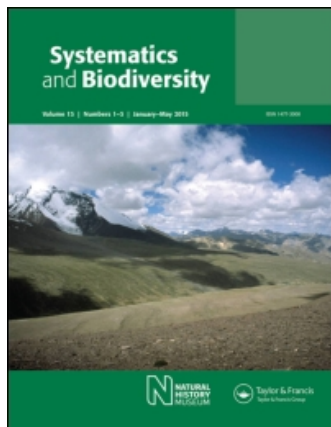


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## Spatial patterns of caddisflies from Austral South America

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Trichoptera are relevant members of the freshwater benthos that can exploit a broad variety of habitats. We explored their distribution patterns in Austral South America using a network quantitative approach applied on point occurrence data. The primary goal was to recognize groups of species connected by strong links of sympatry and secondarily to evaluate the structure of the sympatry network (patterns of connectivity) at higher taxonomic levels. We compiled 2,522 geographic points associated with 446 species. The strength of sympatry links were inferred directly from dot maps. Using the taxonomic resolution of species, we identified two major groups of co-occurring species that mimic in a geographic context the classic zoogeographic division of the study area: the Andean–Patagonian complex (of “cold-adapted” organisms) versus the Extra-Andean domain (of “warm-adapted” organisms) spanning the subtropical belt of the region. Within these major divisions, groups of highly co-distributed species were also found which in turn show a variety of overlapping spatial configurations. Overlap was centred at the following pivoting areas: Yungas of NW Argentina, Paranaense forest of NE Argentina and Valdivian temperate forest of Patagonia. Three very interesting findings emerged from the analyses: (i) Sierras Centrales of Córdoba correspond to the southern portion of many subtropical elements occurring in NW Argentina, (ii) some elements fit the disjunction between NW and NE Argentina and (iii) Uruguay is more closely related to NE Argentina than to Buenos Aires, suggesting that the Pampas region (Uruguay + Buenos Aires) could be an ill-defined biogeographic entity. Patterns at the species level become progressively blurred in going upward through the hierarchical classification.

**Key words:** aquatic insects, biogeography, cleavogram, NAM, Trichoptera, sympatry

### Introduction

Insects of the order Trichoptera constitute one of the main groups of the freshwater benthos. The immature stages are restricted to the aquatic environment and are usually a conspicuous contributor to its total biomass (de Moor & Ivanov, 2008). They can live under a wide range of ecological conditions and are able to reside in a great number of habitats (Ruiz García, Herrera Grao, & Ferreras-Romero, 2006). The high diversity of the group is interpreted as an expression of the great ecological opportunities offered by the secretion of silk by caddisfly larvae that enable them to exploit a variety of resources through the construction of cases, retreats, nets and other structures (Mackay & Wiggins, 1979). On the other hand, caddisfly adults inhabit the riparian area and most of them are weak fliers (Statzner, 1978; Waringer, 1991). They do not disperse far from emergence sites. In considering the worldwide distribution of Trichoptera, de Moor and Ivanov (2008) divided the palaeocontinent of Gondwana into

two closely related regions, namely (i) a temperate Gondwana involving Australia, New Zealand, Patagonia and possibly the southern tip of Africa and southernmost part of Madagascar; and (ii) a tropical Gondwana that includes the remaining portions of South America in addition to Africa, Madagascar and the Indian-part of the Oriental region. Concerning the South American caddisfly fauna inhabiting the area south of the Tropic of Capricorn, the previous general framework agrees well with the primary divisions presented by Flint (1983) who identified two subregions (i.e., the Brazilian and Chilean) for the area. The Chilean subregion includes all of Chile and a large part of western and southern Argentina. The Brazilian subregion, as far as Argentina is concerned, is further divided into three nuclei of diversity differentiation: (1) the main river basins in the central and eastern part of the country known as the Platense area, (2) the northeastern area or Misiones, and (3) the northwestern Andean area. Flint (1983) drew his conclusions following an intuitive approach on the grounds of a limited knowledge about the local fauna. We address here Flint’s conjectures about distribution patterns in Austral South America using a

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quantitative biogeographic analysis on an updated and more complete data set.

The collection localities represent discrete data of the highest available resolution to carry out any prediction of distribution patterns. They can be represented as points of occurrence in geographic space and treated consequently as mathematical objects provided with geographic coordinates. We avoid considering the incidence of points onto predefined OGUs (operative geographic units) as a valid procedure to encode distributions, because it entails loss of information and implicitly brings together portions of the geographic space in an authoritative way (e.g., a cell grid spanning an entire archipelago would force one to consider that archipelago as homogeneous when there is no reason to accept that assumption). In this manner, geographic ranges based on occupied OGUs generate large commission errors (when a species is mistakenly thought to be present) because they assume homogeneous species distributions (Rondinini, Wilson, Boitani, Grantham, & Possingham, 2006). In leaving aside the traditional procedure of using OGUs a new challenge emerges: the analysis of patterns of overlap or sympatry that rely exclusively on the point sets of taxa. The NAM (Network Analysis Method) approach as conceived by Dos Santos, Fernández, Cuezco, and Domínguez (2008) and Dos Santos, Cuezco, Reynaga, and Domínguez (2012) pursues the measurement of sympatric strength between dot sets and the exploration of patterns of connection from the respective sympatry network. NAM seeks groups of species embedded into the global network that are internally sustained by sympatric cohesiveness, but weakly connected (or disconnected) to outgroup entities. These groups satisfying the duality of within-group co-extensive sympatry and between-group disassociation are called henceforth units of co-occurrence (UCs). The areas underlying the resulting UCs are considered to be meaningful entities from a biogeographic standpoint since they are supported by a unique repertoire of co-distributed species.

The aim of this paper is to analyse, through the NAM approach, the sympatry network of Trichoptera from the Southern Cone of South America. The primary goal is to recognize spatial patterns derived from groups of species connected by strong links of sympatry and secondarily to evaluate the structure of the sympatry network but using the taxonomic levels of genus and family as units of study. More succinctly, we ask about the correspondence between the hierarchy in taxonomic classification and the resulting networks of spatial associations between biological entities. In addition to the research questions, we present an updated list of geographic ranges for caddisflies occurring in Argentina, Chile and Uruguay.

## Materials and methods

### Compiling records

Each species of Trichoptera was geographically characterized by the point localities of occurrence gathered from the literature (Angrisano, 1983, 1984, 1986, 1989, 1993, 1994, 1995, 1997, 1998, 2000, 2001, 2002; Angrisano & Burgos, 2002; Angrisano & Sganga, 2005, 2007; Banks, 1920; Bravo & Angrisano, 2003; Cohen, 2004; Flint, 1967a, 1967b, 1969, 1971, 1972, 1973, 1974a, 1974b, 1974c, 1978, 1979, 1980, 1982, 1983, 1989, 1990, 1992, 1997, 1998, 1999; Flint & Angrisano, 1985; Flint & Denning, 1989; Flint, McAlpine, & Ross, 1987; Holzenthal, 1984, 1986, 1988a, 1988b; Jacquemart, 1963, 1980; Kelley, 1983; Mangeaud, 1996; Mosely, 1934, 1939; Navás, 1918, 1920, 1923, 1930, 1934; Prather, 2004; Ross & King, 1951; Rueda Martín, 2006, 2008; Rueda Martín & Sganga, 2011; Rueda Martín, Gibon, & Molina, 2011; Schmid, 1949, 1955, 1957, 1958, 1964, 1989; Sganga & Angrisano, 2005; Sganga & Fontanarrosa, 2006; Ulmer, 1904, 1905, 1907; Valverde & Abelando, 2006; Valverde & Albariño, 1999; Valverde & Miserendino, 1997; Weyenbergh, 1881; Yamamoto, 1966). Other material included in the data set is from the collection of the Instituto de Biodiversidad Neotropical (IBN), CONICET – Facultad de Ciencias Naturales e Instituto Miguel Lillo, UNT.

