ECOGRAPHY 26: 751–767, 2003

# Broad-scale geographical patterns in local stream insect genera richness

**Mark R. Vinson and Charles P. Hawkins**

Vinson, M. R. and Hawkins, C. P. 2003. Broad-scale geographical patterns in local stream insect genera richness. – Ecography 26: 751–767.

Comprehensive global studies of stream invertebrate assemblages are rare and have produced contradictory results. To address this shortcoming, we compiled data from 495 published estimates of local genera richness for three orders of stream-dwelling insects (Ephemeroptera, Plecoptera, Trichoptera) from throughout the world and used these data to describe global geographic patterns in stream insect genera richness and to address two questions: 1) does local stream insect richness vary more with regional historical factors or with local ecological factors?, and 2) to what extent have streams converged in the number of taxa they support?
Maximum genera richness varied sharply across the range of latitude examined from the south to north poles for all three orders of aquatic insects. Ephemeroptera richness showed 3 peaks (~30°S, 10°N, and 40°N) with highest richness near 5–10°N and 40°N latitude. Plecoptera richness was distinctly highest at ~40°N latitude with a similar peak at 40°S latitude. Trichoptera richness showed less latitudinal variation than the other taxa but was slightly higher near the equator and at 40°N and S latitude than at other latitudes. Genera richness generally declined with increasing elevation, except for Plecoptera. Maximum genera richness increased steadily with a measure of regional terrestrial net primary production and declined sharply with a measure of hydrologic disturbance for all orders. Richness varied widely among both biogeographical realms and biomes, although ca 2 times as much variation in richness was associated with biome as biogeographic realm. Richness for each order was highest in different biogeographic realms, but all orders had highest richness in broadleaf forest biomes. These latter results imply that spatial variation in local richness of stream insects is more strongly affected by contemporary ecological factors than by historical biogeography and that maintenance of intact forested landscapes may be critical to the conservation of stream invertebrate faunas.

*M. R. Vinson (aqua@cc.usu.edu) and C. P. Hawkins, Dept of Aquatic, Watershed, and Earth Resources and Ecology Center, Utah State Univ., Logan, UT 84322-5210, USA.*

Much of the recent work on broad-scale patterns in biotic diversity has focused on how local contemporary factors and regional historical processes operate as "landscape filters" to influence the occurrence and persistence of species in local habitats (Tonn 1990, Ricklefs and Schluter 1993a, Poff 1997). Local biotic richness appears to be a function of both the size of regional species pools and local processes (Ricklefs 1987, Cornell and Lawton 1992, Ricklefs and Schluter 1993b, Schluter and Ricklefs 1993, Cornell and Karlson 1996, Caley and Schluter 1997, Hugueny et al. 1997, Karlson and Cornell 1998). The maximum local richness occurring at a site is related to regional richness (Caley and Schluter 1997), which seems to be constrained by both regional environmental conditions (Currie 1991) and biogeographical history (Ricklefs 1987). Below this maximum level, local richness can vary markedly in response to finer-scale variation in factors such as productivity (Rosenzweig and Abramsky 1993), habitat structure (MacArthur 1964, Recher 1969, Vinson and Hawkins 1998), disturbance (Connell 1978), and biotic interactions (Paine 1966). Thus, to interpret the wide

Accepted 5 May 2003

ISSN 0906-7590

variation in species richness observed in local communities, we need to place mechanisms that operate at local contemporary scales within a regional-historical framework (Cornell 1993, Latham and Ricklefs 1993).

Streams should be ideal ecosystems for evaluating global diversity hypotheses because similar local habitats can be found on all continents and within all biomes at all but the highest elevations and latitudes. Because of the universal effects of fluvial processes in creating stream environments, local habitat characteristics (e.g., water depths, water velocities, water temperatures, stream shading, and substrate) can vary greatly at small spatial scales and do not appear to vary systematically with latitude or elevation (Hynes 1970). Indeed, even stream habitats within the same basin can vary considerably. For example, tributary streams are often dissimilar to the streams they flow into, e.g., when a constant temperature and discharge spring flows into a more hydrologically and thermally variable river, or when an intermittent stream flows into a perennial stream, or when a heavily shaded stream flows into a stream that receives full sunlight. Local habitats and thus the structure of stream biotic assemblages may, therefore, be as similar across different continents, which may have markedly different landscapes and biogeographic histories, as they are within the same watershed (Hynes 1970, Statzner and Higler 1986).

