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LATITUDINAL DIVERSITY OF PLECOPTERA (INSECTA) ON LOCAL AND GLOBAL SCALES

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ABSTRACT
Several factors influence the latitudinal distributions of organisms, including habitat heterogeneity, ecological requirements, historical events, and the influence of temperature and latitude, amongst others. We evaluate the distributions and diversity of Plecoptera on local (latitudinal gradient in Chile) and global scales.

In Chile, 66 species from 35 genera and 6 families are recognized, with an endemism of 60 %. Species richness is greatest between the Maipo and Aysén river basins (34-45°S), and especially in the Valdivia region (39-40°S). The most widely distributed species are *Limnoperla jaffueli* and *Antarctoperla michaelseni*. The results of this work extend the distribution of several species and suggest that the latitudinal distribution of the order responds mainly to sampling effort, although lower differences in latitudinal diversity are expected due to the characteristics of Chilean rivers (except in the dry zone, 17-30°S). The two ecological factors that seem to be the most important in Plecoptera distributions, in Chile and around the world, are cold temperatures and good water quality. Thus, at global scale, diversity increases from the Equator toward the poles, with differences in the number of families and species between the Southern and Northern hemispheres, possibly due to differences in the number of studies done at the species level.

Keywords: Plecoptera ecology, distribution, endemism, Chile

INTRODUCTION

The factors that determine diversity include the size of the area, habitat heterogeneity, adaptations to specific niches, ecological requirements, competition, predation, historical events, temperature, and latitude, amongst others (Gaston 2000). The spatial scale is a fundamental factor for determining latitudinal diversity (Boyero 2003; Rahbeck 2005); site diversity is usually assessed on local and regional scales.

Freshwater habitats have received less attention than terrestrial and marine ecosystems, so we must not assume *a priori* that diversity patterns found in terrestrial or marine systems also apply to freshwater systems (Boyero 2002). Some studies show latitudinal patterns in species richness, with macroinvertebrate diversity increasing from the Equator to the poles (e.g. Boyero 2002). However, local studies in streams have failed to show clear latitudinal macro-invertebrate diversity patterns (e.g. Stout & Vandermeer 1975; Vinson & Hawkins 2003). Much more data is required, therefore, to allow us to examine local and global patterns of latitudinal diversity for different species. Chile's unique geography, with a dry zone in the north, Mediterranean climate in the center, and wet-temperate conditions in the south provide a latitudinal gradient for this study. Given these conditions, we expect to find greater diversity in the Mediterranean zone (33-37°S) because it is more heterogeneous and because such zones are recognized hot spots (e.g. Bonada et al. 2005, for caddisflies). Historical factors in Chile such as Pleistocene glaciations could also affect the distribution of these organisms. Since the Plecoptera fauna have been relatively well studied, a theoretical-empirical approach to their latitudinal diversity patterns is possible.

The order Plecoptera is a small order of about 2000 species of exopterygote insects worldwide (Theischinger 1991). These are subdivided into two living suborders, both of which are found in Chilean freshwater systems: Antarctoperlaria (families Eustheniidae, Diamphipnoidae, Austroperlidae, Gripopterygidae) and Arctoperlaria (families Notonemouridae, Perlidae). Pictet (1841) was the first to mention Plecoptera from Chile, followed by more numerous contributions from Illies (1958; 1960a, b, c, d; 1961; 1962; 1963; 1964a, b, c; 1965a, b; 1966; 1969a, b; 1977) and Zwick (1972, 1973, 1979). Recently, the group was reviewed by Vera & Camousseight (2006); these authors collected all the data on the order and included a brief descriptive commentary for each family, but they did not include any new distributions of the order nor *Notoperla macdowalli* (McLellan et al. 2005), a species described from Chile's Metropolitan Region (Mediterranean climate). Other species recently described are *Alfonsoperla flinti* (McLellan & Zwick 2007) and *Uncicauda pirata* (McLellan & Zwick 2007).

The present work reviews Chilean and global Plecoptera distributions. Our aim is to find distribution patterns along the latitudinal gradient imposed by climate and local and regional landscapes and to determine the possible influence of historical factors. New local-scale species distributions and a commentary on the group's local and regional diversity on the global scale are given.

