeable pattern found at the genus than species level is expected considering the different times for evolution and dispersion processes at each level. For example, the genus *Atopsyche* was present all across latitudinal gradients, but this genus has double the number of species at low compared with high latitudes. Although *Atopsyche callosa*, *Atopsyche maxi* and *Atopsyche spinosa* were present at southern sites, *Atopsyche kamesa*, *Atopsyche lobosa* and *Atopsyche yunguensis* were recorded in addition to these three species at northern sites. There are similar examples for the genus *Marilia* and for other species of the families Calamoceratidae and Leptoceridae. In addition, taxonomic improvements could emphasise these differences. Trichoptera is a holometabolous group of insects, which implies that the aquatic larvae are morphologically very different from the aerial adults; because of this, a low percentage of larvae was associated with adults at a species level. Nonetheless, the genus level was informative enough to enable use to recognise latitudinal variation. Another advantage of genus-level analyses is that identifications at this taxonomic level are more plausible. Thus, this result is relevant for ecological studies, because these are mostly at the genus level.

Our results for Trichoptera coincide with the diversity and distribution patterns observed in other taxonomic groups in the Yungas forest. The segregation of the Yungas into northern areas with higher diversity and southern areas with lower diversity is well described primarily for plants (Brown *et al.* 2001), but similar patterns have been reported for amphibians (Lavilla and Manzano 1995), birds (Brown *et al.* 2001) and mammals (Ojeda and Mares 1989). Coincidentally, these previous studies and the present study seem to show an inflection point of the latitudinal gradient, close to 25° and towards the north, where the number of species and genera started to increase. The variables influencing these diversity patterns could be related to ecological factors. For example, when considering the higher plant diversity found in northern Yungas, it could be expected that the forest at this lower latitude produces higher litter diversity than the southern forest. Thus, the northern Yungas could provide a higher diversity of plant litter resources than the southern Yungas. However, the ‘higher consumer diversity at higher levels of resource diversity rule’ does not always come into effect, as observed by Boyero *et al.* (2011) with regard to shredders and plant litter diversity. According to Boyero *et al.* (2017), shredder diversity could be related to leaf litter quality more than to leaf litter diversity.

Variations in assemblage structure across the latitudinal gradient were also evidenced in the results, primarily in genus dominance. It would be interesting to evaluate whether these changes in assemblage dominance could be related to differences in the use of resources by the taxa across the latitudinal gradient. Recent studies have analysed latitudinal variations in diversity patterns of trophic guilds (Wantzen and Wagner 2006; Boyero *et al.* 2011, 2012, 2015) and confirmed the hypothesis that shredders are less diverse in tropical than temperate streams. Following those studies, it could be expected that the proportion of shredders diminishes from the tropical to subtropical Yungas. Nevertheless, different exceptions to this latitudinal trophic pattern have been recorded in many tropical and temperate areas (Pearson and Boyero 2009), such as in the Australian

Wet Tropics (Cheshire *et al.* 2005) or upland Malaysian streams (Yule *et al.* 2009). Hence, that hypothesis must be investigated in the case of the Yungas forest. In addition, it is interesting that although the dominance of genera changed towards the north, the dominant genus in southern zones (*Smicridea*) continued to be very abundant in the north. This could suggest a niche packing process towards lower latitudes.

The results of the present study could also be related to biogeographic processes. Dos Santos *et al.* (2015) analysed distributional patterns of Trichoptera in Austral South America and identified two major groups of co-occurring species that coincided with the classic zoogeographic division of the region: the Andean–Patagonian complex (of ‘cool-adapted’ organisms) and the extra-Andean domain (of ‘warm-adapted’ organisms). Within these major divisions, groups of highly codistributed species were also found and showed many overlapping spatial configurations. The Yungas forest was identified as a high overlapping area including species from the two major divisions. The segregation of the Yungas into northern and southern areas could also be affected by the biogeographical patterns. For example, the northern Yungas shares the presence of some taxa with the rainforest of north-eastern Argentina, which is located in the extra-Andean domain of warm-adapted organisms (Dos Santos *et al.* 2015). These findings imply that temperature is an important variable affecting biodiversity distribution across the Yungas latitudinal gradients, coinciding with global studies of freshwater gradients (Pearson and Boyero 2009; Boyero *et al.* 2011). However, water temperature was not informative about the assemblage ordinations in the present study, probably because the measurements were made only once. Seasonal or annual temperature measurements would be much more appropriate for evaluating variations across latitudinal ranges.

