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# Macroecology of Aquatic Insects: A Quantitative Analysis of Taxonomic Richness and Composition in the Andes Mountains of Northern Ecuador[1]

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## ABSTRACT

To determine the spatial dynamics of Neotropical lotic insect species, specimens were collected from 41 streams on the eastern and western flanks of the Andes Mountains in Ecuador. We examined the manner in which taxonomic richness and composition differed with elevation, latitude, and versant. Statistical analyses were limited to 5 families (Ephemeroptera: Baetidae, Leptohyphidae, Oligoneuriidae; Heteroptera: Naucoridae; Coleoptera: Elmidae), comprising 32 genera and 85 species, for which identifications or morphospecies assignments were reliable. Assessment of taxonomic diversity was based on the richness of genera and species at each site. In addition, each site was characterized by species richness within each of 4 families with more than 10 species. The effects of versant and transect on composition and structure were family-specific. Mean site differences between versants in elmid richness at generic and specific levels depended on transect. Only baetid richness was affected by versant and transect in a consistent manner. Variation among sites in composition based on all genera and species was captured using multidimensional scaling (MDS). Subsequent MANOVAs based on scores from MDS axes revealed that differences between versants were much stronger in the southern transect, although transects differed from each other at specific and generic levels. A Jaccard's similarity matrix was computed for each family to reflect the spatial organization of taxonomic composition. Mesogeographic patterns of species composition for each of the four families were correlated (Mantel analysis) at both the regional level and at the level of the entire study area. At the regional level, the only pair of families to exhibit correlated patterns of species composition was elmids and naucorids in the southwestern region. The pattern of species composition for each family was correlated with the patterns for one or more other families at the level of the entire study area. Thus, spatial dynamics of species composition was similar for the families examined, suggesting that the Andes exert a consistent influence on species distributions within families, regardless of ordinal affiliation. At a local scale, however, the way in which taxonomic composition changed with latitude and versant was family-specific. Mayflies, the most vagile of the taxa studied, had the highest percentage of species overlap between versants. Of three genera of Naucoridae collected, species of *Ambrysus*, of probable Mexican origin, were found only on the eastern versant, corroborating other evidence that the genus is recent in South America. Moreover, dispersion by *Ambrysus* across the Andes Mountains may not have occurred, as it has for *Cryphocricos* and *Limnocoris*, which are of probable South American origin.

*Key words:* *Andes; aquatic insects; distribution; Ecuador; Elmidae; Ephemeroptera; lotic; macroecology; Naucoridae.*

QUANTIFICATION OF SPATIAL PATTERNS IN THE DIVERSITY AND TAXONOMIC COMPOSITION of Neotropical biotas is a contemporary goal of biogeography (Myers & Giller 1988, Rosenzweig 1995, Brown & Lomolino 1998, Willig 2001). Among the best understood patterns of spatial distribution are those concerning trees, mammals, and birds. Among the least understood are those related to invertebrates. Although insects are overwhelmingly dominant organisms with respect to abundance and richness in nearly all Neotropical communities and life zones, their distributional patterns are incompletely documented and poorly understood at best (Jacobsen *et al.* 1997).

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Ecuador has both the highest human population density and biotic diversity per unit area of any South American country. In particular, western Ecuador harbors an exceptionally rich biota and consequently is listed by Conservation International as one of 25 global biodiversity hotspots (Mittermeier *et al.* 2000). The country is sharply bisected by the Andes Mountains into coastal and Amazonian regions. The Ecuadorian Andes comprise two ridges (eastern and western Cordilleras) that reach heights of *ca* 5000 m and form the boundaries of a central paramo having *ca* 2700 m elevation. Traversing an elevational gradient on each versant of the mountains are most major life zones from tundra to tropical rain forest. Although the region portends a rich biota, few systematic reports have been published concerning the insect fauna of Ecuador (*e.g.*, Froeschner 1981, Spangler 1984). No comprehensive systematic work, and only scattered work addressing alpha taxonomy (*e.g.*, Spangler 1980, Perkins & Spangler 1985) and several records of species distributions (*e.g.*, Sites 1990), are available on the aquatic insects of Ecuador.

Few investigations pertaining to environmental correlates of aquatic insect distribution in Ecuador appear in the literature, and most are recent. Seasonal variation in abundance of species was examined in a headwater stream (Turcotte & Harper 1982a); community structure and functional feeding groups were investigated during wet and dry seasons (Jacobsen & Ancalada 1998); patterns of macroinvertebrate drift were studied in streams of the paramo (Turcotte & Harper 1982b); and elevational and latitudinal effects on the structure and diversity of the macroinvertebrate fauna were compared among regions in Ecuador and Denmark (Jacobsen *et al.* 1997). In a broad regional assessment of factors accounting for familial-level distribution in relation to Andean slopes, Monaghan *et al.* (2000) found that elevation affected familial composition more so than it controlled familial richness.

Most research quantifying distributional patterns of tropical aquatic insects are constrained by poor taxonomic resolution. Consequently, these studies have focused at familial or generic levels because of the difficulty in obtaining authoritative identifications or in assigning reliable identities to morphospecies. Recognizing that finer resolution has the potential to yield greater insight into biogeographic patterns and processes, the purpose of our research was to (1) document the species composition and richness of a number of Andean streams, (2) assess the degree to which local richness at generic and specific levels differ among regions defined by versant or latitudinal position, and (3) evaluate patterns of compositional similarity within and among regions as evinced by different insect families.

