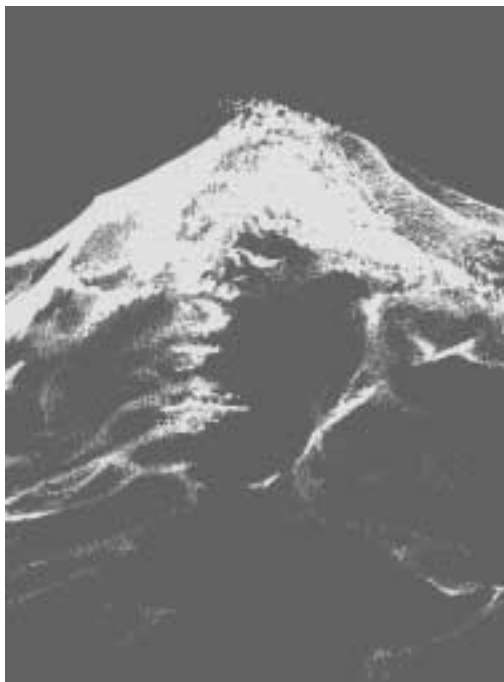


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Insect biodiversity in freshwater ecosystems: is there any latitudinal gradient?

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The ecological literature is full of qualitative and quantitative studies of diversity, from local surveys of communities or selected groups of organisms, to estimates of the total number of species on Earth (e.g. May 1988). In search of global patterns, ecologists were early to recognize an enormous diversity in the tropics compared with temperate and cold zones (Hawkins 2001). Although this latitudinal gradient has been discussed for more than a century, a consensus about its cause does not yet exist (Rosenzweig 1997; Rohde 1999). Whereas many groups of organisms have been shown to be more diverse in the tropics (e.g. bats, Rosenzweig 1992), a few groups present 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. Moreover, studies on tropical lakes or streams are scarce compared with those in temperate zones (Lewis 1987; Boyero 2000), so we must not assume *a priori* that diversity patterns found in terrestrial or marine systems also apply to freshwaters. Available data on macroinvertebrate diversity (fish are not considered in this paper) are very sparse and disconnected, both at the local and regional scale. Local studies in streams have failed to show any clear latitudinal pattern of macroinvertebrate diversity. Stout and Vandermeer (1975) estimated insect diversity from rock samples and found greater species richness in neotropical than in temperate streams (for theoretical samples of 100 rocks). Haynes (1987) employed the same method in a tropical stream, finding low species richness (6–9 species per rock sample) compared with Stout and Vandermeer's results for both North America (8–40) and Central and South America (23–62). Other results have suggested a greater local diversity in tropical streams than in temperate ones (Lake *et al.* 1994), but some have shown the opposite pattern (Arthington 1990) or no latitudinal gradient (Flowers 1991).

To my knowledge, there are no studies comparing the biodiversity of macroinvertebrate taxa at tropical and temperate latitudes at a regional scale. Here I conduct the first step by comparing existing biodiversity data of two taxa,

Ephemeroptera and Odonata, from different latitudes in America. I considered it an appropriate region for the study of latitudinal gradients because it presents a wide latitudinal range and it includes tropical and temperate zones in both hemispheres. I divided the region into four zones: North America (NA), which includes Canada, The United States and Mexico, and represents the temperate zone in the Northern Hemisphere; Central America (CA), comprising the countries from Guatemala to Panama; Tropical South America (TSA), composed of the northern half of South America, from Colombia to Bolivia; and Austral South America (ASA), comprising Argentina, Chile, Uruguay and Paraguay. It would have been more appropriate to divide the region exactly by the Tropics and the Equator, but the selection of zones was necessary owing to the arrangement of the species lists available.

Table 1 shows the number of families, genera and species per unit area (10^6 km^2) for the two taxa in the four zones. The most remarkable finding is the high number of taxa per unit area known for CA. Despite the relative scarcity of studies carried out in CA, there are about 29 times more species of Odonata per unit area in CA than in NA, 38 times more genera and 44 times more families. Comparing the two tropical zones, 13 times more species of Ephemeroptera per unit area were found in CA than TSA, 16 times more genera and 29 times more families.