The fact that we compared regional diversity patterns within the same ecoregional landscape could have helped avoid environmental heterogeneity that led to bias between regional comparisons (Heino *et al.* 2018). Boyero *et al.* (2009) acknowledged that tropical streams can flow through variable landscapes, such as rainforest, deciduous forest, grasslands or deserts. It is well known that macroinvertebrate assemblages can differ among ecoregions or river types (Hawkins *et al.* 2000; Verdonschot and Nijboer 2004), and macroinvertebrate assemblages (including Trichoptera) from north-western Argentina showed significant variations among ecoregions (Pero *et al.*, in press). Therefore, it is important to consider those landscape variations in latitudinal analyses. In addition, it is important to recognise the narrow latitudinal diversity pattern for the development of regional bioassessment and biomonitoring programs. Further studies including other ecoregions must be performed to increase our knowledge of regional diversity patterns. For example, a greater sampling effort is needed in streams of others ecoregions from north-western Argentina, such as the Western Dry Chaco or Monte shrubland, which cover a similar latitudinal range from tropical to subtropical or temperate regions. However, even within the same ecoregion, environmental heterogeneity could be found (Pero *et al.*, in press). Although Trichoptera assemblages varied with latitude, discharge and altitude were also important predictors at smaller spatial scales (i.e. local).

In conclusion, Trichoptera showed a diversity gradient across the Yungas forest, with higher richness at lower latitudes.

The factors affecting that gradient are likely to be ecological and biogeographical features, such as plant litter diversity or distribution of cool- and warm-adapted organisms. Further studies encompassing other taxa and a broader latitudinal range within the Yungas forest and other ecoregions are needed to explore whether the diversity gradient found in this study is replicated at those levels.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

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Appendix 1

Table A1 Sampling site locations, geographical coordinates and latitudinal range
A°, arroyo (stream)

Sampling site	Geographical coordinates	Latitudinal range	Location
Huaico Grande	22°16'44"S, 64°42'39"W	A	Baritú National Park, Salta
Los Naranjos	22°25'47"S, 64°44'20"W	A	Baritú National Park, Salta
Río Baritu	22°25'47"S, 64°44'20"W	A	Baritú National Park, Salta
El Sunchal	23°34'45"S, 64°58'6"W	B	Calilegua National Park, Jujuy
San Lorenzo	23°45'52"S, 64°51'7"W	B	Calilegua National Park, Jujuy
A° Yuto	23°38'40"S, 64°35'53"W	B	Calilegua National Park, Jujuy
A° Aguas Negras	23°45'38"S, 64°50'54"W	B	Calilegua National Park, Jujuy
A° San Roberto	24°42'58"S, 64°38'36"W	C	El Rey National Park, Salta
Los Noques	24°44'44"S, 64°38'11"W	C	El Rey National Park, Salta
Popayán	24°43'44"S, 64°34'42"W	C	El Rey National Park, Salta
Aguas Negras	24°41'39"S, 64°36'46"W	C	El Rey National Park, Salta
Palo Largo	25°31'4"W, 65°03'10"W	D	Metán, Salta
Garabatal	26°43'39"S, 65°30'45"W	E	Lules, Tucumán
Anfama	26°44'52"S, 65°31'10"W	E	Lules, Tucumán
Las Juntas 1	26°45'30"S, 65°29'31"W	E	Lules, Tucumán
Las Juntas 2	26°46'9"S, 65°28'20"W	E	Lules, Tucumán
Jaya	27°17'44"S, 65°50'55"W	F	Campo de Los Alisos National Park, Tucumán
Pavas	27°12'39"S, 65°55'39"W	F	Campo de Los Alisos National Park, Tucumán
A° Grande	27°13'36"S, 65°54'57"W	F	Campo de Los Alisos National Park, Tucumán
Tributary of A° Grande	27°13'2"S, 65°55'47"W	F	Campo de Los Alisos National Park, Tucumán