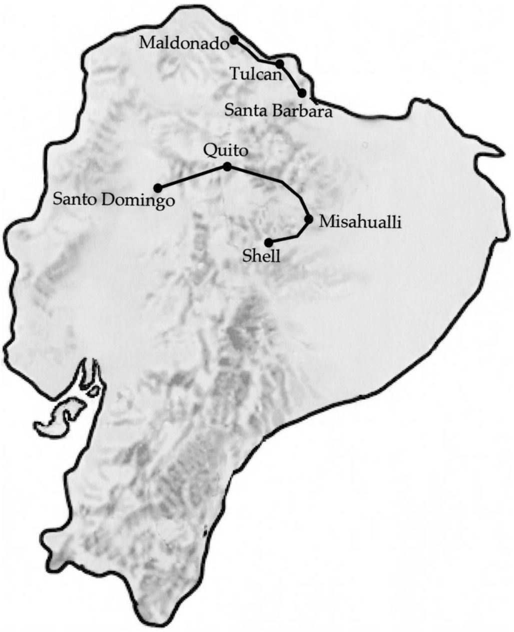

FIGURE 1. Diagrammatic representation of Ecuador and transects along which streams were sampled.

## MATERIALS AND METHODS

Specimen collection.—Aquatic insects were collected from 41 sites (river reaches) along two east–west transects in northern Ecuador during July 1993 (Fig. 1; Appendix 1). The northern transect, near the Colombian border, comprised 13 sites divided approximately equally between eastern ($N = 6$) and western ($N = 7$) versants of the Andes, and extended from Santa Barbara to Maldonado. The southern transect comprised 28 sites, equally divided between eastern and western versants of the Andes, and extended from Puerto Napo and Shell to Santo Domingo de los Colorados. In the northern transect, the distance traveled and number of sites sampled were constrained because of political instability and the limited availability of gasoline. At each site, elevation and water temperature were recorded, and all discernible habitats (*e.g.*, riffles, pools, margins, emergent vegetation) were sampled within a reach of each river. Macroinvertebrates were collected by kick-sampling the substrate while holding an aquatic D-net immediately downstream. Marginal vegetation was sampled by vigorously sweeping the D-net through plants beneath the water near the surface and at the substrate level. Pools were sampled by agitating the substrate and vigorously sweeping the net through the water column above the disturbed substrate. Net contents were emptied into a white, plastic pan, and insects were placed into a jar with 70 percent ethanol. In addition, rocks were examined for tightly clinging taxa that may not have been dislodged by kick-sampling (*e.g.*, Elmidae). Alcohol was changed later during the same day of collection to compensate for dilution. Sampling continued at each site until no additional morphospecies were taken in at least three consecutive samples by each of three collectors.

In the laboratory, insects were sorted to morphospecies and counted. Taxonomic specialists provided identifications for Ephemeroptera (W. P. McCafferty, C. Lugo-Ortiz, T. Wang; Purdue University), Elmidae (C. Barr; University of California–Berkeley), and Naucoridae (RWS). Voucher specimens were deposited in the insect collections of Universidad Catolica, el Museo Ecuatoriano de Ciencias Naturales, Quito in Ecuador, and at Purdue University, University of California–Berkeley, and University of Missouri–Columbia in the United States.

Quantitative analysis.—Recognizing that elevational zonation exists in the macroinvertebrate communities of mountain streams (Macan 1961, Hynes 1970, Allan 1975) and that richness predictably increases in mid-order streams and is lower in headwaters and high orders (Vannote *et al.* 1980), data were collected in a sufficiently rigorous manner to assess the presence or absence of species from each river reach at a series of elevations and ordinal stream categories. Thus, we examined the manner in which taxonomic richness and composition differed with elevation, transect (a northern and southern latitude), and versant (east or west flank of the Andes). All statistical analyses were conducted using SPSS (1990) statistical software, version 4.0 (SPSS Inc., Chicago, Illinois) unless noted otherwise.

Diversity.—We estimated taxonomic diversity at two hierarchical levels based on the richness of genera and species at each site. In addition, we characterized each site by species richness within each of four families (*i.e.*, those with >10 species represented in our collections; Baetidae, Leptohyphidae, Naucoridae, and Elmidae). For each of six indices of richness (generic and specific levels for each family except Naucoridae), we conducted two-way (transect vs. versant) analyses of covariance (elevation) to assess spatial patterns of richness. In addition, we conducted more powerful orthogonal *a priori* comparisons of eastern and western versants within each latitudinal transect, and comparisons of northern and southern transects as well. Because Naucoridae did not occur in the northern transect, resulting in zero variance for richness, we conducted a one-way (versant) ANCOVA (elevation) on sites from the southern transect. Northern and southern transects did not contain a similar distribution of sites with respect to elevation. To avoid attributing differences in richness to transect that were confounded by latitude, we used elevation as a covariate in all analyses.

Taxonomic composition.—Similarities in taxonomic composition were quantified using Jaccard's index (Sneath & Sokal 1973, Magurran 1988) based on a presence–absence matrix for the insect fauna of each river. More specifically, similarity ($\mathbf{S_{ij}}$) between any pair of sites **i** and **j** is given by: $\mathbf{S_{ij} = a/(a + b + c)}$, where **a** is the number of taxa shared in common, **b** is the number of taxa in site **i** but not site **j**, and **c** is the number of taxa in site **j** but not site **i**. Joint absences (taxa that did not occur in either site **i** or **j**) of taxa found at other sites in the study were not considered to be informative in these calculations of similarity. The ecological interpretation of Jaccard's index is straightforward given its mathematical simplicity. Nonetheless, the index is sensitive to sampling effort, especially when effort is low compared to actual species richness of a site. Fortunately, our intensive collection of specimens at each site until no new species were obtained in three consecutive samples by each of three collaborators greatly diminished the likelihood that measures of similarity were biased by this phenomenon (*i.e.*, the absence of species from our sample likely is an accurate reflection of its absence from the site). The relationship among sites in taxonomic composition as estimated by Jaccard's index was subjected to multidimensional scaling (MDS). MDS is a nonparametric data reduction technique that is analogous to principal components analysis, but has fewer restrictive assumptions (Gower 1984). Axis scores from MDS represent the position of sites in multidimensional space defined by species composition. The degree to which biogeographical constraints affected species composition was assessed by two-way multivariate analysis of variance (MANOVA), with six axis scores from MDS as dependent variables and transect and versant as categorical variables. More powerful *a priori* tests evaluated if differences existed between eastern and western versants within the northern and southern transects, separately as well as between northern and southern transects, after combining versants.