METHODOLOGY

The Chilean Plecoptera literature was reviewed (e.g. Cekalovic 1976; Vera & Camousseight 2006). These data were analyzed and used to obtain more recent distributions of the order throughout Chile, and new sites for several species were registered based on our studies of freshwater systems. The group's latitudinal diversity was analyzed through a species distribution matrix with ranks of 1° latitude between 17°S and 56°S for obtaining local diversity. The Plecoptera diversity in other regions of the world was obtained from: Argentina (Albariño 1997 and pers. comm.), Brazil (Olifiers et al. 2004), South Africa (Villet 2007), New Zealand (McLellan 2006), and Australia (Australian Biological Resources Study 2007) (Southern Hemisphere); North America (Stark et al. 2008), Iberian Peninsula and Balearic Islands (Tierno de Figueroa et al. 2003), and Europe (Fochetti & Tierno de Figueroa 2007) (Northern Hemisphere); Costa Rica (Stark 1998) (Central America). Colombia (Zúñiga & Stark 2007, Zúñiga et al. 2007) and Venezuela (Maldonado et al. 2002). Later, all the families, genera, and species were compared between both the Northern and Southern hemispheres, along the American continent, and on a global scale.

RESULTS

Plecoptera distributions along Chile are clearly bimodal (Fig. 1). Diversity is high in the southern Mediterranean area (33-45°S), specifically between the Maipo and Aysén river basins. A second peak in species richness occurs in the Magallanes zone (49-54°S). Plecoptera species are absent from 47°S to 48°S and species diversity is low in northern Chile.

A total of 66 species are listed with an endemism of 60%. Table 1 shows the presence of species along the latitudinal gradient (discriminated every 1°). The most widely distributed species is *Limnoperla jaffueli* (21 latitudinal degrees), followed by *Antarctoperla michaelseni* (15 degrees). The stoneflies with the narrowest distribution range (< 1°) throughout Chile are *Austronemoura araucana*, *Austronemoura caramavidensis*, *Austronemoura auberti*, *Austronemoura flintorum*, *Austronemoura decipiens*, *Chilenoperla puerilis*, *Diamphipnopsis beschi*, *Megandiperla kuscheli*, *Notoperla macdowalli*, *Neonemoura illiesi*, *Plegoperla borggreenae, Plegoperla punctata, Rhithroperla penai, and Teutoperla auberti*. The distribution of other species such as *Andiperla willinki*, *Andiperlodes holdgatei*, *Antarctoperla andersoni*, *Megandiperla kuscheli*, and *Notoperla tunelina* are restricted to the Aysén and Magallanes regions (southern Chile).

Globally, the Plecoptera distribution varies between the north, center, and south, being widely diverse toward high latitudes in both hemispheres (Table 2). The Northern Hemisphere presents greater diversity of families than the Southern Hemisphere, and North America is clearly more diverse than Europe and the Iberian Peninsula at the family and genus levels. Within the Southern Hemisphere, Australia and New Zealand have the most species diversity, whereas Chile and Argentina have the greatest diversity in families and genera.