In contrast to other taxa (see reviews by Huston 1994, Rosenzweig 1995), there have been few comprehensive global studies of taxa richness patterns for any group of stream biota among continents or terrestrial biomes (Minshall 1988, Allan and Flecker 1993, Oberdorff et al. 1995, 1997, Hugueny et al. 1997, Guegan et al. 1998). Broadscale geographical studies to describe patterns in stream invertebrates are even rarer. Comparisons of diversity between tropical and temperate streams are limited in scope and contradictory in results (Covich 1988, Allan and Flecker 1993 and papers cited within). To address this knowledge gap, we compiled 495 published local genera richness estimates for stream dwelling insects from throughout the world. We then used these data to describe global geographic patterns in stream insect genera richness and to address two questions: 1) does local stream insect richness vary more with regional historical factors or with local ecological factors?, and 2) to what extent have streams converged in the number of taxa they support (Schluter 1986, Schluter and Ricklefs 1993)?

## Methods

### Aquatic insect data

Data on local stream insect assemblage richness were collected by searching 88 aquatic sciences, general ecology, entomology, and natural history journals for published taxa lists and using further citations from selected papers. We concentrated on literature published between the years 1970–1997, but earlier years were searched in those journals that yielded more data. A list of journals and years searched and the data used in the analyses are available in Vinson (1998) and from the senior author. We defined local assemblages as individual sampling sites or composite samples collected within short stream reaches (0.1–1 km or $10^1$–$10^2$ channel widths long). Minimum critera for inclusion in the analyses were: 1) multiple benthic larval insect samples were collected from at least two seasons and 2) sampling had to have been conducted upstream of any dams, water diversions, or conspicuous sources of pollution. These minimum data requirements forced us to exclude several well-known (e.g. Hynes and Williams 1962, Illies 1964, Patrick 1966, Williams and Hynes 1971, Hynes 1975, Barnard and Biggs 1988) and many more lesser known works from poorly studied areas, but improved the consistency of the data we did evaluate. Each richness estimate was thus based on a rigorous sampling effort, 1–2 yr studies, that would have likely collected all but the rarest taxa at a site. The number of samples used for each richness estimate ranged from 2 to 520, with a mean and median of 67 and 54.

The data set consisted of 495 estimates of local genera richness; 146 samples were from North America and 349 samples were from outside continental North America (Fig. 1). Analyses presented here were limited to the insect orders Ephemeroptera (mayflies, $n = 382$), Plecoptera (stoneflies, $n = 446$), and Trichoptera (caddisflies, $n = 351$). These three orders were selected because their larvae are wholly aquatic, they have widespread distributions, their ecological requirements are fairly well known, their taxonomy is generally well established on a worldwide basis, considerably more data were available for these groups than other taxa, and trends in Ephemeroptera, Plecoptera, and Trichoptera richness are often strongly correlated with trends in overall richness (Perry and Schaeffer 1987). The number of genera was used rather than species because the predominance of data was available at this taxonomic level. However, the relationship between genera and species was highly significant ($p < 0.0001$ for all taxa groups) for those studies that provided species level identifications. Pearson correlation coefficients between genera and species richness were 0.82 for Ephemeroptera ($n = 203$), 0.88 for Plecoptera ($n = 261$), 0.93 for Trichoptera ($n = 172$), and 0.74 for combined Ephemeroptera, Plecoptera, and Trichoptera (EPT, $n = 177$) genera. Furthermore, genera of aquatic insects appear to be natural groupings that describe clear ecological trends in adaptive radiation (Wiggins and Mackay 1978). For consistency, only data from benthic larvae collections were used; thus, richness values are likely underestimates.