For each family, we considered the site-by-site matrix of Jaccard's index to reflect the spatial organization of taxonomic composition. If two families exhibit similar patterns of spatial organization, then their site-by-site matrices should be correlated. We assessed correlations between families in the spatial organization of taxonomic composition at two spatial scales: within each of the four areas defined by combinations of transect and versant, and within the entire study area. If biogeographic barriers associated with ascending the Andes (versant) or traversing long distances (transect) contribute to differences in the faunal composition of sites, then correlations at one scale of analysis should be different than correlations at another. Because some regions contained a larger proportion of low elevational sites (<2195 m) than others (proportions for NE, NW, SW, and SE regions were 0/6, 0/7, 11/14, and 7/14, respectively) and some taxa have strong elevational limits (*e.g.*, naucorids do not extend ≥2195 m in the region), we repeated the same suite of pairwise Mantel correlations for an elevationally restricted subset of sites (*i.e.*, those ≥2195 m). In all cases, Mantel matrix correlations were executed using the R package of Legendre and Vaudor (1991).

## RESULTS

To conduct analyses using data with reliable species-level resolution, the lotic taxa available for statistical analyses were limited to 5 families, 32 genera, and 85 species (Table 1). Although taxa of other families and orders were collected, these were not included in the analyses because of unreliable identifications or assignments to morphospecies. Systematic collections from these regions of the Andes are not common, and as a result our work has discovered at least 26 new species (Wang *et al.* 1998) and 4 new genera of mayflies alone, including *Prebaetodes* (Baetidae) (Lugo-Ortiz & McCafferty 1996) and 3 undescribed genera.

The four regions defined by combinations of transect and versant contained distinctive faunas. Within transects, only 25 and 33 percent of the fauna were shared between versants in the north and south, respectively. Within versants, only 17 and 28 percent of the fauna were shared between transects in the east and west, respectively, although this likely is an underestimate because of the disparity in representation of elevation by sites in the north and south (Table 2). Similarly, distinctive regional faunas appear when attention is restricted to particular families (Table 2).

TAXONOMIC DIVERSITY.—Considerable variability in richness characterized these montane streams at the generic and species levels (Table 3). For each family at generic and specific levels, richness of a site was consistently higher in western than eastern versants and higher in southern than northern transects; however, once the effects of elevation were removed from considerations of variation in richness, differences with respect to transect or versant were family-specific (Table 4). In particular, mean site differences with respect to versant and transect for both generic and species richness were not significant for leptohyphids and naucorids. Mean site differences between versants in elmid richness at generic and specific levels depended on transect (significant interaction). Only baetid richness was affected by versant and transect in a consistent and significant manner, and this was true at both generic and specific levels.

TAXONOMIC COMPOSITION.—Multidimensional scaling effectively captured variation among sites in composition based on all genera (stress = 0.082; $R^2 = 0.916$) and on all species (stress = 0.094; $R^2 = 0.883$). Consequently, the MANOVA based on axis scores from MDS was an efficacious approach for assessing the effects of versant and transect on taxonomic composition of sites. The effect of versant on generic or species composition depended on transect (significant interactions; Table 5). Differences between versants were much stronger in the south (genera, $P = 0.037$; species, $P = 0.015$) than in the north (genera, $P = 0.147$; species, $P = 0.071$) based on *a priori* analyses. Moreover, the northern transect was quite different from the southern transect in terms of taxonomic composition at the generic ($P = 0.005$) and specific ($P = 0.004$) levels.

Mesogeographic patterns in species composition within areas defined by combinations of transect and versant were family-specific (Fig. 2). No pairwise correlations of site-by-site matrices for families were significant in three of the four regions defined by combinations of transect and versant

TABLE 1. *Taxa collected from 41 streams in northern Ecuador that were included in statistical analyses.*

| | North | | South | |
|---|---|---|---|---|
| Taxon | East | West | East | West |
| EPHEMEROPTERA | | | | |
| Baetidae | | | | |
| *Acerpenna* sp. | | X | X | X |
| *Baetis levis* Mayo | X | X | X | X |
| *Baetodes proiectus* Mayo | | | X | X |
| *B. spinae* Mayo | | | X | X |
| *Baetodes* sp. 1 | | X | X | X |
| *Baetodes* sp. 2 | | | | X |
| *Baetodes* sp. 3 | | | | X |
| *Bernerius* sp. | | X | | X |
| *Camelobaetidius* sp. 1 | | X | X | X |
| *Camelobaetidius* sp. 2 | | X | X | X |
| *Camelobaetidius* sp. 3 | | | | X |
| *Cloeodes redactus* Waltz & McCafferty | | | X | X |
| *Guajirolus* sp. | | | | X |
| *Moribaetis ellenae* (Mayo) | X | X | X | X |
| *Paracloeodes* sp. | X | | | |
| *Prebaetodes sitesi* Lugo-Ortiz & McCafferty | X | X | X | X |
| Undescribed genus 2 | X | X | X | X |
| Undescribed genus 3 | | X | X | X |
| Undescribed genus 4 | | | X | X |
| Leptohyphidae | | | | |
| *Haplohyphes huallaga* Allen | X | X | X | X |
| *Leptohyphes echinatus* Allen & Roback | | | | X |
| *L. ecuador* Mayo | | | X | |
| *L. hirsutus* Allen & Roback | | | X | X |
| *L. liniti* Wang, Sites, & McCafferty | | X | X | X |
| *L. maculatus* Allen | | | | X |
| *L. myllonatus* Allen & Roback | | X | X | X |
| *L. nicholsae* Wang, Sites, & McCafferty | | | | X |
| *L. tuberculatus* Allen | | | X | |
| *Tricorythodes* sp. 1 | | | X | |
| *Tricorythodes* sp. 2 | | X | | X |
| *Tricorythodes* sp. 3 | | | X | |
| *Tricorythodes* sp. 4 | | | X | |
| *Tricorythodes* sp. 5 | | | X | X |
| *Tricorythodes* sp. 6 | | | X | |
| *Tricorythodes* sp. 7 | | | X | |
| Oligoneuriidae | | | | |
| *Lachlania* sp. | X | | X | X |
| HETEROPTERA | | | | |
| Naucoridae | | | | |
| Cryphocricinae | | | | |
| *Ambrysus crenulatus* Montandon | | | X | |
| *A. fossatus* Usinger | | | X | |
| *Cryphocricos barrozii* Signoret | | | | X |
| *C. breddini* Montadon | | | | X |
| *C. peruvianus* De Carlo | | | X | |
| Limnocorinae | | | | |
| *Limnocoris* sp. 1 | | | X | |
| *Limnocoris* sp. 2 | | | X | X |
| *Limnocoris* sp. 3 | | | | X |
| *Limnocoris* sp. 4 | | | | X |
| *Limnocoris* sp. 5 | | | X | |
| *Limnocoris* sp. 6 | | | | X |