### Distributional analyses

Dot maps were directly employed to infer the sympatry network of included species. The R package SyNet (Dos Santos, 2011), freely available on the website of the R platform (<http://www.cran-r.project>), was used to analyse the respective sympatry network under the NAM (Network Analysis Method) approach (Dos Santos *et al.*, 2008, 2012). To explore patterns of spatial connections between species, NAM relies exclusively on the distributional evidence provided by the geometrical layout of point records. If two species are assumed to occupy a common underlying area, their respective set of points (or dot clouds) are expected to fulfil two geometric properties, namely proximity and interpenetration. NAM estimates the coefficient of spatial association between point sets by measuring the degree of proximity (through the profiles of nearest neighbour distances) and interpenetration (through changes in the length of minimum spanning trees) between the respective dot clouds. Once the weighted network is constructed, meaningful links are filtered via a thresholding operation. In the resulting sympatry network, a pair of species can be directly linked (1) or not linked (0). NAM can compensate for sampling bias. Indeed, it gives differential weights (or values of relevance) to the different points of a dot cloud depending

on how clumped or disaggregated they are. In doing so, the contribution of many very close points to the overall profile of nearest neighbour distances is lower than the contribution of a few records broadly separated from each other. A beneficial consequence of this procedure is that we can achieve the skeleton or basic shape of a dot cloud by recruiting only the subset of heaviest (most relevant) points.

Intermediary species facilitate links between pairs of species otherwise disconnected from each other. By removing intermediary species, NAM identifies groups of species with the following duality: (1) intragroup cohesive connection, and (2) intergroup disconnection. The rationale for this condition is that species groups spatially shaped by common factors (either historical or ecological) are compartmentalized into separable, connected clusters of the sympatry network. The iterative removal of intermediary species (guided by the betweenness score) leads to a disaggregation of the sympatry network into components successively smaller in size. The entire process of node removal of the network can be summarized in a cleavogram (Dos Santos et al., 2012). This graphical tool helps to visualize the different connected species groups that emerge with the progressive removal of intermediary species. We report here the main components emerging during the removal process going from the more to the less inclusive ones.

Colorimetric maps (Dos Santos, 2012) were generated to show the geographic context of selected groups of connected species. To generate these maps we established a rectangular lattice of points over the study region (as dense as possible depending on the computational limitations) and then measured the geographic distance between these imaginary sampling points and the dot clouds of included species. For a given group composed of  $n$  species, the intensity value  $I$  of a sampling point is obtained through the summation of the species incidences on it. The larger the gap between the species point set and the sampling point, the lower the incidence of such species on the sampling point. This inverse relationship can be translated mathematically by the following formula for calculating the intensity value  $I$  that corresponds to a given sampling point  $m$ :

$$I_m = \sum_{i=1, n} \min(1; r/d_{im}),$$

where  $d_{im}$  denotes the shortest distance between the sampling point  $m$  and the point set associated with the species  $i$  of a given group. The parameter  $r$  (here 100 km) represents a value of tolerance used in testing whether the above spatial gap is negligible. Therefore, the proximity of a given species to the sampling point at a distance below the tolerance  $r$  means a perfect incidence ( $= 1$ ) of that species over the sampling point  $m$ . The value of  $r$

adopted is around the average arc length of the calculated minimum spanning trees. Note that the maximum score for  $I_m$  equals the number of species considered. Thus, if we consider a group comprised of 10 connected species, the sampling point  $m$  will have an intensity score of 10 if the totality of species converges towards the sampling point under consideration. In the next step of map delineation, a contour map is derived and the respective levels plotted by using the intensity previously calculated as  $z$ -scores. The spatial expressions derived from colorimetric maps were finally compared with current biogeographic schemes. Colorimetric maps help to understand the geographic context of a given group in a continuous spatial scenario. They also assist us in recognizing extralimital noise from the distributional core of each spatial expression.

Although the taxonomic level of species represents the desirable resolution to carry out biogeographic analysis since species are evolutionary units, we are also interested in the spatial patterns associated with the more inclusive taxonomic categories of genus and family. Consequently, we treat each taxonomic category by separate distributional analyses, pooling the records of involved species as a way to infer the distribution of each genus or family considered.

### Statistical inference for species co-occurrence

We have devised a novel test statistic called Group Separability (GS) as a single measure of the main network attribute we are interested in: the arrangement of nodes into disjoint and numerous clusters that are connected within, but disconnected between them when intermediary elements are removed. We will test if the calculated statistic is larger than the value expected by chance alone. For that purpose, the significance of GS should be established by comparison with the statistic calculated on null-hypothesis networks. Although randomly generated, null-hypothesis networks preserve basic characteristics of the original network. Here, null-hypothesis networks have random topology (links between different nodes are equally likely) and each edge is included with probability  $p$  independent from every other edge (Erdős–Renyi null model). We set  $p$  equals to the density of the original network (fraction of present connections to possible connections).

Given a binary sympatry matrix  $\mathbf{S} = [s_{ij}]$  and a cleavogram associated with its NAM analysis, GS is defined in terms of pairs of nodes with no direct link connecting them ( $s_{ij} = 0$ ) and the maximum size of disjoint cleavogram branches to which those pairs belong to. Formally, let  $B_i$  and  $B_j$  be two cleavogram branches that include the species  $i$  and  $j$  respectively, and notation # standing for

the size of such branches (i.e., number of species subtended by them),

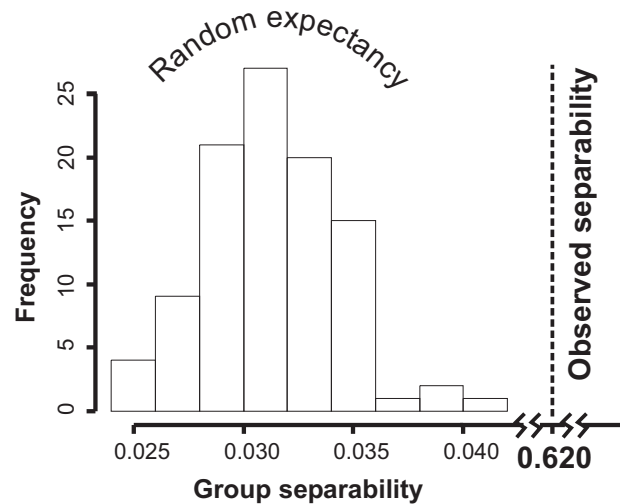
$$GS = \sum_{i>j, s_{ij}=0} \max_{B_i \cap B_j = \emptyset} (B_i + B_j)$$

In order to normalize the GS score into the unit interval, we calculate  $GS' = 2GS/(n^3 - n^2)$  that represents the average value of GS across all pairs of species relative to the total number of species ( $= n$ ). GS is sensitive to the proper balance between presence and absence of links in a network, that is to say, the trade-off of conditions that make possible the emergence of clusters (i.e., presence of intragroup links for cohesiveness and absence of intergroup links for distinctiveness). In doing so, GS accounts for the differential membership of nodes to mutually exclusive sets of connected species. If large groups of species can be separated from each other as the network is deflated by nodes breaking off, then GS increases, suggesting thus a modular structure that deserves to be studied more in depth.

## Results

A data set consisting of 2,522 non-duplicated geographic points associated with 446 species was constructed. The assignment of each spatial record to the respective species was carefully checked. A supplementary Table provides, for each species, the ranges of occurrence in both latitude and longitude (see online supplemental material, which is available from the article's Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2015.1045954>).