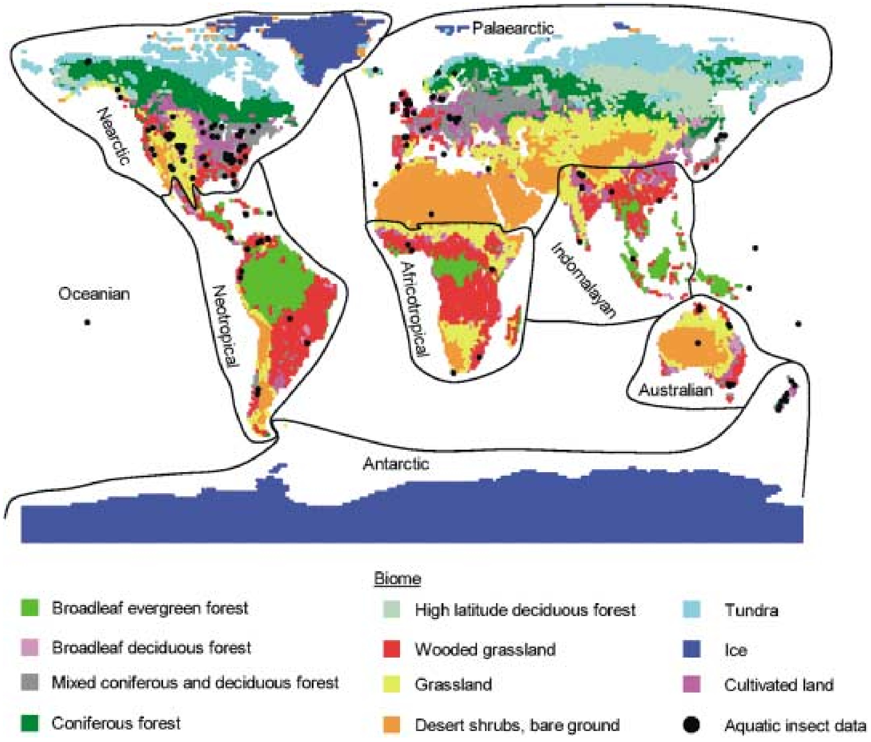

Fig. 1. Distribution of 8 biogeographical realms (Udvardy 1975), 11 biomes (Defries and Townshend 1994, Meeson et al. 1995, Sellers et al. 1995), and the locations of sampling sites used in the analyses. Each stream insect sampling location represents a single sampling station or a group of closely clustered sites. Considerable overlap of points exists.

## Geographical and environmental data

Each local richness estimate was placed within a biogeographical realm (Udvardy 1975) and a terrestrial vegetation biome (Table 1, Defries and Townshend 1994, Meeson et al. 1995, Sellers et al. 1995). Similarly, estimates of regional terrestrial net primary production (NPP) and hydrologic disturbance were determined for each richness estimate using a standardized 1° × 1° equal angle latitude/longitude area data set compiled by Meeson et al. (1995) and Sellers et al. (1995). Udvardy's (1975) biogeographical classification delineated 8 realms throughout the world based on unifying features of history, geology, and flora and fauna biogeography (Fig. 1) and is similar to previous global biogeographic classification systems dating back to Wallace (1876, also see Brown and Gibson 1983). Biomes were delineated based on phenological differences among terrestrial vegetation types reflected in the temporal variations in the Normalized Difference Vegetation Index (NDVI) derived from satellite data (Defries and Townshend 1994). Following Dodds (1997), we combined biomes that would potentially have similar influences on stream biota with respect to riparian vegetation inputs and shading: $C_3$ and $C_4$ grasslands were placed into a single grassland class, $C_3$ and $C_4$ wooded grasslands were combined into a single wooded grassland class, and desert, shrubs and bare ground were combined into a single shrub-desert class.

Mean annual NDVI values, derived from monthly NDVI values for 1987, were used as a measure of regional terrestrial NPP. NDVI values are related to the physical properties of vegetation and have been correlated with leaf area index, the fraction of photosynthetic active radiation absorbed by the green portion of the vegetative canopy, percent leaf area greenness, net primary production, atmospheric $CO_2$ dynamics, and actual evapotranspiration (Sellers 1985, Tucker et al. 1986, Goward and Dye 1987, Box et al. 1989, Los et al. 1994, Sellers et al. 1994, 1996). Higher NDVI values reflect greater net primary productivity. Mean annual NDVI values varied greatly both within and across latitudinal bands (Fig. 2). These data clearly support Lugo and Brown's (1991) observation that simple generalizations between tropical and temperate environments, such as equatorial regions being predominately characterized by highly productive broadleaf evergreen forests, are often inaccurate and fail to reflect the diversity of environments found in both tropical and temperate regions.

Coefficients of variation (CV) in monthly precipitation were used as a measure of regional hydrologic disturbance. Precipitation data were area average monthly precipitation totals derived from rain-gauge measurements, satellite observations and numerical weather prediction results for January 1987 through December 1988 (Anon. 1993). Coefficient of variation in monthly precipitation describes the annual variation

Table 1. Number of genera richness estimates by biome and biogeographic realm. Where sample size varied among insect orders the range is shown.