TABLE 1. *Continued.*

| Taxon | North | | South | |
|---|---|---|---|---|
| | East | West | East | West |
| COLEOPTERA | | | | |
| Elmidae | | | | |
| Elminae | | | | |
| *Heterlemis* sp. 1 | X | X | X | |
| *Heterlemis* sp. 2 | X | | | X |
| *Heterlemis* sp. 3 | | | | X |
| *Heterlemis* sp. 4 | | | | X |
| *Heterlemis* sp. 5 | | | | X |
| *Heterlemis* sp. 6 | | | X | X |
| *Heterlemis* sp. 7 | | | | X |
| *Macrelmis* sp. 1 | | | | X |
| *Macrelmis* sp. 2 | | | X | |
| *Macrelmis* sp. 3 | | X | | |
| *Macrelmis* sp. 4 | | | | X |
| *Macrelmis* sp. 5 | | | X | X |
| *Macrelmis* sp. 6 | | | X | |
| *Macrelmis* sp. 7 | | | | X |
| *Macrelmis* sp. 8 | | | | X |
| *Macrelmis* sp. 9 | | | | X |
| *Neoelmis* sp. 1 | | X | | X |
| *Neoelmis* sp. 2 | | X | | |
| *Cylloepus* sp. 1 | | | X | X |
| *Cylloepus* sp. 2 | | X | | X |
| *Cylloepus* sp. 3 | | | | X |
| *Cylloepus* sp. 4 | | | | X |
| *Cylloepus* sp. 5 | | | | X |
| *Cylloepus* sp. 6 | | | X | X |
| *Cylloepus* sp. 7 | | | | X |
| *Cylloepus* sp. 8 | | | X | X |
| *Cylloepus* (or near) sp. 1 | | | | X |
| *Cylloepus* (or near) sp. 2 | | | X | |
| *Microcylloepus* sp. | | | | X |
| *Austrolimnius eris* | | | | X |
| *A.* nr. *tarsalis* | | | | X |
| *Austrolimnius* sp. | | | | X |
| *Stenhelmoides* sp. | | | | X |
| *Austrelmis* sp. | | | X | X |
| *Onychelmis* sp. | | | X | |
| Larainae | | | | |
| *Hexanchorus* sp. | X | | | |
| near *Hexanchorus* | | X | | X |
| *Pharcoenus* (or near) | | | X | X |

(NE, NW, or SE). In the southwest region, the only pair of families to exhibit correlated mesogeographic patterns of species composition were elmids and naucorids ($P < 0.001$). In contrast, the geographic pattern of species composition for each family was correlated with the patterns for one or more other families at the level of the entire study area (Fig. 1). These mesogeographic patterns generally were also true when Mantel analyses of regions were restricted to sites at 2195 m elevation or greater. No pairwise correlation of site-by-site matrices for families were significant in any of the four regions. In part, this likely was a consequence of reduced power in Mantel randomizations for matrices of low rank, especially in the southwest region (rank = 3). At the scale of the entire study area, the pairwise similarities of species composition for families at elevationally restricted sites corresponded closely to those when all sites were in the analysis, but with two exceptions. First, in the elevationally restricted data set, no analyses could be performed for naucorids because of their absence at sites at 2195 m elevation or greater. Second, the correlation of mesogeographic patterns of

TABLE 2. *Number of species shared between versants or transects of total species possible for each of five families of lotic insects from northern Ecuador.*

| | Comparisons of Versants | | Comparisons of Transects | |
|---|---|---|---|---|
| Taxon | North E–W | South E–W | East N–S | West N–S |
| Baetidae | 4/11 | 13/18 | 4/14 | 10/18 |
| Leptohyphidae | 1/4 | 5/16 | 1/12 | 4/9 |
| Oligoneuriidae | 0/1 | 1/1 | 1/1 | 0/1 |
| Naucoridae | — | 1/11 | — | — |
| Elmidae | 1/8 | 7/35 | 1/14 | 3/33 |
| Total | 6/24 | 27/81 | 7/41 | 17/61 |
| Percent | 25 | 33 | 17 | 28 |

compositional similarity between the Baetidae and Leptohyphidae were less strong and nonsignificant ($P = 0.146$) in elevationally restricted analyses compared to the situation in the elevationally unrestricted analyses ($P < 0.05$). This diminution in significance may be associated with a loss of power in Mantel analyses involving matrices for which rank is 23 (elevationally restricted data) versus 41 (elevationally unrestricted data).