Here, we consider the sympatry network at the taxonomic level of species. The calculated GS score ( $= 0.62$ ) departed significantly from chance expectation (Fig. 1) after processing 100 random networks. The iterative removal of intermediary species is summarized in the cleavogram for species (Fig. 2), which is also coupled with the colorimetric maps of selected branches. Since each branch of the cleavogram represents a group of spatially connected species differentiated from the remainder, the respective colorimetric maps anchored on them represent the explicit geographic context behind those data processed in terms of network analysis. Table 1 details the species composition for each one of the selected branches in the previous cleavogram. Selected branches follow a nested sequence. Most inclusive branches are labelled in capital letters, whereas intermediate and less inclusive branches are denoted with Roman and Arabic numbers, respectively. As a whole, patterns A and B match the major zoogeographic division recognized for the study area, namely an Andean-Patagonian pattern (or “cold-adapted”) versus an Extra-Andean Brazilian pattern (or “warm-adapted”) comprising mainly the subtropical belt

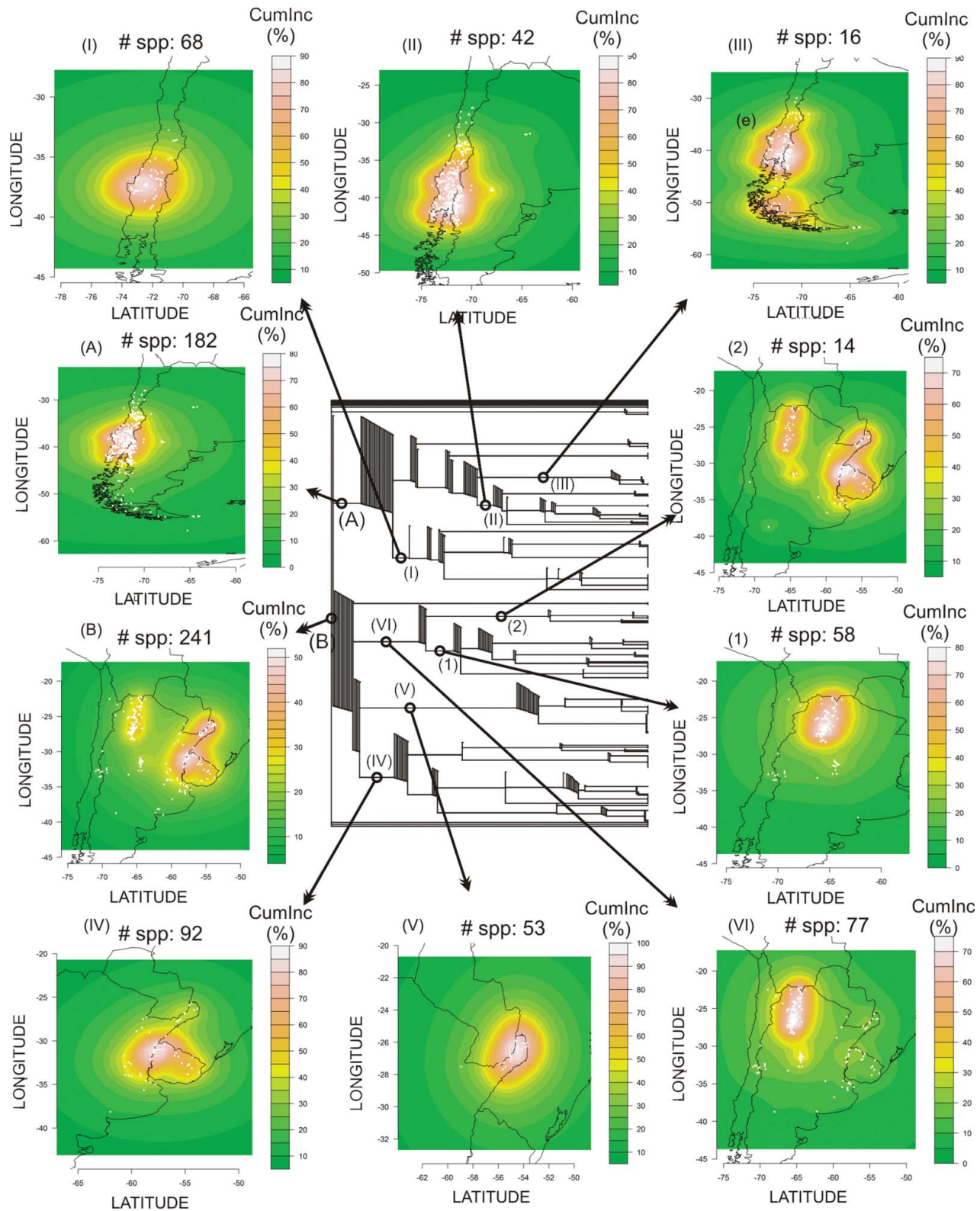


**Fig. 1.** Statistical inference of species co-occurrence structure. Histogram reflects the frequency distribution for normalized GS (Group Separability) scores across 100 random replications. Note the extreme value achieved by the observed network, suggesting a non-random packing of species into mutually exclusive clusters (sets of connected species).

of the region. In turn, we can discriminate three components within the elements that belong to pattern A; all of them with the Valdivian region as a pivotal area of occupancy. These include, group A-I restricted to this hotspot, group A-II expanded northward and group A-III extended southward. Further, we recognize three spatial nuclei where the Extra-Andean elements are expressed. Pattern B-IV conforms to the lower portion of the Uruguay river, group B-V spans the forested area of Misiones, and group B-VI occupies basically (but not necessarily confined to) the freshwater environments of the Yungas rainforest in northwestern Argentina, in addition to the Sierras de Córdoba. Interestingly, this last component can be further divided into group B-VI-1 (its spatial core of occurrence falls in the Yungas) and group B-VI-2 (with an affinity between NW and NE Argentina).

Figures 3, 4 show the cleavograms (with colorimetric maps associated with relevant branches) obtained after processing the sympatry networks for genera and families, respectively. Ninety-one out of 98 genera included can be split into two distributional configurations (cold temperate versus subtropical) located respectively to the south and north of a diagonal line in arid southern South America from the Atacama Desert to the dry steppes of Patagonia. Notwithstanding, this separation is equivocal and some genera are on either side of it, such as *Austrotinodes*, *Smicridea*, *Iguazu*, *Metrichia*, *Polycentropus* and *Triplectides* grouped in a common cleavogram branch. At the family level (Fig. 4), the two major groups of co-occurring taxa overlap geographically in Patagonia.





**Fig. 2.** Cleavogram associated with the sympatry network inferred from dot maps of austral South American Trichoptera species. Color-metric maps highlight the geographic context of selected groups of connected species. White dots represent the actual localities associated with the pooled set of records for the group under consideration. #spp: total number of species belonging to the selected branch of the cleavogram (group of connected species). CumInc: cumulative incidence of taxa (expressed as a percentage of the theoretical maximum) derived from their geographic proximity to hypothetical sampling points scattered throughout the study area. See text for explanation of incidence values represented in the accompanying colour scale bar.

**Table 1.** Species composition for each of the selected branches in the cleavogram (Fig. 2). The correspondence between each branch and the spatial core of their spatial expressions are as follows: A = Andean–Patagonian pattern, A-I = Concentrated in the Valdivian forest, A-II = Valdivian, but expanded northward, A-III = Valdivian, but expanded southward; B = Extra-Andean pattern, B-IV = lower portion of Uruguay river, B-V = forested area of Misiones, B-VI = Centred in the Yungas rainforest including Sierras Centrales of Córdoba, B-VI-1 = Circumscribed to Yungas in NW Argentina, B-VI-2 = Disjunction between NW and NE Argentina.