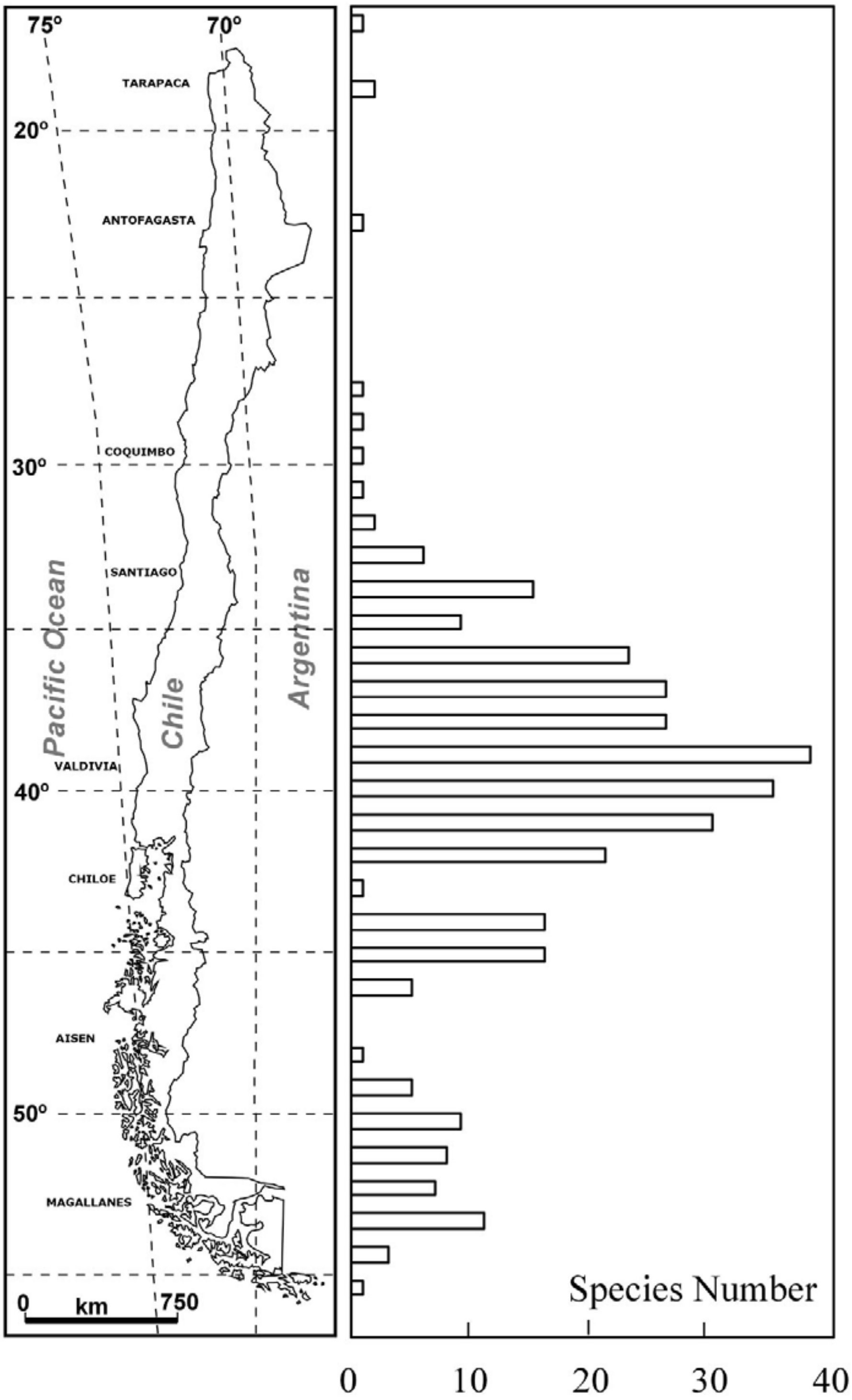

Fig. 1. Diversity and distribution of Plecoptera species in Chile.

Regions of Chile	Tarapaca				Antofagasta					Atacama				Coquimbo			Stgo-Mau			Conc-Ara			Val-Osor-Chil				Aisen						Magallanes							
O. Plecoptera / °L.S.	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Neuroperlopsis patris Illies, 1960.																	2	2		1	1		1	1	1															
Neuroperla schedingi (Navás, 1929).																					2	2	1	1	1	2														
Diamphipnoa annulata (Brauer, 1869).																		1	1	1		2	1		1	2		1	1											
Diamphipnoa helgae Illies, 1960.																						1	1	1	1															
Diamphipnoa virescentipennis (Blandchard, 1851).																				1	1																			
Diamphipnopsis beschi Illies, 1960.																							1																	
Diamphipnopsis samali Illies, 1960.																					1	2	1	1	1	1								1	1					
Andesobius barilochensis (Illies, 1960).																						2	2	1	2			2		1			1	1			2			
Klapopteryx armillata Navás, 1928.																				2	2	1	1	1				2												
Klapopteryx kuscheli Illies, 1960.																					2		1	1	1	1											1			
Penturoperla barbata Illies, 1960.																		1		1	1	1	1	1	2			2	1	1										
Alfonsoperla flinti McLellan & Zwick, 2007																					1	1		1																
Andiperla willinki Auber, 1956.																																1	1	1	1					
Andiperlodes holdgatei Illies, 1963.																												2	2							1				
Antarctoperla anderssoni Enderlein, 1905.																																	1		1	1		1		
Antarctoperla michaelseni (Klapalek, 1904).																	1	1	1	1	1	1	1	1	1	2			1	1				1	1		1			
Araucanioperla brincki (Froehlich, 1960).																							1	1	1	2	1	2	2											
Araucanioperla bullocki (Navás, 1933).																					1				1															
Aubertoperla illiesi (Froehlich, 1960).																		1	1	1	1	1	2	1	1	2		1	1	1										
Aubertoperla kuscheli Illies, 1963.																					1							1		1						2	1			
Ceratoperla fazi (Navás, 1934).																						1	1	1	1															
Ceratoperla schwabei Illies, 1963.																							1	1																
Chilenoperla beschi Illies, 1963.																		1		1		2	1																	
Chilenoperla puerilis Illies, 1963.																									1															
Chilenoperla semitincta Illies, 1963.																							1		1															
Claudioperla tigrina (Klapalek, 1904).			2				1					2											1	1																
Limnoperla jaffueli (Navás, 1928).	2		2										2	1	2	1	1	2	1	1	1	1	1	1	1	1								1	1	1	1	1		
Megandiperla kuscheli Illies, 1960.																																	1							
Notoperla archiplatae (Illies, 1958).																	1	1	1	1					1															
Notoperla tunelina (Navás, 1917).																												1	1					1	1		2			
Notoperla macdowalli McLellan & Mercado, 2005.																	1																							
Notoperlopsis femina Illies, 1963.																				1		1	1		2				1											
Pelurgoperla personata Illies, 1963.																				1		1	1	1	1	1			1											
Plegoperla borggreenae Illies, 1965.																					1																			
Plegoperla punctata (Froehlich, 1960).																					1																			
Potamoperla myrmidon (Mabille, 1891).																1		1	1	1	1		1	1				2	2					1			1			