## DISCUSSION

The latitudinal gradient in diversity is one of the most pervasive patterns characterizing life on earth (Hawkins 2001, Willig 2001), with tropical regions, especially those in the New World, harboring the most species-rich biotas. Indeed, approximately one-third of the megadiversity countries of the world (Brazil, Colombia, Ecuador, Peru, and Venezuela) are in South America (Mittermeier *et al.* 1997). Moreover, the tropical Andes ranks first among global biodiversity hotspots (Myers 2001) in terms of endemic species richness for plants and vertebrates (6.7 and 5.7% of world total, respectively). Unfortunately, our understanding of how taxonomic richness of stream invertebrates is related to nonaquatic environmental gradients, including latitude (Boyero 2002), is poor.

The richness of any large region, such as the tropical Andes, is a consequence of the richness of each of the smaller constituents and the turnover in species composition among them (Whittaker 1960, 1977; Schneider 2001; Koleff & Gaston 2002). Elevation is an important environmental factor that would enhance turnover of species (beta diversity) among Andean sites (alpha diversity), consequently leading to high regional (gamma) diversity (Rahbek 1995).

Patterns of biotic distribution in South America have been shaped in part by the mid-Miocene uplift of the Andes Mountains and the late-Miocene incursion of inland embayments and semi-marine seaways near the eastern base of the Andes (Hoorn 1993, Räsänen *et al.* 1995). Following the Andean uplift, continental patterns of drainage reversed from a northwestward flow toward the Guyana Shield to an eastward flow (Hoorn 1993). Further, following the Pliocene establishment of the Isthmus of Panama land bridge, immigration of elements of the North American fauna contributed to the faunal composition of Amazonia (Simpson & Haffer 1978). These factors, acting in concert with local evolutionary (*i.e.*, cladogenic) processes, likely had a profound effect on and are responsible in part for the present day patterns of distribution of aquatic biota in South America (Räsänen *et al.* 1995). Current distributional patterns of aquatic insects are constrained by clade-specific dispersal attributes that differ regarding vagility. For example, adults of Anisoptera (dragonflies) are capable of powerful and directed flight and would be expected to disperse more widely and readily than taxa with reduced propensity for dispersion, such as flightless insect taxa. Similarly, insect clades with elevational restrictions would be expected to be geographically constrained when presented with a barrier of substantial topographic relief, such as the Andes Mountains.

Regional distribution patterns of aquatic biodiversity are thought to be largely reflective of those of terrestrial biodiversity (Illies 1969). In addition to endemic clades, elements of the South American fauna have been attributed to a Central American origin (Simpson & Haffer 1978). More specifically, origins of the Colombian Pacific fauna (which includes the Choco faunal subcenter in Ecuador [Müller 1973]) include elements of both the Central American and Amazonian faunas (Müller 1973). Possible routes of interchange for terrestrial elements of the Amazonian faunal center and the Colombian Pacific faunal center were explored by Chapman (1923), Miller (1952), and Koepcke (1961). The most likely routes of distribution are thought to include Porculla Pass (2150 m elev.) in northern Peru and the Loja route in southern Ecuador (Chapman 1923, Müller 1973).

TAXONOMIC DIVERSITY.—Species of three insect orders that differ widely in biological attributes were examined in this study (Ephemeroptera, Heteroptera, and Coleoptera). Generally, differences in taxonomic richness and community composition were

TABLE 3. *Descriptive statistics of richness per region for species and genera in each of four families of insects from 41 sites in northern Ecuador.*

| | Baetidae | | | | Leptohyphidae | | | | Naucoridae[a] | | | | Elmidae | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | North | | South | | North | | South | | North | | South | | North | | South | |
| | E | W | E | W | E | W | E | W | E | W | E | W | E | W | E | W |
| Specific Level | | | | | | | | | | | | | | | | |
| Mean | 1.3 | 2.6 | 1.9 | 3.1 | 0.2 | 0.7 | 1.3 | 1.4 | — | — | 0.8 | 1.0 | 0.8 | 0.9 | 0.9 | 3.9 |
| SD | 1.5 | 1.1 | 1.4 | 1.6 | 0.4 | 1.1 | 1.7 | 1.2 | — | — | 1.3 | 0.9 | 0.8 | 1.2 | 1.5 | 2.4 |
| Minimum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | — | — | 0 | 0 | 0 | 0 | 0 | 0 |
| Maximum | 4 | 4 | 5 | 6 | 1 | 3 | 6 | 5 | — | — | 4 | 2 | 2 | 3 | 5 | 8 |
| Generic Level | | | | | | | | | | | | | | | | |
| Mean | 1.3 | 2.6 | 1.9 | 2.7 | 0.2 | 0.6 | 0.9 | 1.3 | — | — | 0.6 | 0.9 | 0.8 | 0.9 | 0.8 | 3.1 |
| SD | 2.5 | 1.1 | 1.4 | 1.3 | 0.4 | 0.8 | 1.0 | 1.0 | — | — | 0.9 | 0.8 | 0.8 | 1.2 | 1.3 | 2.1 |
| Minimum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | — | — | 0 | 0 | 0 | 0 | 0 | 0 |
| Maximum | 4 | 4 | 5 | 5 | 1 | 2 | 3 | 3 | — | — | 2 | 2 | 2 | 3 | 4 | 8 |
| Elevation[b] | | | | | | | | | | | | | | | | |
| Mean | 2.85 | 2.71 | 2.24 | 1.42 | 2.60 | 2.60 | 1.72 | 1.37 | — | — | 0.85 | 0.92 | 2.95 | 2.46 | 1.80 | 1.42 |
| SD | 0.34 | 0.33 | 1.23 | 0.94 | — | 0.43 | 1.01 | 0.81 | — | — | 0.32 | 0.57 | 0.32 | 0.24 | 1.23 | 0.94 |
| Minimum | 2.51 | 2.20 | 0.58 | 0.31 | 2.60 | 2.20 | 0.50 | 0.31 | — | — | 0.05 | 0.31 | 2.60 | 2.20 | 0.58 | 0.31 |
| Maximum | 3.18 | 3.16 | 3.83 | 3.10 | 2.60 | 3.05 | 3.15 | 2.71 | — | — | 1.23 | 1.95 | 3.25 | 2.67 | 3.83 | 3.10 |

[a] Naucoridae were not collected in the northern transect.