Species	Selected branches of clivogram	Species	Selected branches of clivogram
<i>Parasericostoma laterale</i>	A	<i>Smicridea (Rhyacophylax) argentina</i>	B-IV
<i>Dolophilodes spinifera</i>	A	<i>Nectopsyche nigricapilla</i>	B-IV
<i>Smicridea (Smicridea) tregala</i>	A	<i>Smicridea (Rhyacophylax) vilela</i>	B-IV
<i>Verger curtior</i>	A	<i>Neotrichia salada</i>	B-IV
<i>Tolhuaca cupulifera</i>	A	<i>Leptonema columbianum</i>	B-IV
<i>Iguazu flavofuscum</i>	A	<i>Cyrnellus bifidus</i>	B-IV
<i>Austrotinodes recta</i>	A	<i>Smicridea (Rhyacophylax) voluta</i>	B-IV
<i>Metacosmoecus nigrofasciatus</i>	A	<i>Cernotina medioloba</i>	B-IV
<i>Verger capillatus</i>	A	<i>Synoestropsis ecliptica</i>	B-IV
<i>Clavichorema trancasicum</i>	A	<i>Ascotrichia frontalis</i>	B-IV
<i>Austrotinodes cekalovici</i>	A	<i>Nectopsyche multilineata</i>	B-IV
<i>Dolophilodes chilensis</i>	A	<i>Marilia salta</i>	B-IV
<i>Smicridea (Smicridea) manzanara</i>	A	<i>Marilia lateralis</i>	B-IV
<i>Clavichorema complicatissimum</i>	A	<i>Cernotina cacha</i>	B-IV
<i>Brachysetodes trifidus</i>	A	<i>Bredinia alza</i>	B-IV
<i>Verger affinis</i>	A	<i>Smicridea (Smicridea) travertinera</i>	B-IV
<i>Parasericostoma rufum</i>	A	<i>Smicridea (Rhyacophylax) palmar</i>	B-IV
<i>Austrotinodes lineatus</i>	A	<i>Rhyacopsyche yatay</i>	B-IV
<i>Chiloecia lacustris</i>	A	<i>Polypectropus paysandu</i>	B-IV
<i>Polycentropus chilensis</i>	A	<i>Oxyethira ritae</i>	B-IV
<i>Austrocentrus valgiiformis</i>	A	<i>Oxyethira petei</i>	B-IV
<i>Tripletides chilensis</i>	A	<i>Oxyethira mocoï</i>	B-IV
<i>Tripletides nigripennis</i>	A	<i>Neotrichia charrua</i>	B-IV
<i>Pangullia faziana</i>	A	<i>Nectopsyche muelleri</i>	B-IV
<i>Clavichorema chiloeanum</i>	A	<i>Marilia alata</i>	B-IV
<i>Heterochorema paradoxicum</i>	A	<i>Neotrichia brevispina</i>	B-IV
<i>Stenochorema crassicozum</i>	A	<i>Cernotina fallaciosa</i>	B-IV
<i>Apatanodes brachytergum</i>	A	<i>Cyrnellus mammillatus</i>	B-IV
<i>Metachorema gregarium</i>	A	<i>Mortoniella unota</i>	B-IV
<i>Celaenotrichia edwardsi</i>	A	<i>Neotrichia abbreviata</i>	B-IV
<i>Austrotinodes picada</i>	A	<i>Acostatrichia plaumanni</i>	B-IV
<i>Australobiosis araucanica</i>	A	<i>Neotrichia tertia</i>	B-IV
<i>Microthremma bipartitum</i>	A	<i>Flintiella andreae</i>	B-IV
<i>Microchorema penai</i>	A	<i>Hydroptila producta</i>	B-IV
<i>Trichovespula macrocera</i>	A	<i>Betrichia hamulifera</i>	B-IV
<i>Mastigoptila ruizi</i>	A	<i>Neotrichia dikeros</i>	B-IV
<i>Notidobiella chacayana</i>	A	<i>Cernotina perpendicularis</i>	B-IV
<i>Dolophilodes bispinosa</i>	A	<i>Neotrichia angulata</i>	B-IV
<i>Polycentropus valdiviensis</i>	A	<i>Neotrichia chana</i>	B-IV
<i>Isochorema flintorum</i>	A	<i>Cernotina carbonelli</i>	B-IV
<i>Anomalopsyche minuta</i>	A	<i>Neotrichia aequispina</i>	B-IV
<i>Helicopsyche caligata</i>	A	<i>Neotrichia noteuna</i>	B-IV
<i>Androchorema chilense</i>	A	<i>Neotrichia durior</i>	B-IV
<i>Dolophilodes elongatoides</i>	A	<i>Polycentropus sarandi</i>	B-IV
<i>Dolophilodes appendiculata</i>	A	<i>Costatrichia noite</i>	B-IV
<i>Metachorema griseum</i>	A	<i>Protoptila uruguayensis</i>	B-IV

(continued)

Table 1. (Continued)

Species	Selected branches of clivogram	Species	Selected branches of clivogram
<i>Neatopsyche chilensis</i>	A	<i>Neotrichia picada</i>	B-IV
<i>Smicridea (Smicridea) mucronata</i>	A	<i>Neotrichia novara</i>	B-IV
<i>Smicridea (Smicridea) frequens</i>	A	<i>Cyrnellus risi</i>	B-IV
<i>Monocosmoecus obtusus</i>	A	<i>Cyrnellus rianus</i>	B-IV
<i>Smicridea (Smicridea) decora</i>	A	<i>Smicridea (Smicridea) mesembrina</i>	B-IV
<i>Apatanodes sociata</i>	A	<i>Neotrichia bullata</i>	B-IV
<i>Vergler obliquus</i>	A	<i>Austrotinodes uruguayensis</i>	B-IV
<i>Monocosmoecus pulcher</i>	A	<i>Neotrichia filifera</i>	B-IV
<i>Neatopsyche brevispina</i>	A	<i>Cernotina sexpinosa</i>	B-IV
<i>Austrocentrus bifidus</i>	A	<i>Cernotina artiguensis</i>	B-IV
<i>Smicridea (Smicridea) redunda</i>	A-I	<i>Betrichia zilbra</i>	B-IV
<i>Austrotinodes quadripina</i>	A-I	<i>Acostatrachia simulans</i>	B-IV
<i>Mystacopsyche longipilosa</i>	A-I	<i>Oxyethira obscura</i>	B-IV
<i>Austrotinodes armiger</i>	A-I	<i>Orthotrichia cristata</i>	B-IV
<i>Charadropsyche penicillata</i>	A-I	<i>Neotrichia lucrecia</i>	B-IV
<i>Neochorema jaula</i>	A-I	<i>Oxyethira acegua</i>	B-IV
<i>Microchorema extensum</i>	A-I	<i>Atopsyche (Atopsaura) uruguayensis</i>	B-IV
<i>Dolophilodes spinosella</i>	A-I	<i>Abtrichia antennata</i>	B-IV
<i>Polycentropus obtusus</i>	A-I	<i>Smicridea (Rhyacophylax) spinulosa</i>	B-IV
<i>Nothotrichia cautinensis</i>	A-I	<i>Itaouara plaumanni</i>	B-IV
<i>Microthremma caudatum</i>	A-I	<i>Smicridea (Rhyacophylax) dentifera</i>	B-IV
<i>Dolophilodes bifida</i>	A-I	<i>Marilia eleutheria</i>	B-IV
<i>Microchorema larica</i>	A-I	<i>Cernotina verna</i>	B-IV
<i>Mystacopsyche ochracea</i>	A-I	<i>Polyplectropus dubitatus</i>	B-IV
<i>Contulma cranifer</i>	A-I	<i>Cyrnellus arotron</i>	B-IV
<i>Smicridea (Smicridea) turgida</i>	A-I	<i>Betrichia argentinica</i>	B-IV
<i>Pseuroladema spinosissima</i>	A-I	<i>Tripletides gracilis</i>	B-IV
<i>Neochorema lobiferum</i>	A-I	<i>Smicridea (Rhyacophylax) discalis</i>	B-IV
<i>Monocosmoecus minor</i>	A-I	<i>Smicridea (Rhyacophylax) appendiculata</i>	B-IV
<i>Dolophilodes paxillifera</i>	A-I	<i>Oecetis punctipennis</i>	B-IV
<i>Polycentropus quadripinosus</i>	A-I	<i>Nyctiophylax neotropicalis</i>	B-IV
<i>Brachysetodes bifurcatus</i>	A-I	<i>Nectopsyche separata</i>	B-IV
<i>Nothotrichia illiesi</i>	A-I	<i>Achoropsyche duodecimpunctata</i>	B-IV
<i>Clavichorema pillimipilli</i>	A-I	<i>Polyplectropus fuscatus</i>	B-IV
<i>Alloecentrellodes obliquus</i>	A-I	<i>Nectopsyche muhni</i>	B-IV
<i>Brachysetodes spinosus</i>	A-I	<i>Chimarra parana</i>	B-V
<i>Austrotinodes triangularis</i>	A-I	<i>Leptonema viridianum</i>	B-V
<i>Smicridea (Smicridea) complicatissima</i>	A-I	<i>Nectopsyche bruneofasciata</i>	B-V
<i>Austrotinodes irwini</i>	A-I	<i>Smicridea (Rhyacophylax) unguiculata</i>	B-V
<i>Austrotinodes brevis</i>	A-I	<i>Nectopsyche aureovittata</i>	B-V
<i>Pseudostenopsyche gracilis</i>	A-I	<i>Smicridea (Rhyacophylax) vermiculata</i>	B-V
<i>Pseudosericoctostoma simplissimum</i>	A-I	<i>Smicridea (Smicridea) paranensis</i>	B-V
<i>Pomphochorema chilensis</i>	A-I	<i>Polyplectropus elongatus</i>	B-V
<i>Polycentropus aspinosus</i>	A-I	<i>Nectopsyche splendida</i>	B-V
<i>Parasericoctostoma drepanigerum</i>	A-I	<i>Marilia misionensis</i>	B-V
<i>Parasericoctostoma corniculatum</i>	A-I	<i>Phylloicus pirapo</i>	B-V
<i>Parasericoctostoma abruptum</i>	A-I	<i>Helicopsyche lobata</i>	B-V
<i>Austrocentrus griseus</i>	A-I	<i>Chimarra ypsilon</i>	B-V
<i>Neochorema sinuatum</i>	A-I	<i>Helicopsyche monda</i>	B-V