| Biome | Biogeographical realm | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Africotropical | Antarctica | Australian | Indomalayan | Nearctic | Neotropical | Palaearctic | Oceanian | Total |
| Broadleaf evergreen forest | 0 | 0 | 2 | 4 | 0 | 11 | 0 | 2 | 19 |
| Broadleaf deciduous forest and woodland | 0 | 0 | 0 | 0 | 33 | 0 | 0 | 0 | 33 |
| Mixed coniferous and broadleaf forests | 0 | 0 | 3 | 2 | 26–39 | 0–6 | 10–57 | 0 | 41–107 |
| Coniferous forest and woodland | 0 | 10 | 0 | 0 | 4 | 0 | 5 | 0 | 19 |
| Wooded grasslands | 12 | 0 | 36–37 | 1 | 4–5 | 23–26 | 25–30 | 1 | 102–108 |
| Grasslands | 2 | 0 | 1 | 1 | 35 | 0 | 2 | 0 | 40–41 |
| Cultivated lands | 0 | 6 | 0 | 5–7 | 29 | 0 | 19–62 | 1 | 60–105 |
| Desert shrubs and bare ground | 0 | 0 | 6 | 0 | 0 | 0–9 | 8 | 0 | 14–23 |
| Tundra | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Total | 14 | 16 | 48–49 | 12–15 | 131–145 | 36–49 | 70–158 | 4 | 329–446 |

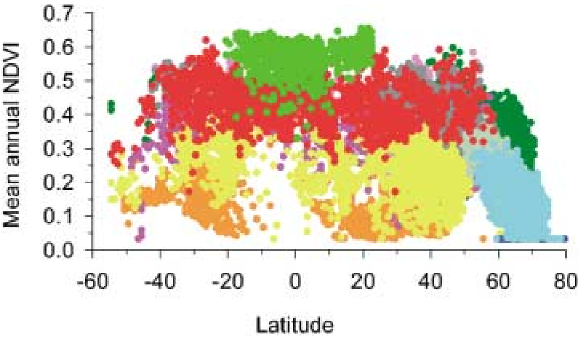

Fig. 2. Relationships between latitude and regional (1° × 1° latitude-longitude) mean annual Normalized Difference Vegetation Index (NDVI) derived from monthly satellite NDVI values for 1987 (Defries and Townshend 1994). Data are from Meeson et al. (1995) and Sellers et al. (1995). Symbol colors represent biomes as in Fig. 1. Considerable overlap of points exists.

in monthly precipitation standardized by the mean without accounting for the temporal sequence of the variation. Coefficients of variation in climate variables are commonly used as indices of ecological and hydrological variability and disturbance (e.g., Ricklefs 1980, Hughes and James 1989, Poff 1996) and are correlated with other measures of stability and predictability, e.g., Colwell's Index (Colwell 1974, Poff and Ward 1989, Poff 1996). Poff (1996) found that CVs in mean monthly streamflow were an acceptable single descriptor of discharge variability in streams across the US, and Finlayson and McMahon (1988) found that the CV in streamflow increased linearly with the CV in precipitation. In the absence of a more direct measure of disturbance, CV in monthly precipitation provides a reasonable approximation of hydrologic disturbance in terms of both the potential high and low water events experienced by some stream biota. CV's in monthly precipitation were highest in desert biomes, lowest in tropical broadleaf evergreen forests, and peaked at ca 20° north and south latitudes, but considerable variability in CV's existed both within and across latitudes (Fig. 3).

## Data analyses

### Preliminary data analyses

Sampling intensity and basin area are known to influence stream taxa richness estimates (Vinson and Hawkins 1998). To examine the effect of these variables on richness values, we collected data on the duration of each study, the number of samples collected as the basis for each richness estimate, basin area, distance downstream from the stream source, and stream order, when these data were included in publications. Unfortunately, none of these variables were consistently re-

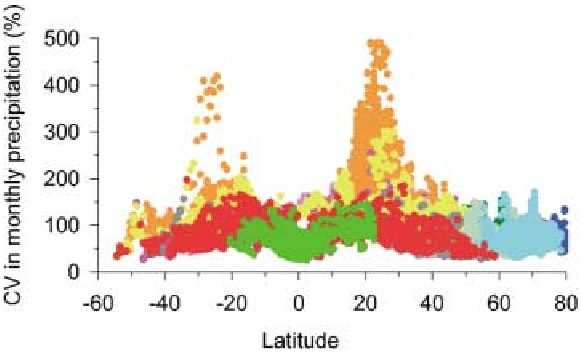

Fig. 3. Relationship between latitude and regional (1° × 1° latitude-longitude) coefficient of variation in monthly precipitation. Precipitation data were area average monthly precipitation totals derived from rain-gauge measurements, satellite observations and numerical weather prediction results for January 1987 through December 1988 (Anon. 1993). Data were from Meeson et al. (1995) and Sellers et al. (1995). Symbol colors represent biomes as in Fig. 1. Considerable overlap of points exists.

ported and thus their inclusion in an overall analysis would have reduced the number of samples that could be included in an analysis by up to 88%. However, study duration, number of samples, and basin area were reported in a sufficient number of samples that we could estimate the magnitude of error associated with not including these variables in our primary analyses. These factors were evaluated separately using regression analyses. We also used the number of samples collected in a study as a covariate in a 2-factor ANOVA to assess the effects of biogeographic realm and biome on genera richness. The results of this analysis were then compared to those derived from an ANOVA without the covariate to assess the degree to which sampling intensity confounded our overall results.