[b] Elevations are expressed as kilometers.

TABLE 4. P*-values of two-way (transect and versant) analyses of covariance (elevation) for generic and species richness in four families of aquatic insects from 41 streams in the Andes of Ecuador. Because Naucoridae were absent from the northern transect, a one-way (versant) analysis of covariance (elevation) was conducted for both generic and species richness in the southern transect. The number of genera or species in a fauna is indicated parenthetically beneath the taxonomic level in the heading.*

| | Baetidae | | Leptohyphidae | | Naucoridae | | Elmidae | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|
| Factors | Genera (13) | Species (19) | Genera (3) | Species (16) | Genera (3) | Species (11) | Genera (12) | Species (38) | Genera (31) | Species (84) |
| ANCOVA | | | | | | | | | | |
| Elevation | 0.033 | 0.108 | 0.155 | 0.127 | <0.001 | <0.001 | 0.827 | 0.622 | 0.561 | 0.280 |
| Transect (T) | 0.079 | 0.066 | 0.181 | 0.336 | — | — | 0.099 | 0.052 | 0.034 | 0.036 |
| Versant (V) | 0.006 | 0.006 | 0.393 | 0.719 | 0.367 | 0.226 | 0.041 | 0.027 | 0.027 | 0.045 |
| T × V | 0.911 | 0.827 | 0.770 | 0.498 | — | — | 0.039 | 0.023 | 0.301 | 0.325 |
| A priori | | | | | | | | | | |
| North (versants) | 0.066 | 0.102 | 0.477 | 0.524 | — | — | 0.990 | 0.993 | 0.433 | 0.497 |
| South (versants) | 0.020 | 0.011 | 0.622 | 0.793 | — | — | <0.001 | <0.001 | 0.007 | 0.012 |
| North vs. South | 0.079 | 0.066 | 0.181 | 0.336 | — | — | 0.099 | 0.052 | 0.034 | 0.036 |

related to versants defined by the Andes or latitudinal distance. Primarily because of differences associated with elevational constraints, most taxa of each order were collected in streams of the southern transect. Moreover, within the southern transect, more taxa of Baetidae were found in western streams (18 of 19 taxa), whereas more taxa of Leptohyphidae were found in eastern streams (12 of 16 taxa). Similarly, the vast majority of Elmidae were found in western streams of the southern transect (30 of 38 taxa). The number of taxa within the naucorid subfamilies Cryphocricinae and Limnocorinae were distributed evenly on both versants of the mountains in the southern transect.

Because the Andes serve as a substantial biogeographic barrier for the eastern and western faunas, and because of the intervening high paramo, stream capture is not a probable mechanism of dispersal between versants. Of the three orders in our analyses, mayflies are appreciably more vagile and have greater predisposition to dispersal by wind or directed flight. Documentation of flight in Naucoridae is nonexistent, except for records of one genus at light traps in Paraguay (Hungerford 1941), and flight of Elmidae is known predominantly for emerging adults searching for aquatic habitats after terrestrial pupation (Brown 1972, Seagle 1980). Moreover, elmids exhibit elevational limitations above which they do not occur (Williams & Hynes 1971) and naucorids similarly are constrained to elevations below *ca* 2000 m. Ele-

TABLE 5. P*-values of multivariate analysis of variance for the compositional similarity of 41 sites based on all species of five families from northern Ecuador.*

| Factor | Genera | Species |
|---|---|---|
| MANOVA | | |
| Transect (T) | 0.005 | 0.004 |
| Versant (V) | 0.072 | 0.079 |
| T × V | 0.047 | 0.064 |
| A priori | | |
| North (versants) | 0.071 | 0.147 |
| South (versants) | 0.037 | 0.015 |
| North vs. South | 0.005 | 0.004 |

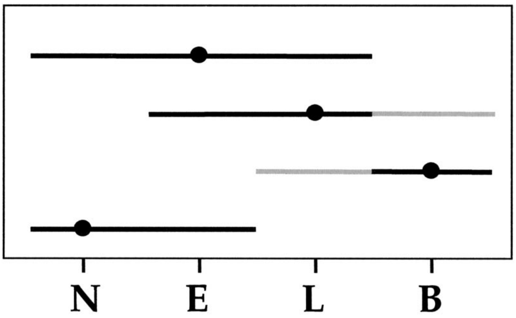

FIGURE 2. Compositional similarity for each of four families (N, Naucoridae; E, Elmidae; L, Leptohyphidae; B, Baetidae) of lotic insects collected in 41 streams in northern Ecuador. All families appearing below a particular line are not significantly different from the family represented by the focal centroid with respect to their geographic pattern of faunal similarities. The gray line represents a significant correlation for the latitudinally unrestricted data set that is weak to nonsignificance in the elevationally restricted data set (only sites >2195 m).