Table A2 Species list from national park historical records

Taxon	Baritu	El Rey	Calilegua	Campo de los Alisos
Family Hydropsychidae		X		
<i>Smicridea bifida</i>		X		
<i>Smicridea (Rhyacophylax) murina</i> McLachlan			X	
<i>Smicridea (Rhyacophylax) pampeana</i> Flint			X	
<i>Smicridea (Rhyacophylax) peruana</i> (Martynov)	X	X	X	
<i>Smicridea</i> sp.				X
<i>Leptonema boliviensis boliviensis</i>	X			
<i>Leptonema</i> sp.				X
Family Philopotamidae				
<i>Chimarra argentinica</i> (Ulmer)			X	
<i>Chimarra</i> sp.	X	X		
Family Polycentropodidae				
<i>Polycentropus joergenseni</i>				X
Family Xiphoxentronidae				
<i>Xipocentron</i> sp.	X	X		
Family Glossosomatidae				
<i>Mortoniella argentinica</i>				X
<i>Mortoniella wigodzinskii</i>	X			
<i>Mortoniella</i> sp.		X		
<i>Protoptila dubitans</i> Mosely			X	
<i>Protoptila julieta</i> Robertson & Holzenthal			X	
<i>Protoptila</i> sp.	X			
Family Hydroptilidae				
<i>Anchitrichia trifurcate</i>	X			
<i>Alisotrichia benji</i> Rueda Martín			X	
<i>Hydroptila argentinica</i> Flint		X	X	
<i>Hydroptila bidens</i>		X		

(Continued)

Table A2 (Continued)

Taxon	Baritu	El Rey	Calilegua	Campo de los Alisos
<i>Hydroptila</i> sp.	X			
<i>Ithytrichia ferni</i>	X			
<i>Leucotrichia alisensis</i>		X		X
<i>Metrichia argentina</i>		X		
<i>Metrichia</i> sp.	X			
<i>Neotrichia barite</i>		X		
<i>Neotrichia falsifera</i> Flint			X	
<i>Neotrichia gotera</i> Flint			X	
<i>Neotrichia sala</i>		X		
<i>Neotrichia</i> sp.	X			X
<i>Oxyethira batiru</i>	X			
<i>Oxyethira parce</i> (Edwards & Arnold)		X	X	
Family Hydrobiosidae				
<i>Atopsyche callosa</i>	X	X		
<i>Atopsyche lobosa</i>	X			
<i>Atopsyche</i> sp.inosa	X			
<i>Atopsyche yunguensis</i>	X			
<i>Atopsyche maxi</i>	X	X		
<i>Atopsyche kamesa</i>	X			
<i>Cailloma lucidula</i>				X
Family Calamoceratidae				
<i>Banyallarga argentina</i>	X			
<i>Banyallarga loxana</i> (Navás)	X		X	
<i>Banyallarga yungensis</i> Flint	X		X	
<i>Phylloicus lituratus</i>	X			
Family Helicopsychidae				
<i>Helicopsyche turbida</i>		X		
<i>Helicopsyche</i> sp.	X	X		
Family Leptoceridae				
<i>Grumichella flaveola</i> (Ulmer)	X		X	
<i>Grumichella</i> sp.		X		
<i>Nectopsyche</i> sp.	X			X
<i>Oecetis excisa</i> Ulmer			X	
<i>Oecetis knutsoni</i> Flint	X		X	
<i>Oecetis</i> sp.		X		
Family Limnephilidae				
<i>Limnephilidae</i>				X
Family Odontoceridae				
<i>Marilia cinerea</i> Navás	X	X	X	
<i>Marilia elongata</i>	X			
<i>Marilia flexuosa</i> Ulmer			X	
Total number of species	28	20	18	9