The difference between the two temperate zones is also important. The number of species of Odonata per unit area found in ASA is three times greater than in NA, the number of genera is four times greater, and the number of families is five times greater. Between TSA and ASA, the pattern is more variable: for Odonata, the number of species is 1.2 times greater in TSA than ASA, but there are almost twice the number of genera and three times more families in ASA. All of these data appear to show a high relative diversity of tropical regions, mainly of CA. Although North American streams are among the best studied in the world, NA is relatively poor in species, genera and families. It is highly likely that there are many more unrecorded species in CA and TSA than NA.

Table 1. Number of families, genera and species of Ephemeroptera and Odonata, total and per unit area (10⁶ km²)

North America (NA), Central America (CA), Tropical South America (TSA) and Austral South America (ASA) (see text for definition of these zones). Data for Ephemeroptera from <http://168.223.36.3/acad/research/mayfly/>, updated September 1999. Data for Odonata from North America (NA) from <http://www.afn.org/~iori/nalist.html> and <http://www.afn.org/~iori/zyglist.html>, updated December 1999 and August 1999 respectively; Central America (CA) from <http://www.ups.edu/biology/museum/ODofMA.html>, updated October 1999; Tropical South America (TSA) and Austral South America (ASA) from <http://www.ups.edu/biology/museum/ODofSA.html>, updated July 1999. Total area data is from, 'The 21st Century World Atlas' (Trident Press International 1998).

	Total area km ²	Total number of taxa			Number of taxa per unit area		
		Families	Genera	Species	Families	Genera	Species
Ephemeroptera							
NA	21 457 874	21	84	679	0.98	3.91	31.64
CA	523 270	9	35	108	17.20	66.89	206.39
TSA	13 600 539	8	58	224	0.59	4.26	16.47
ASA	4 119 993	11	45	156	2.67	10.92	37.86
Odonata							
NA	21 457 874	14	93	526	0.65	4.33	24.51
CA	523 270	15	86	375	28.67	164.35	716.65
TSA	13 600 539	15	143	1157	1.10	10.51	85.07
ASA	4 119 993	13	77	284	3.16	18.69	68.93

The higher diversity of ASA with respect to NA is also remarkable. As noted by Platnick (1991), this suggests the possibility of different diversity patterns in the temperate zones of the two hemispheres. The relatively high diversity of CA with respect to TSA, and ASA with respect to NA, can be understood from a historical point of view. Central America was the focal point of the 'Great American Biotic Interchange', when the formation of the Isthmus of Panama created a land bridge between North and South America that allowed mass migrations from both north to south and south to north (Webb, 1997). Although ASA is within the temperate region of the southern hemisphere, it is part of the neotropical biogeographic region, and its biota is directly related to that of TSA.

We need much more data on freshwater macroinvertebrate biodiversity at regional and local scales to properly examine latitudinal gradients. At a regional scale, lists of species are scarce for tropical zones, so large-scale comparisons are not realistic. At a local scale, there have been very few quantitative studies in tropical freshwaters, and the identification of tropical species is difficult for non-specialists (particularly as species lists are scarce). Family-level identification might be an alternative for local studies given that it has been a good predictor of species richness for freshwater macroinvertebrates (Wright *et al.* 1998). Moreover, Roy and Foote (1997) suggested that the importance of tropical diversity not only resides in the number of species present, but also in the greater diversity of form, and higher taxa generally reflect greater morphological divergence than species. The number of species per family may not be constant in different geographical areas and there are data that suggest that South

American aquatic insect families do contain more species than North American and European families (Jacobsen *et al.* 1997), but this does not necessarily mean that each family is represented by more species at a local scale.

Besides collecting biodiversity data in different regions to detect latitudinal patterns, it is important that we try to understand the causes of those patterns. There have been some excellent reviews of hypotheses that explain latitudinal gradients of biodiversity (e.g. from Pianka 1966 to Rohde 1992). These hypotheses are worthy of being tested in freshwater ecosystems.

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