TABLE 6. *Species of* Ambrysus *with published records from Andean countries.*

| Species | Countries | References |
|---|---|---|
| *A. acutangulus* Montandon | Argentina | Montandon 1897a, De Carlo 1950 |
| *A. attenuatus* Montandon | Argentina | Montandon 1897b, De Carlo 1950 |
| *A. bergi* Montandon | Argentina | Montandon 1897b, Lopez-Ruf 1985 |
| *A. colombicus* Montandon | Colombia | Montandon 1909 |
| *A. crenulatus* Montandon | Colombia, Ecuador | Montandon 1897b, Sites 1990 |
| *A. fossatus* Usinger | Colombia, Ecuador, Peru | Usinger 1946, Roback 1966, Roback & Nieser 1974, Sites 1990 |
| *A. fucatus* Berg | Argentina | Berg 1879, De Carlo 1950 |
| *A. gemignanii* De Carlo | Argentina | De Carlo 1950 |
| *A. horvathi* Montandon | Peru[a] | Montandon 1909 |
| *A. ochraceus* Montandon | Argentina, Bolivia | Montandon 1909, De Carlo 1950, Bachmann 1963, Lopez-Ruf 1990 |
| *A. peruvianus* Montandon | Peru | Montandon 1909 |
| *A. p. planus* La Rivers | Ecuador, Peru | La Rivers 1951a, b |
| *A. teutonius* La Rivers | Colombia | La Rivers 1951b, Roback & Nieser 1974 |
| *A. tricuspis* La Rivers | Colombia | La Rivers 1974 |

[a] Specific locality was not given.

vational limitations may be related to maximum stream temperatures, as suggested by studies on Danish and Ecuadorian streams (Jacobsen *et al.* 1997). Thus, of these three orders, mayflies may have had the greatest predisposition to be dispersed widely, and across the Andes Mountains. Therefore, it is not surprising that mayflies, many genera of which are temperate and not as elevationally restricted as are naucorids and elmids, had the highest percentage overlap in species occurrence between versants. This was particularly true for Baetidae, which had 36 and 72 percent shared species between versants for the northern and southern transects, respectively. Because we did not sample in streams below 2000 m in the northern transect, naucorids were not encountered. In the southern transect, however, only a 9 percent overlap in naucorid species occurrence was found between versants. Similarly, the elmid fauna exhibited versant restrictions for each transect. Specifically, 12 and 20 percent of the faunas were in common between versants for the northern and southern transects, respectively. Thus, the extreme elevational barrier of the Andes Mountains, in concert with the limited flight abilities of the naucorids and elmids, likely prevents appreciable dispersion of these insects across the mountains. Further, within a versant, the turnover in species composition among sites is high, as shared species of Elmidae was only 7 and 9 percent for the western and eastern streams, respectively. Thus, in addition to the mountain barrier, the ranges of Elmidae appear to encounter substantial latitudinal restriction. This partially may be accounted for by the elevational exclusion of certain elmid taxa in the streams of the northern transect. Thus, by virtue of their propensity to occur in streams at lower elevations (higher water temperature), the faunal similarity within versant and between transects naturally would be low. For mayflies, however, the percentage of shared species within a versant was considerably higher: Baetidae, 29 and 56 percent; and Leptohyphidae, 8 and 44 percent (for the western and eastern streams, respectively, indicating broader ranges of species in these families).

The number of species and percent species overlap also is shaped in part by the particular evolutionary history of each taxon. In the Naucoridae, the genus *Ambrysus* most likely radiated northward and southward from its origin in the Neotropics of Mexico where it is most species-rich. A Pliocene infiltration into South America predictably would funnel lowland Central American taxa southward along the Pacific coastal lowlands or eastward into the northern Guyana Shield, the two faunas of which are partially bisected by the northern limit of the Andes. We found species of *Ambrysus* only in the eastern versant. In addition, all published records of the genus from Andean countries also are from the eastern versant (Table 6), although Colombian records of *A. colombicus* Montandon and *A. crenulatus* Montandon are from the intermountain regions near Panama. Further, published records of the genus from Chile, which predominantly occupies the western versant of the Andes, are nonexistent. Thus, the occurrence of *Ambrysus* in South America appears to be of sufficiently recent origin that dispersion across the Andes Mountains from the Amazonian faunal center may not have occurred, as it has for other naucorid genera of probable South American origin. More specifically, the genera *Limnocoris* and *Cryphocricos* are most species-rich in South America and are found in both versants of the Andes in Ecuador, in part because they have had sufficient time to disperse, although species co-occurrence is low; however, the specific Neotropical center of origin of these genera is unclear. The *Limnocoris* fauna was diverse and only one morphospecies was shared in both versants. Because this species-rich genus (71 described species) requires taxonomic revision, specific determinations are not reported here.

Most of the faunal interchange by mayflies through Central America was represented as South American taxa infiltrating northward to Central and North America. The few mayfly groups that moved from North America into South America largely were Nearctic and temperate, and thus most were restricted to montane conditions available in the Andes Mountains (McCafferty 1998). Similar dispersion of other insects (Halffter 1987) and plants have been documented to follow this montane distribution corridor, although a northward bias in the number of infiltrating taxa has been suggested (Halffter 1987, McCafferty 1998).

TAXONOMIC COMPOSITION.—In our samples, we detected *a priori* differences in compositional similarity between transects and between versants in the southern transect only. Clear distinction in taxonomic composition between versants in the northern transect was obscured in part because of our limitation in sampling at lower elevations. Because of political and logistical limitations, we were restricted to elevations above 2512 m in the east and above 2195 m in the west. Communities were influenced taxonomically in part by the absence of Naucoridae, which were not collected at elevations above 1950 m. In addition, Elmidae is thought to be a tropical family with incursions into temperate regions and higher elevations; thus, the diversity of the elmid fauna can be expected to be lower in the northern transect, although the covariate of elevation should account for any differences in richness between versants (which is linearly associated with elevation). The lack of representation of lower elevation streams in the northern transect likely was a factor in our detection of stronger differences in generic and species compositions between versants in the southern transect than in the northern transect.

On a landscape scale, interfamilial correlations in the change of taxonomic composition among sites were significant (Mantel analysis), suggesting that the way in which taxonomic composition changes is similar for the families examined. This result was robust in that elimination of sites below 2195 m from analyses did not appreciably change interpretation of patterns. This suggests that the Andes Mountains exert a consistent influence on species-level distributions within families, regardless of ordinal affiliation. On a regional level (*i.e.*, NE, NW, SE, and SW), however, only a single pairwise interfamilial correlation was significant, and this was not even evident in the elevationally restricted analysis. This implies that the way in which intrafamilial composition changes among sites in a region differs among families. At this finer level of spatial resolution, presence or absence of taxa is controlled by particular environmental features that directly affect the ability of the taxon to exist (*e.g.*, water quality, substrate condition, temperature). Not surprisingly, the lone significant correlation was between the elevationally restricted Naucoridae and Elmidae in the southwestern region, which harbored the most species-rich fauna of both families.