## Primary analyses

Richness for each order was analyzed separately and as combined EPT genera (Ephemeroptera + Plecoptera + Trichoptera). Patterns of maximum genera richness with latitude, elevation, terrestrial NPP, and the coefficient of variation in monthly precipitation were evaluated using two different statistical approaches: quantile regression (Cade et al. 1999, BLOSSOM software ver. W2000.12; < http://www.mesc.usgs.gov/blossom > and locally weighted sums of squares (LOWESS)). Bivariate scattergrams of the relationships are provided to convey the distribution of all of the data points; however statistical analyses were performed on maximum richness values rather than means derived from the entire data set because distinct edges or "factor ceilings" (sensu Thomson et al. 1996) were readily visible in the data clouds and we were interested in determining if the independent variables acted as landscape filters (sensu Poff 1997) to limit the maximum local richness possible at a site. In descriptive studies such as this, many sites will exhibit values smaller than the factor ceiling because of the additional constraints imposed by other factors. When subjected to traditional statistical analyses these unmeasured factors can obscure potentially important relationships (Thomson et al. 1996, Cade et al. 1999). In our data set, local genera richness was certainly dependent on a number of both local and regional factors that we could not account for, but we sought evidence regarding how maximum biotic richness may be limited by several ecologically relevant broad-scale factors. We evaluated these trends in maximum richness using both quantile and LOWESS regression techniques because they offer objective means of describing trends in data and both methods offer substantial improvement over simple linear regression or visual descriptions for the type of data we examine here. However, we emphasize that their application and interpretation must still be tempered by either how well the data fit the assumptions of the model (quantile regression) or the lack of quantitative criteria to determine if trends are different from random patterns (LOWESS).

Quantile regression is useful in detecting constraints of an independent variable on the upper limit of a response variable (e.g., triangular shaped relationships), but assumes a linear relationship between the maximum possible value of a response variable and the independent variable. Although choice of the quantile to be used is somewhat arbitrary, we used the 90th quantile rather than 95th or 99th quantiles to balance Type I (apparent relationship caused by outliers) and Type II (did not detect relationship) errors of inference. Quantile regression was applied separately for 0–30°N latitude and 30–70°N latitude bands of data because visual inspection showed a marked break in richness at about this latitude, and application of quantile regression to the entire range of latitudes would have clearly violated the assumption that maximum richness values were linearly related to latitude. This analysis was not done in southern latitudes because fewer data were available. Selection of 30°N latitude as a breakpoint was somewhat subjective, but this value was consistent with that observed for several other taxonomic groups that also do not exhibit a smooth latitudinal gradient in biotic richness. For example, Currie (1991, Fig. 3) showed a rapid decline in North American Amphibia and Mammalia richness at latitudes < 35 and 40°N and McGowan and Walker (1993) found a sharp increase in marine zooplankton richness above ca 40°N.

In contrast to quantile regression, LOWESS is a regression technique designed to identify the underlying trend in a data set without a priori specification of a model (Cleveland 1979) and is especially useful in detecting complex, nonlinear trends in data (Trexler and

Travis 1993). Currie (1991) used LOWESS to identify trends in animal and plant species richness patterns across North America. We used LOWESS to evaluate how maximum richness varied with latitude, elevation, NDVI and CV in monthly precipitation. We determined the maximum richness within regularly spaced intervals throughout the range of values of the independent variables (intervals were latitude = 5°, elevation = 200 m, NDVI = 0.05 units, and the coefficient of variation in precipitation = 20%). These intervals were arbitrarily selected to get a minimum data set of 20 values. We set the tension parameter in the LOWESS models to 0.5, the mid-point value. Lower tension values tend to emphasize minor variations in the data, whereas higher values may obscure important trends.

ANOVA was used to test for differences in richness among biogeographical realms and biomes. The Type I experimentwise error rate was managed by setting the critical alpha value to 0.0125 ($\alpha = 0.05/4$ taxa groups) for all ANOVAs and by using the Ryan-Einot-Gabriel-Welsch multiple range test (Anon. 1988), which controls the Type I error for multiple comparisons. This test was used to determine all significant pairwise differences in richness between categories. Because of the unbalanced sampling (Table 1), Type III two-factor fixed effects ANOVAs were used to assess the degree to which streams draining similar biomes in different biogeographical realms supported similar numbers of taxa. The relative importance of historical and ecological factors in influencing local biotic richness was judged by the relative amount of variation in local richness associated with biogeographic realm (history) and biome (ecology). Data from islands were examined and are presented but were excluded from statistical analyses because richness estimates were always much lower than those for mainland faunas.