(continued)



**Table 1.** (Continued)

Species	Selected branches of clivogram	Species	Selected branches of clivogram
<i>Microthremma villosum</i>	A-I	<i>Smicridea (Rhyacophylax) forcipata</i>	B-V
<i>Microthremma griseum</i>	A-I	<i>Helicopsyche velligera</i>	B-V
<i>Mastigoptila ecornuta</i>	A-I	<i>Nectopsyche pantosticta</i>	B-V
<i>Dolophilodes spectabilis</i>	A-I	<i>Nectopsyche fuscumaculata</i>	B-V
<i>Dolophilodes elongata</i>	A-I	<i>Cernotina chelifera</i>	B-V
<i>Verger quadrispinus</i>	A-I	<i>Synoestropsis pedicillata</i>	B-V
<i>Australobiosis bidens</i>	A-I	<i>Smicridea (Rhyacophylax) weidneri</i>	B-V
<i>Parasericostoma dinocephalum</i>	A-I	<i>Smicridea (Rhyacophylax) pallidivittata</i>	B-V
<i>Mastigoptila curvicornuta</i>	A-I	<i>Phylloicus plaumanni</i>	B-V
<i>Dolophilodes pectinifera</i>	A-I	<i>Metrichia cuniapiru</i>	B-V
<i>Parasericostoma acutum</i>	A-I	<i>Plectromacronema comptum</i>	B-V
<i>Amphichorema monicae</i>	A-I	<i>Oxyethira misionensis</i>	B-V
<i>Austrotinodes recurvatus</i>	A-I	<i>Macrostemum santaeritae</i>	B-V
<i>Pseudostenopsyche davisorum</i>	A-I	<i>Smicridea (Smicridea) minima</i>	B-V
<i>Polycentropus tuberculatus</i>	A-I	<i>Smicridea (Rhyacophylax) minuscula</i>	B-V
<i>Mastigoptila bicornuta</i>	A-I	<i>Polyplectropus hamulus</i>	B-V
<i>Isochorema curvispinum</i>	A-I	<i>Atopsyche (Atopsaura) longipennis</i>	B-V
<i>Dolophilodes scopula</i>	A-I	<i>Leptonema aspersum</i>	B-V
<i>Dolophilodes proluxa</i>	A-I	<i>Helicopsyche opalescens</i>	B-V
<i>Dolophilodes dupliplex</i>	A-I	<i>Chimarra scopuloides</i>	B-V
<i>Clavichorema purgatorium</i>	A-I	<i>Chimarra piraya</i>	B-V
<i>Alloecentrellodes elongatus</i>	A-I	<i>Chimarra cultellata</i>	B-V
<i>Psilopsyche chillana</i>	A-I	<i>Chimarra conica</i>	B-V
<i>Notidobiella parallelipipeda</i>	A-I	<i>Triplectides misionensis</i>	B-V
<i>Microthremma crassifimbriata</i>	A-I	<i>Smicridea (Rhyacophylax) nanda</i>	B-V
<i>Microchorema recintoi</i>	A-I	<i>Smicridea (Rhyacophylax) iguazu</i>	B-V
<i>Helicopsyche chilensis</i>	A-I	<i>Polyplectropus ulmeriana</i>	B-V
<i>Clavichorema capillatum</i>	A-I	<i>Oecetis iguazu</i>	B-V
<i>Parasericostoma peniai</i>	A-I	<i>Atopsyche (Atopsaura) misionensis</i>	B-V
<i>Verger vespersus</i>	A-II	<i>Marilia infundibulum</i>	B-V
<i>Myotrichia murina</i>	A-II	<i>Marilia humerosa</i>	B-V
<i>Oxyethira andina</i>	A-II	<i>Leptonema pallidum</i>	B-V
<i>Parasericostoma cristatum</i>	A-II	<i>Itauara guarani</i>	B-V
<i>Neopsilochorema tricarinatum</i>	A-II	<i>Iguazu ulmeri</i>	B-V
<i>Psilopsyche molinai</i>	A-II	<i>Helicopsyche lambda</i>	B-V
<i>Austrotinodes nielseni</i>	A-II	<i>Grumichella aequiunguis</i>	B-V
<i>Australobiosis glaciocincta</i>	A-II	<i>Cyrnellus misionensis</i>	B-V
<i>Monocosmoecus aberrans</i>	A-II	<i>Alisotrichia gabriel</i>	B-V
<i>Oxyethira bidentata</i>	A-II	<i>Protoptila truncata</i>	B-V
<i>Schajovskoya neuquensis</i>	A-II	<i>Ithytrichia ferni</i>	B-VI
<i>Neatopsyche unispina</i>	A-II	<i>Helicopsyche turbida</i>	B-VI
<i>Parasericostoma ovale</i>	A-II	<i>Nectopsyche jenseni</i>	B-VI
<i>Monocosmoecus vanderweeli</i>	A-II	<i>Chimarra argentinica</i>	B-VI
<i>Notidobiella inermis</i>	A-II	<i>Banyallarga argentinica</i>	B-VI
<i>Smicridea (Smicridea) pucara</i>	A-II	<i>Oecetis knutsoni</i>	B-VI-1
<i>Parachorema bifidum</i>	A-II	<i>Grumichella flaveola</i>	B-VI-1
<i>Triplectides jaffuelli</i>	A-II	<i>Neotrichia baritu</i>	B-VI-1
<i>Mastigoptila longicornuta</i>	A-II	<i>Mortoniella pocita</i>	B-VI-1
<i>Psilopsyche kolbiana</i>	A-II	<i>Smicridea (Smicridea) piraya</i>	B-VI-1