The extreme elevational relief of the Andes Mountains presents a barrier to taxa adapted to lowland tropical environments that is difficult for even insects to circumvent without the help of incidental transport by humans. Although organisms adapted to temperate conditions, including North American invading taxa, have higher coefficients of overlap between versants, there still exists a substantial faunal-isolating effect of the Andes Mountains in Ecuador.

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APPENDIX 1. *Collection data for localities included in analyses. Region refers to versant and transect position (Fig. 1). A locality number is given for each collection, most of which have a corresponding photograph of the collecting site available via a link from the internet site of the Enns Entomology Museum, University of Missouri–Columbia.*

| Province | Region | Specific Locality | Elevation (m) | Temp. (°C) | Locality |
|---|---|---|---|---|---|
| Carchi | NE | 13.3 km E Pan-American Hwy, middle road to La Bonita | 3252 | 11.0 | L-1 |
| Carchi | NE | 15.0 km E Pan-American Hwy, middle road to La Bonita | 3176 | 10.0 | L-2 |
| Carchi | NE | 15.7 km E Pan-American Hwy | 3115 | 9.5 | L-3 |
| Carchi | NE | 11 km W Santa Barbara | 2749 | 17.5 | L-4 |
| Carchi | NE | Rio Chingual, 4 km W Santa Barbara | 2512 | 11.5 | L-5 |
| Carchi | NE | 2.1 km W Santa Barbara | 2603 | 17.0 | L-6 |
| Carchi | NW | Rio Bobo, 4.4 km E Tufiño | 3045 | 10.0 | L-8 |
| Carchi | NW | 33.7 km W Tufiño | 3158 | 11.5 | L-12 |
| Carchi | NW | 39.0 km W Tufiño | 2804 | 15.0 | L-13 |
| Carchi | NW | 40.8 km W Tufiño | 2682 | 13.0 | L-14 |
| Carchi | NW | 45.2 km W Tufiño | 2573 | 12.0 | L-15 |
| Carchi | NW | 49.1 km W Tufiño | 2505 | 16.5 | L-17 |
| Carchi | NW | Rio San Juan, 1.8 km E Maldonado | 2195 | 18.0 | L-18 |
| Pichincha | SW | Rio Peripa at Puerto Limon | 314 | 24.0 | L-20 |
| Pichincha | SW | Rio Chila, 1 km E San Pedro de Laurel | 314 | 24.0 | L-21 |
| Pichincha | SW | Rio Mache, 9.6 km W San Jacinto de Bua | 329 | 26.0 | L-22 |
| Pichincha | SW | tributary of Rio Toachi, 5.9 km W Tinalandia | 701 | 22.0 | L-23 |
| Pichincha | SW | tributary of Rio Toachi, 2.2 km W Tinalandia | 725 | 22.0 | L-24 |
| Pichincha | SW | Rio Toachi near footbridge, 0.3 km E Tinalandia | 741 | 20.0 | L-25 |
| Pichincha | SW | tributary of Rio Toachi, 2.6 km S La Union del Toachi | 975 | 22.0 | L-27 |
| Pichincha | SW | Rio Dos Rios at Dos Rios, 7.0 km NE on Old Quito Rd. | 1292 | 20.0 | L-28 |
| Pichincha | SW | 13.4 km NE on Old Quito Rd. | 1509 | 18.0 | L-29 |
| Pichincha | SW | Rio Guajalito at Las Palmeras, 36.2 km NE on Old Quito Rd. | 1949 | 15.0 | L-30 |
| Pichincha | SW | Rio Soloya at Escuela Jose, Joaquin Olmeda, Old Road to Quito | 2100 | 11.0 | L-50 |
| Pichincha | SW | 25.3 km W Barrio de Libertad, Old Road to Quito | 2316 | 12.0 | L-51 |
| Pichincha | SW | 20.2 km W Barrio de Libertad, Old Road to Quito | 2707 | 12.0 | L-52 |
| Pichincha | SW | 14.2 km W Barrio de Libertad, Old Road to Quito | 3097 | 11.0 | L-53 |
| Napo | SE | 2.4 km E of shrine on road to Baeza | 3833 | 9.0 | L-31 |
| Napo | SE | 9.1 km E of shrine on road to Baeza | 3420 | 7.0 | L-32 |
| Napo | SE | Rio Papallacta at Papallacta below spillway at EMAP plant | 3146 | 10.0 | L-33 |
| Napo | SE | tributary of Rio Papallacta, 4 km E Papallacta | 2975 | 9.0 | L-34 |
| Napo | SE | 5.6 km E Papallacta | 2880 | 11.0 | L-35 |
| Napo | SE | Rio Maspa, 13.5 km E Papallacta | 2975 | 9.0 | L-36 |
| Napo | SE | stream at Cuyuja | 2475 | 12.0 | L-37 |
| Napo | SE | Rio Quebrada Juve | 1996 | 15.0 | L-38 |
| Napo | SE | 6.2 km S Baeza (old town) | 1865 | 16.0 | L-40 |
| Napo | SE | 33.2 km S Cosanga | 1219 | 20.0 | L-42 |
| Napo | SE | 48.7 km S Cosanga | 835 | 22.0 | L-44 |
| Napo | SE | Rio Sinde, 5.5 km E Puerto Napo | 501 | 25.0 | L-47 |
| Napo | SE | 5.5 km E Puerto Napo | 579 | 24.0 | L-48 |
| Napo | SE | Rio Pindo at Shell | 1120 | 21.0 | L-49 |