# Results

## Preliminary analyses

For the subset of samples analyzed, sampling duration, number of samples, and basin area individually explained 0–13% of the observed variation in genera richness (Fig. 4). Richness generally increased with number of samples ($r^2 \leq 0.03$) and study duration ($r^2 \leq 0.04$) and decreased with increasing basin area ($r^2 \leq 0.13$). Including the number of samples as a covariable in ANOVAs evaluating the influence of biogeographic realm and biome accounted for little additional variance in richness. Model adjusted $R^2$ values increased by 5% for Ephemeroptera and 2% for EPT and there was no increase for either Plecoptera and Trichoptera. Excluding these 3 factors did not therefore appear to seriously bias our analyses. In fact, our statistical tests based on the full data set were conservative in that some systematic variation in richness associated with these factors were included as part of the error term in regressions and ANOVAs thus decreasing our ability to detect real patterns. This loss of power was offset, however, by the larger sample sizes that resulted from dropping these factors from our analyses. Furthermore, there was no evidence that sampling intensity or basin area varied systematically with latitude, elevation, biogeographic realm, or biome.

## Latitudinal patterns

Genera richness for all three orders of aquatic insects varied strongly across the range of latitudes examined from the south to north poles (Fig. 5). Our combined analyses showed that Ephemeroptera genera richness was generally highest near 30°S, 10°S and N, and 40°N latitude, lowest near the poles, and intermediate near the equator and 20°N latitude. Plecoptera genera richness clearly peaked near 40° latitude in both the southern and northern hemisphere. All Plecoptera richness estimates at $< 30°$ latitude were low relative to temperate latitudes with the exception of a single tropical stream in Malaysia (Bishop 1973), which resulted in an apparent secondary peak in Plecoptera richness near the equator. Latitudinal trends in Trichoptera genera richness were much less marked. Maximum Trichoptera genera richness was similar at most latitudes, although both LOWESS and quantile regression analyses revealed depressed richness between 20 and 30°N latitude. The LOWESS analysis also showed that Trichoptera richness, like Ephemeroptera, Plecoptera, and combined EPT genera richness, dropped steeply at latitudes $> 60°$N. Combined EPT genera richness was highest near 10°N and 40°N latitude and showed no evidence of a distinct peak in the southern hemisphere. Variation in richness within latitudes was nearly as great as that across latitudes, and richness on islands was consistently less than that on mainland streams for all 3 orders. The dips in richness between 10°–30°N latitude coincide with areas with high coefficients of variation (CV) in monthly precipitation (Fig. 3).

Quantile regression revealed a similar decline in genera richness between 0° and 30° and between 30° and 70°N latitude. Although the slopes of these relationships were steep with the exception of Trichoptera richness between 30° and 70°, most relationships were only marginally significant (Fig. 5).

## Elevational patterns

Maximum genera richness did not vary as strongly with elevation as it did with latitude (Fig. 6). Quantile