(continued)

Table 1. (Continued)

Species	Selected branches of clivogram	Species	Selected branches of clivogram
<i>Brachysetodes quadrifidus</i>	A-II	<i>Smicridea (Smicridea) nigerrima</i>	B-VI-1
<i>Brachysetodes forcipatus</i>	A-II	<i>Oxyethira parce</i>	B-VI-1
<i>Brachysetodes extensus</i>	A-II	<i>Anomalocosmoecus argentinicus</i>	B-VI-1
<i>Smicridea (Smicridea) penai</i>	A-II	<i>Marilia flexuosa</i>	B-VI-1
<i>Verger bispinus</i>	A-II	<i>Neotrichia gotera</i>	B-VI-1
<i>Neoatopsyche spinosella</i>	A-II	<i>Neotrichia elongata</i>	B-VI-1
<i>Eosericoctoma inaequispinum</i>	A-II	<i>Leptonema boliviense boliviense</i>	B-VI-1
<i>Dolophilodes flavipunctata</i>	A-II	<i>Hydroptila catamarcensis</i>	B-VI-1
<i>Austrotinodes angustior</i>	A-II	<i>Smicridea (Smicridea) olivacea</i>	B-VI-1
<i>Smicridea (Smicridea) annulicornis</i>	A-II	<i>Xiphocentron caenina</i>	B-VI-1
<i>Hudsonema flaminii</i>	A-II	<i>Metrichia disparilis</i>	B-VI-1
<i>Verger kuscheli</i>	A-II	<i>Leptonema boliviense plumosum</i>	B-VI-1
<i>Phylloicus aculeatus</i>	A-II	<i>Protoptila julieta</i>	B-VI-1
<i>Austrotinodes talcana</i>	A-II	<i>Leucotrichia alisensis</i>	B-VI-1
<i>Smicridea (Smicridea) smilodon</i>	A-II	<i>Xiphocentron pintada</i>	B-VI-1
<i>Smicridea (Smicridea) anticura</i>	A-II	<i>Xiphocentron cuyensis</i>	B-VI-1
<i>Mastigoptila brevicornuta</i>	A-II	<i>Smicridea (Rhyacophylax) valeni</i>	B-VI-1
<i>Neotrichia chilensis</i>	A-II	<i>Mortoniella punensis</i>	B-VI-1
<i>Amphichorema costiferum</i>	A-II	<i>Mortoniella argentinica</i>	B-VI-1
<i>Brachysetodes major</i>	A-II	<i>Merionoptila wygodzinskyi</i>	B-VI-1
<i>Metrichia patagonica</i>	A-II	<i>Nectopsyche gemma</i>	B-VI-1
<i>Metrichia bidentata</i>	A-II	<i>Nectopsyche flaveola</i>	B-VI-1
<i>Scotiotrichia ocreata</i>	A-III	<i>Leptonema agraphum</i>	B-VI-1
<i>Mastigoptila ventricornuta</i>	A-III	<i>Smicridea (Rhyacophylax) peruana</i>	B-VI-1
<i>Platycosmoecus beaumonti</i>	A-III	<i>Marilia cinerea</i>	B-VI-1
<i>Verger appendiculatus</i>	A-III	<i>Cailloma lucidula</i>	B-VI-1
<i>Rheochorema robustum</i>	A-III	<i>Smicridea (Rhyacophylax) dithyra</i>	B-VI-1
<i>Cailloma pumida</i>	A-III	<i>Metrichia neotropicalis</i>	B-VI-1
<i>Cailloma rotunda</i>	A-III	<i>Metrichia argentinica</i>	B-VI-1
<i>Verger lutzky</i>	A-III	<i>Polycentropus jorgenseni</i>	B-VI-1
<i>Verger fuscovittata</i>	A-III	<i>Helicopsyche muelleri</i>	B-VI-1
<i>Austrocosmoecus hirsutus</i>	A-III	<i>Atopsyche (Atopsaura) spinosa</i>	B-VI-1
<i>Rheochorema tenuispinum</i>	A-III	<i>Smicridea (Smicridea) chicoana</i>	B-VI-1
<i>Rheochorema lobuliferum</i>	A-III	<i>Smicridea (Rhyacophylax) bifida</i>	B-VI-1
<i>Neoatopsyche obliqua</i>	A-III	<i>Neotrichia sala</i>	B-VI-1
<i>Eosericoctoma aequispinum</i>	A-III	<i>Smicridea (Rhyacophylax) elisae</i>	B-VI-1
<i>Verger stenopterus</i>	A-III	<i>Leucotrichia lerma</i>	B-VI-1
<i>Verger michaelsoni</i>	A-III	<i>Banyallarga yunguensis</i>	B-VI-1
<i>Mortoniella albolineata</i>	B	<i>Banyallarga loxana</i>	B-VI-1
<i>Nectopsyche punctata</i>	B	<i>Atopsyche (Atopsyche) maxi</i>	B-VI-1
<i>Protoptila dubitans</i>	B	<i>Mortoniella wygodzinskii</i>	B-VI-1
<i>Smicridea (Rhyacophylax) mesembrina</i>	B	<i>Atopsyche (Atopsaura) callosa</i>	B-VI-1
<i>Mortoniella teutonia</i>	B	<i>Hydroptila bidens</i>	B-VI-1
<i>Hydroptila pulestoni</i>	B	<i>Hydroptila coscaroni</i>	B-VI-1
<i>Smicridea (Rhyacophylax) coronata</i>	B	<i>Phylloicus lituratus</i>	B-VI-1
<i>Smicridea (Rhyacophylax) pampeana</i>	B	<i>Oxyethira baritu</i>	B-VI-1
<i>Nectopsyche bruchi</i>	B	<i>Atopsyche (Atopsyche) kamesa</i>	B-VI-1
<i>Neotrichia tubulifera</i>	B	<i>Atopsyche (Atopsaura) yunguensis</i>	B-VI-1
<i>Hydroptila sauca</i>	B	<i>Atopsyche (Atopsaura) lobosa</i>	B-VI-1

(continued)