Regions of Chile	Tarapaca				Antofagasta					Atacama				Coquimbo			Stgo-Mau			Conc-Ara			Val-Osor-Chil				Aisen						Magallanes							
O. Plecoptera / °L.S.	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Rhithroperla penai Illies, 1963.																										1														
Rhithroperla rossi (Froehlich, 1960).																		2		1			1	1	1	1			1					1	1		1	1	1	
Senzilloides panguipulli (Navás, 1929).																		2		1	2	2	1	2	2			2	2						1		2			
Teutoperla auberti Illies, 1965.																					1																			
Teutoperla brundini Illies, 1963.																								1	1	1														
Teutoperla rothi Illies, 1963.																					1	1	1	1	1	1														
Uncicauda pirata McLellan & Zwick, 2007																					1	1																		
Austronemoura araucana Aubert, 1960.																					1																			
Austronemoura auberti McLellan & Zwick, 1996																						1																		
Austronemoura caramavidensis Aubert, 1960.																					1																			
Austronemoura chilena Aubert, 1960.																						1	1	1	1			2	2											
Austronemoura decipiens McLellan & Zwick, 1996																								1																
Austronemoura encoensis Aubert, 1960.																							1		1															
Austronemoura eudoxiae Froehlich, 1960.																				1	1	1	1	2	1	1														
Austronemoura flintorum McLellan & Zwick, 1996																										1														
Austronemoura quadrangularis Aubert, 1960.																								1					1					1	1					
Neofulla areolata (Navás, 1929).																							1	1	1			1								1	1			
Neofulla biloba (Aubert, 1960).																								2	1															
Neofulla spinosa (Aubert, 1960).																	2						1	2				2												
Neonemoura barrosi Navás, 1920.																	1	2	1	1	1	1	1	1	1	2			1						1					
Neonemoura illiesi Zwick, 1973.																										1														
Udamocercia antarctica (Enderlein, 1905).																				2			1	1												1	1			
Udamocercia arumifera Aubert, 1960.																							1	1	1															
Udamocercia frantzi Illies, 1961																							1	1	1															
Inconeuria porteri (Navás, 1920).																				1	1	1	1	1	1	1														
Kempnyella genualis (Navás, 1918).																		2	1	1	1	1	1	1	1	1			1											
Kempnyella walperi Illies, 1964.																		2		1		1	1									1								
Nigroperla costalis Illies, 1964.																			1	1	1	1																		
Pictetoperla gayi (Pictet, 1841).																		2	1			2	2		1	1		2					2	1	1	1	1			
Pictetoperla repanda (Banks, 1920).																	2		1		1					1	1	2	1											
Total number of species by degree	1	0	2	0	0	0	1	0	0	0	0	1	1	1	1	2	8	15	11	22	28	27	38	35	34	21	2	16	17	5	0	2	5	10	11	7	12	3	1	0

Table 1. Distribution of Plecoptera in Chile by one latitudinal degree. The three principal biogeographical zones of the analysis are emphasized: North (17-32° S); southern-Mediterranean (33-45° S), and Magallanes (46-56° S). Chilean regions refer to the country's political divisions (Stgo: Santiago, Mau: Maule, Conc: Concepción, Ara: Arauco, Val: Valdivia, Oso: Osorno, Chil: Chiloé). The numbers represent 1: bibliographic records, 2: new records, no number: lack of species.