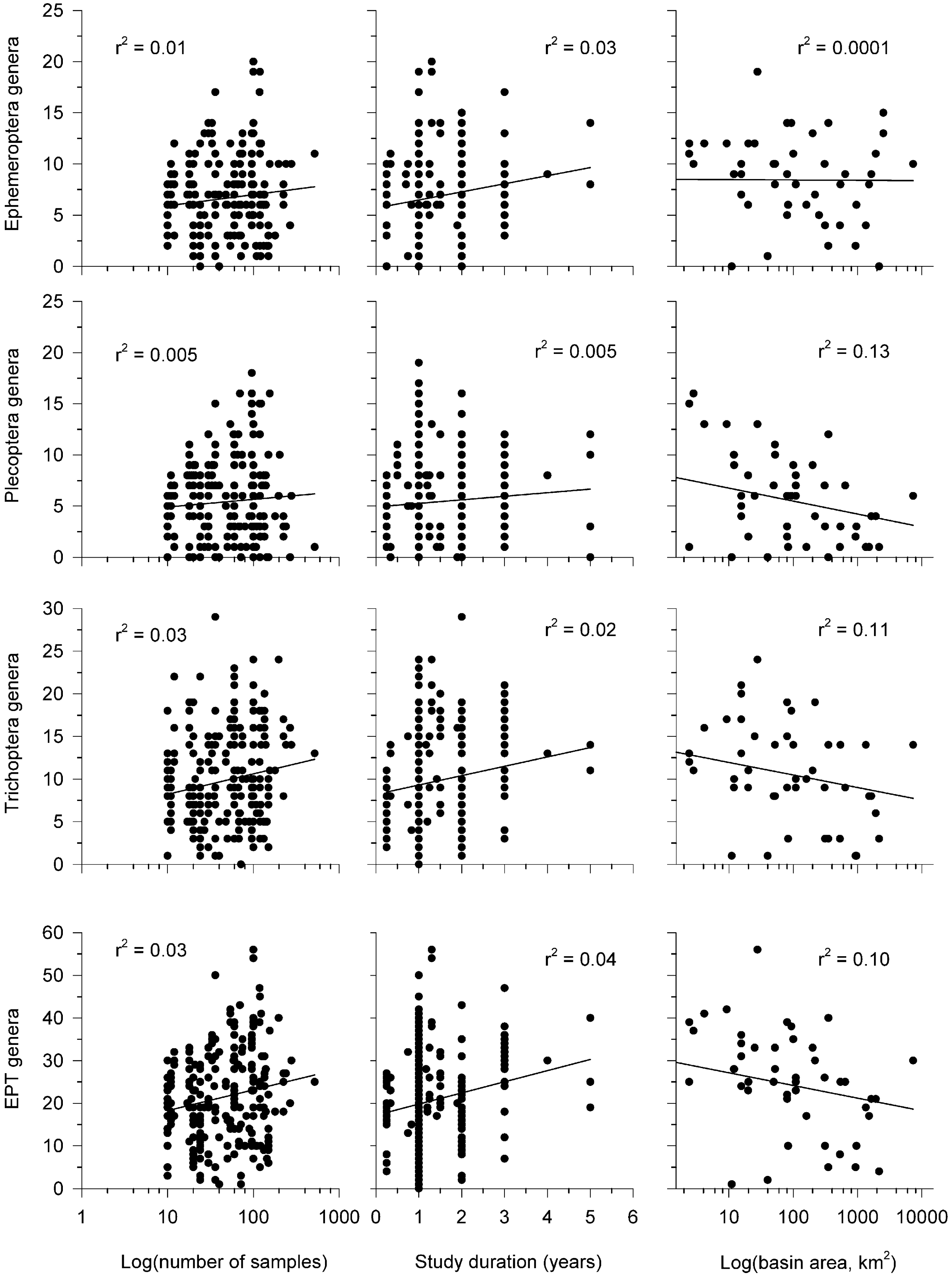

Fig. 4. Relationships between log (number of samples), study duration, and log (basin area) and local genera richness of Ephemeroptera, Plecoptera, Trichoptera, and combined EPT. Although not all relationships were statistically significant, adjusted $r^2$ values estimate the maximum amount of variation in richness that would have been associated with these factors if they were included in analyses of the effects of biogeographic realm and biome.