**Table 1.** (Continued)

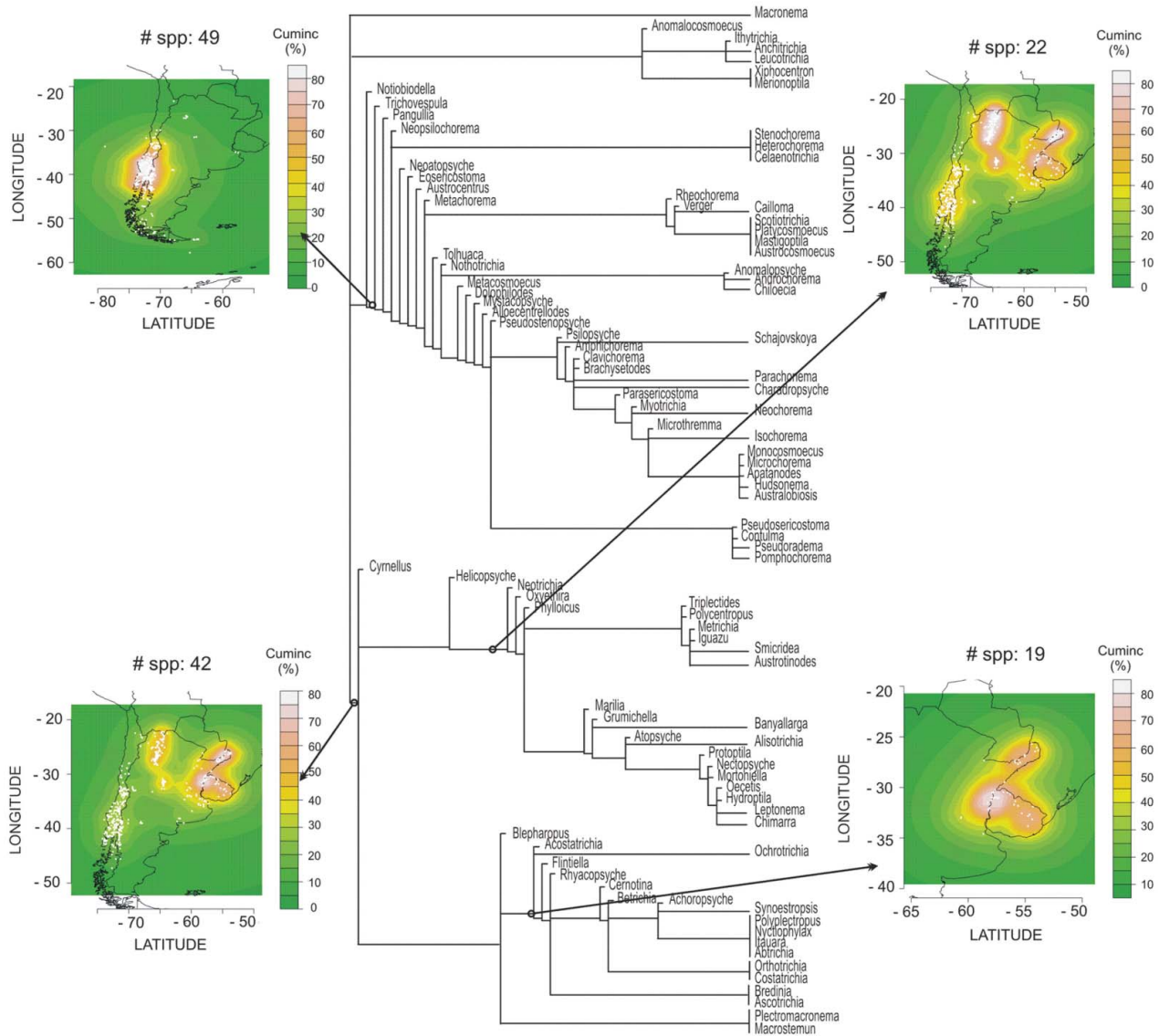
Species	Selected branches of clivogram	Species	Selected branches of clivogram
<i>Ochrotrichia cebollati</i>	B	<i>Leucotrichia yungarum</i>	B-VI-1
<i>Chimarra plaumani</i>	B	<i>Anchitrichia trifurcata</i>	B-VI-1
<i>Rhyacopsyche hagenii</i>	B	<i>Alisotrichia benji</i>	B-VI-1
<i>Nyctiophylax tacuarembó</i>	B	<i>Smicridea (Rhyacophylax) thermophila</i>	B-VI-1
<i>Nectopsyche adusta</i>	B	<i>Oxyethira lagunita</i>	B-VI-2
<i>Blepharopus diaphanus</i>	B	<i>Hydroptila argentinica</i>	B-VI-2
<i>Leptonema crassum</i>	B	<i>Cynnellus ulmeri</i>	B-VI-2
<i>Chimarra hyoeides</i>	B	<i>Smicridea (Rhyacophylax) atrobasis</i>	B-VI-2
<i>Cynnellus collaris</i>	B-IV	<i>Phylloicus angustior</i>	B-VI-2
<i>Neotrichia palma</i>	B-IV	<i>Oxyethira circaverna</i>	B-VI-2
<i>Itauara brasiliana</i>	B-IV	<i>Marilia elongata</i>	B-VI-2
<i>Polyplectropus flavicornis</i>	B-IV	<i>Oxyethira ulmeri</i>	B-VI-2
<i>Leptonema rostratum</i>	B-IV	<i>Protoptila misionensis</i>	B-VI-2
<i>Oxyethira zilaba</i>	B-IV	<i>Oecetis excisa</i>	B-VI-2
<i>Betrichia uruguayensis</i>	B-IV	<i>Nectopsyche flavofasciata</i>	B-VI-2
<i>Oecetis paranensis</i>	B-IV	<i>Oxyethira argentinensis</i>	B-VI-2
<i>Neotrichia abbreviatoides</i>	B-IV	<i>Chimarra brasiliana</i>	B-VI-2
<i>Cynnellus fraternus</i>	B-IV	<i>Oxyethira santiaguensis</i>	B-VI-2
<i>Oecetis amazonica</i>	B-IV		

## Discussion

In a broad survey of the diversity of Trichoptera around the world, de Moor and Ivanov (2008) stressed the relevance of mountainous landscapes or areas of high rainfall as drivers of great concentration of species. Our results favour this statement, since the cores of diversity across the different taxonomic levels are expressed in humid forested hills of austral South America, namely Andean Patagonian forests, NW Argentina Yungas forests, and Paranaense Atlantic forests. The same authors also mentioned a major faunistic split within South America, called tropical (or Neotropical) and temperate (or Patagonian) Gondwana. Strong linkages between family and genera occur between temperate South America and the Australian regions. With regards to tropical South America, there are meaningful phylogenetic links with Africa, Madagascar and India (de Moor & Ivanov, 2008). The division between tropical and temperate Gondwana runs across our study area and matches the primary division of the Neotropical region into Brazilian and Chilean subregions proposed by Flint (1983). This continental bisection is indeed pervasive throughout the biogeographic literature. For instance, Ringuet (1961) recognizes two major pools of aquatic insects (Chile and Patagonian elements) and Posadas and Morrone (2003) refer to the Andean region as a biotic complex separated from the rest of South America. In our data, as we move from the family to the species levels of analysis this division is also

evident (see spatial expressions of the most inclusive branches in the cleavogram concerning species).

The zoogeographic proposals of Flint (1983), as far as Trichoptera found south of the Tropic of Capricorn are concerned, are the most adequate reference point to understand the relevance of our results. Flint (1983) speculated on three marked divisions in the Brazilian fauna of Argentina: one centred in the Andean area of NW Argentina, a very small division centred in Misiones in NE Argentina, and another centred in the main river basins of the central and eastern part of the country. Although Misiones has been confirmed as a distinctive centre of diversification, previous appraisals about the biogeographic nature of the central and western portions of the country need to be revised. Examination of different branches of the cleavograms at different taxonomic levels suggests that austral South America is a complex landscape where different structures of distribution arise. Important findings are the hybrid nature of Patagonia at the family level, but clearly differentiated from the rest at the species level. Families restricted to Patagonia in Fig. 4 have either a southern Gondwana distribution (Helicophidae, Tasimiidae, Philorheithridae, Kokiriidae) or are common in other temperate cold-water habitats (Limnephilidae, Sericostomatidae, Stenopsychidae). Anomalopsychidae is the only caddisfly family fully endemic to the Neotropics, distributed in forested mountainous regions as well as above the tree line in the northern Andes (Holzenthall & Robertson, 2006).