DISCUSSION AND CONCLUSIONS

Unexpectedly, the southern-Mediterranean zone (33-45°S) rather than the Mediterranean zone was the most diverse in stonefly species. Our results showed new distribution records for several species that were restricted to a few areas (e.g. *Klapopteryx kuscheli*, Table 1), suggesting a change in the latitudinal distribution of the order, possibly as a consequence of greater sampling effort. The older records were centered in central-southern Chile, principally between 36°S and 41°S. This reflected the location of the specialists (e.g. Illies in the Valdivian region, 39°S) and not a restriction of the species produced by the latitudinal environmental gradient (e.g. riparian structure, substrate diversity). Thus, we now see increased distributions for *Claudioperla tigrina* (23-19°S) and *Limnoperla jaffueli* (30-17°S), the most northerly distributed species of the country.

Plecoptera	Chile	Argen-tina	Brazil	S.Africa	New Zealand	Australia	Costa Rica	Colombia	Venezuela	N.America	Iberian P.	Europe
Families	6	6	2	2	4	4	1	2	1	9	7	7
Genera	35	31	8	7	21	26	1	4	3	105	26	35
Species	66	47	100	34	104	192	26	63	40	>662	140	426

Table 2. Plecoptera diversity for different world regions, expressed in the number of families, genera, and species.

It should be noted that 14 Plecoptera species displayed only one degree of distribution throughout Chile and many of these were mentioned only when they were first described, with no known new records. Likewise, one of the most conspicuous features of the current knowledge of Chilean Plecoptera is the absence of *Anacroneuria*, a stonefly with wide South American presence. This genus is actually present in Argentina with at least 22 species (Stark 2007), but in Chilean waters it is unknown until now. Probably, this could be due to a lack of studies in several specific regions of the country as well as a lack of specialists in this group, making the works of Illies in the sixties highly relevant. On the other hand, sampling intensity and the basin area selected for study influence fluvial taxa richness estimates (Vinson & Hawkins 1998). Unfortunately, the sampling efforts were not found in the literature review on the Plecoptera distribution in Chile, although we can suppose that the taxa richness was highest where the specialists were located. More and newer studies are necessary in order to examine the real Plecoptera distribution in Chile; the entire country (or most of it) should be sampled and the sampling effort should be standardized to obtained better conclusions. For example, the area between 43°S and 48°S has a low occurrence of species even though it is next to the latitude with the most diversity; this is probably because the former area is a zone of Patagonian ice development and has not been studied.

The global Plecoptera distribution pattern is interesting. North America has the greatest number of families and genera, suggesting the group originated in this zone, although Zwick (2000) indicates that the group originated in the Pangean breakup. One possible explanation for this pattern is the amount of specialists in this group and the works published in this particular zone and in the boreal zone in general (Platnick 1991). Nevertheless, the number of families in the Northern Hemisphere is effectively larger than in the Southern Hemisphere, and few families are found near the tropics.

Differences also exist within the Southern Hemisphere at all levels of analysis (family, genus, species). Diversity in terms of the number of families and genera is greatest in Chile and Argentina, but lower in terms of species than in Australia and New Zealand. The difference in species richness is probably due to the lower degree of taxonomical studies and sampling efforts in South America, whereas, at family level, the main difference is due to the restriction of Diamphipnoidae to South America and the worldwide distribution of the family Perlidae that excludes only Oceania. On the other hand, within South America the families and genera in Chile and Argentina are highly similar, but this is not the case with Brazil, whereas a comparison between New Zealand and Australia (Oceania) showed that only *Notonemoura* is shared at genus level (McLellan 2006). Likewise, the families Austroperlidae and Eustheniidae are found only in Australia, New Zealand, Argentina, and Chile.