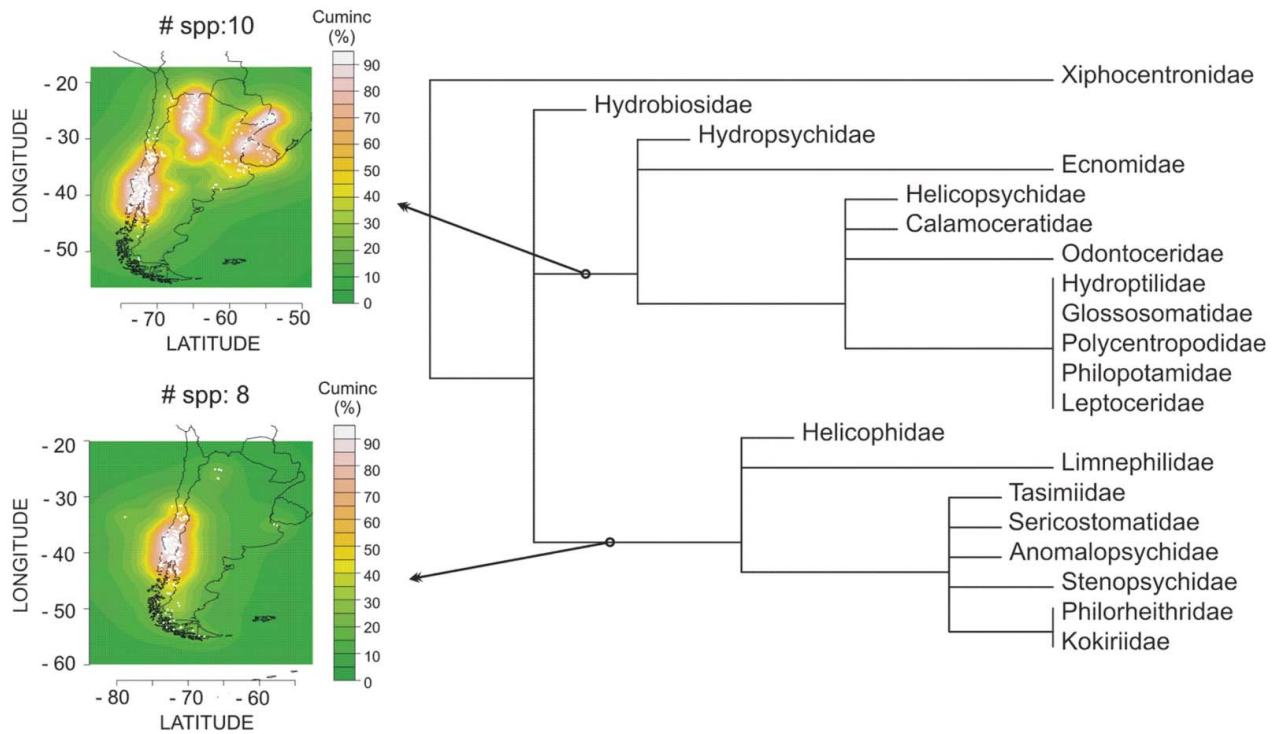


**Fig. 3.** Cleavogram and colorimetric maps obtained after processing the sympatry network between caddisfly genera. White dots represent the actual localities associated with the pooled set of records for the group under consideration. #spp: total number of species belonging to the selected branch of the cleavogram (group of connected species). CumInc: cumulative incidence of taxa (expressed as a percentage of the theoretical maximum) derived from their geographic proximity to hypothetical sampling points scattered throughout the study area. See text for explanation of incidence values represented in the accompanying colour scale bar.

Consequently, the interaction between historical and ecological factors can be thought as the operating mechanism behind the diversity of caddisflies in Patagonia.

In the cleavogram based on genera, the successive division of the subtropical group ends up separating a component centred in NE Argentina. In general, these taxa also have representatives in other tropical areas of South America, but mostly to the east. Another component retrieved by the analysis occupies the northern portion of Argentina in a broad sense (including Sierras Centrales of Córdoba). Here, supporting genera are commonly found throughout the mountainous running waters from the Andean ranges, in high gradient channels (steeply sloped

streams), going as far north as Central America. Noticeably, a genus with a marked functional role predator, *Atopsyche*, is replaced by other genera of Hydrobiosidae in Patagonia (Holzental & Cressa, 2002). Finally, a group conformed by widespread genera is also recognized. *Austrotinodes*, *Smicridea*, *Metrichia* and *Triplectides* are present in all America, whereas *Polycentropus* is cosmopolitan. *Iguazu* has two described species; one for Patagonia and the other from Misiones, but probably the latter has been mislabelled (Flint, Holzental, & Harris, 1999). Because of their wide distribution and geographic segregation of included species, these genera are valuable to carry out phylogeographic studies as well as



**Fig. 4.** Cleavogram and colorimetric maps obtained after processing the sympatry network between caddisfly families. White dots represent the actual localities associated with the pooled set of records for the group under consideration. #spp: total number of species belonging to the selected branch of the cleavogram (group of connected species). CumInc: cumulative incidence of taxa (expressed as a percentage of the theoretical maximum) derived from their geographic proximity to hypothetical sampling points scattered throughout the study area. See text for explanation of incidence value represented in the accompanying colour scale bar.

ecogeographic analysis of traits. Thus, for example, the Andean–Patagonian species of *Austrotinodes* are morphologically different to the Paranaense group. A similar situation follows for *Smicridea*.

At the species level, NW Argentina seems to be a confluence area for many species, some of them restricted there and others with ranges extending either southward to Sierras de Córdoba or eastward to Misiones. Northeast Argentina has its own suite of species and also shares elements with Uruguay, a remarkable Paranaense linkage recovered even with records pooled by common membership to genera. Uruguay has been included in the Pampas region by Morrone (2006), but we disagree with that interpretation. The Trichoptera fauna of Uruguay is more closely related to NE Argentina than to the humid pampas of Buenos Aires. The same conclusion was reached by Emmerich (2012) after analysing the distribution of Ephemeroptera.

Caddisflies contribute to many of the ecosystem services intrinsic to freshwater systems, so knowledge of their distribution is critical for delineating priority areas for conservation of freshwater resources. We consider that four sources of information are needed to guide conservation decisions, namely knowledge of the richness, phylogeny, life history, and distribution of taxa occurring in the target area. A certain measure of diversity can be derived from each source, but distributional diversity is usually not

included in assessments of priority conservation areas. Thus, if a given area holds a mix of species with different types of distributions (i.e., species spread across different branches of the cleavogram), that area could be considered high priority because it is likely supported by a heterogeneous set of species in the sense of their life histories. This is the case, for instance, for the Yungas of NW Argentina.

Although we have made progress since Flint's (1983) assessment, our knowledge of the Trichoptera fauna of South America's Southern Cone is incomplete. We still lack a complete picture of the fauna's taxonomic richness and distributional patterns. Some large areas are almost devoid of records, including the high altitude Puna grasslands and the various environments of the Chacoan region. The patterns presented here may change when additional records are analysed. Notwithstanding, we have made progress in the urgent task of outlining the spatial structure of the area's known Trichoptera biodiversity. Concluding, our findings strengthen and broaden Flint's conjectures: (1) peaks of diversity occur across the forested dense drainage networks of the study area (under the influence of Valdivian, Southern Andean Yungas and Paranaense rainforests), (2) different sets of strongly co-distributed species overlap in these diversity nuclei (they act as pivot areas of different distributional patterns), (3) Sierras Centrales of Córdoba and Uruguay seem to be



the southern limit of subtropical elements, (4) the divergence between Andean–Patagonian and Brazilian elements is marked at the species level but became somewhat blurred in considering more inclusive taxa like families. However, the presence of families unique to the Andean–Patagonian domain reveals once again the singularity of this region compared with the rest of the continental landmass.

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## Supplemental data

Supplemental data for this article can be accessed <http://dx.doi.org/10.1080/14772000.2015.1045954>.

## Disclosure Statement

No potential conflict of interest was reported by the authors.

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