The great differences observed on the regional scale in Plecoptera diversity between the Northern and Southern hemispheres are probably due to different diversity patterns in the temperate zones of the two hemispheres (Platnick 1991). Jacobsen et al. (1997) indicated differences in the number of families and general diversity in tropical as compared to temperate zones, with higher richness and diversity in the tropics than in the temperate zones. Boyero (2002) found a similar pattern for Ephemeroptera and Odonata. Vinson & Hawkins (2003) reported slightly higher Trichoptera richness near the equator, a tendency for less variability across latitudes than Plecoptera or Ephemeroptera, and more richness in temperate zones. The results of our work show the same pattern for Plecoptera, with increased diversity from the Equator toward the poles, perhaps related to the ecological preference of the species for cool, well-oxygenated waters for nymph development (Hynes 1976; Theischinger 1991; Albariño 1997; Vinson & Hawkins 2003). Nevertheless, it is interesting to stress that the *Anacroneuria* species diversity does not seems to fit the model that Plecoptera shows; in fact, this genus seems to exhibit an opposite pattern increasing diversity from the poles toward the equator. Perhaps this could be analyzed from some of the recent systematic studies (e.g. Colombia, Ecuador, Peru and Bolivia). In this sense, if this is true, it is probable that the ecological preference of *Anacroneuria* species is warmer waters, and this could be the cause of its absence in Chilean waters. Future research about it is needed.

In general, these two ecological factors (cold temperatures and good water quality) seem to be the most important in determining latitudinal diversity of Plecoptera in Chile and around the world, even though other sets of environmental variables are described as having an important influence on the distribution of organisms in freshwater systems, including basin characteristics (i.e. geology, basin area), reach (i.e. channel width, stream order, conductivity, riparian structure), and bedform (i.e. riffles vs. pool, substrate diversity, heterogeneity elements) (Townsend et al. 2003; Bonada et al. 2005). A study carried out by Céréghino et al. (2003) supports our conclusion: these authors used four environmental variables (elevation, stream order, distance from source, maximum water temperature) to predict the species richness of four major orders of aquatic insects (Plecoptera, Ephemeroptera, Trichoptera, Coleoptera); only Plecoptera was correlated with the upper mountainous sections of the stream systems, and species richness relationships between Plecoptera and the other three orders was not significant. Another study by Vinson & Hawkins (2003) showed the same pattern; Plecoptera diversity was higher in temperate streams near 40° latitude in both hemispheres.

Our results extend the distribution of many species throughout Chile. Moreover, we expect to find a more continuous distribution for several species that currently present discontinuous latitudinal distributions in Chilean rivers (e.g. bimodal distribution, Fig. 1); although there is a latitudinal environmental gradient imposed by climate, the water temperature is approximately 2 to 17°C from the beginning of the Mediterranean zone southward due to the Andean origins of several Chilean rivers. Moreover, the water upstream in the riffle areas is well oxygenated and of good quality (e.g. Figueroa et al. 2007). Thus, water quality and temperature may explain the low stonefly diversity in northern Chile, where the landscape is characterized by few streams, warm waters, and high mineral contents. It will be interesting to test this idea with more data and to verify whether this same pattern occurs on the other side of the Andes Mountains in Argentina.

Historical events appear to have less influence on the distribution of several taxa than the ecological requirements (e.g. Vinson & Hawkins 2003 for Trichoptera, Plecoptera, and Ephemeroptera; Bonada et al. 2005 for Trichoptera). It seems that the Pleistocene glaciations that affected Chile did not have a great influence on Plecoptera distributions although these glaciations likely had an important effect on the order's high degree of endemism. The glaciation episodes may have occurred so long ago that they no longer influence the current macroinvertebrate distribution, especially because the Plecoptera adults fly, showing relatively high dispersion and colonization capabilities (Sheldon 1984). However, this idea must be corroborated with further studies.

Finally, in our work, we argue that two ecological factors (cold temperatures and good water quality) seem to be the most important in local and global Plecoptera distributions. This suggests that the order is fragile given changes in freshwater quality and properties, being very susceptible to changes of water courses; any effluent that reduces the oxygen content or increases the water temperature could quickly eliminate the Plecoptera. More studies are necessary in the neotropical region, perhaps at higher elevations where cool streams can be found, because a greater number of species are expected in such high diversity zones. More studies are also required in freshwater ecosystems in order to determine local and regional biodiversity and to examine latitudinal gradient patterns in the Southern Hemisphere and around the world.

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