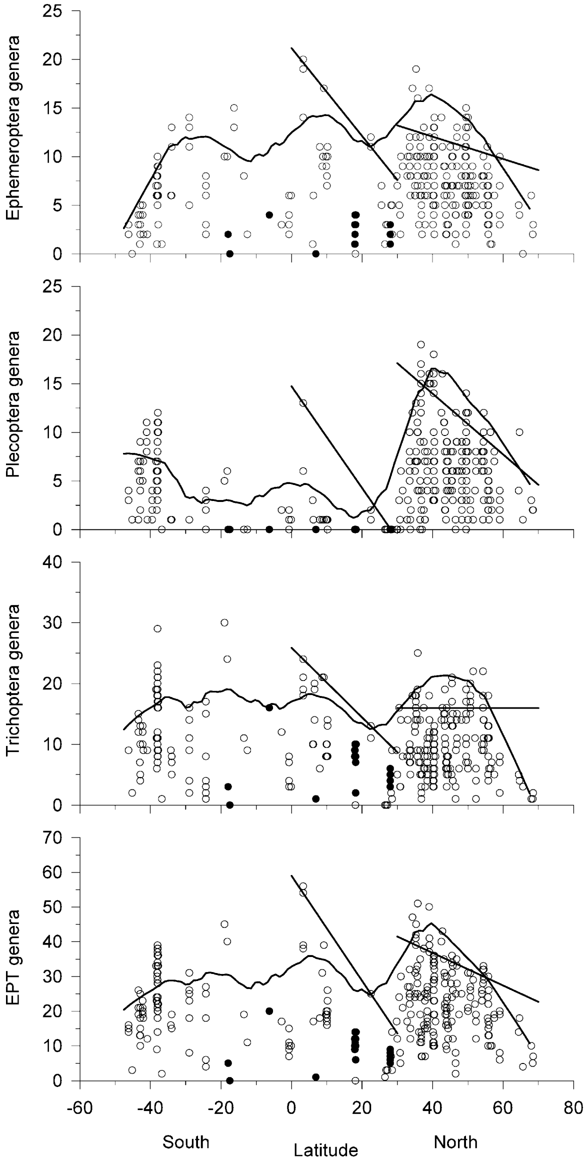

Fig. 5. Relationships between latitude and local Ephemeroptera, Plecoptera, Trichoptera, and combined EPT genera richness. Curved lines were fit using LOWESS regression (tension = 0.5) through maximum genera richness values at 5° latitude intervals. Straight lines are 90th quantile regression estimates for genera richness as functions of latitude for 0–30°N and 30–70°N latitude. For latitudes 0–30°, Ephemeroptera genera richness = 21.2 − 0.5 × latitude, $n = 27$, $p = 0.0686$, Plecoptera genera richness = 14.7 − 0.5 × latitude, $n = 24$, $p = 0.0542$, Trichoptera genera richness = 25.9 − 0.6 × latitude, $n = 27$, $p = 0.1086$, EPT genera richness = 59.0 − 1.5 × latitude, $n = 24$, $p = 0.0542$. For latitudes 30–70°, Ephemeroptera genera richness = 16.7 − 0.1 × latitude, $n = 243$, $p = 0.0625$, Plecoptera genera richness = 26.5 − 0.3 × latitude, $n = 297$, $p = 0.0004$, Trichoptera genera richness = 16.0 − 0.0 × latitude, $n = 213$, $p = 0.5813$, EPT genera richness = 55.6 − 0.5 × latitude, $n = 195$, $p = 0.0086$. ○ = continental streams, ● = island streams.

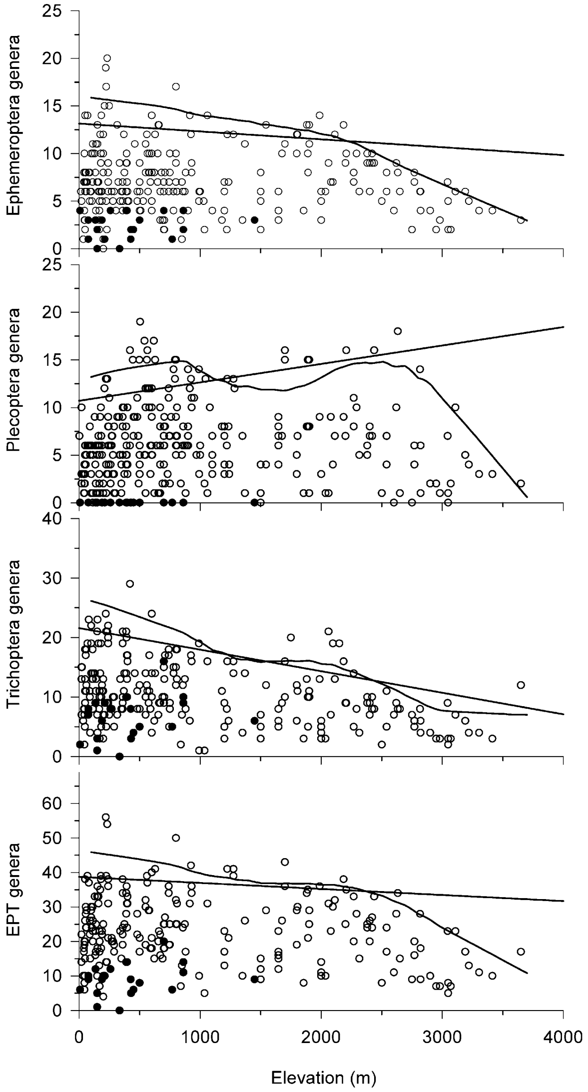

Fig. 6. Relationships between elevation and local Ephemeroptera, Plecoptera, Trichoptera, and combined EPT genera richness. Straight lines are 90th quantile regression estimates for genera as a function of elevation. Curved lines were fitted by LOWESS regression (tension = 0.5) through maximum genera richness values at 200 m intervals. For 90th quantile regressions: Ephemeroptera genera richness = 13.1 − 0.0009 × elevation, $n = 360$, $p = 0.7522$, Plecoptera genera richness = 10.7 + 0.002 × elevation, $n = 424$, $p = 0.0014$, Trichoptera genera richness = 21.6 − 0.004 × elevation, $n = 328$, $p = 0.0207$, EPT genera richness = 38.7 − 0.002 × elevation, $n = 307$, $p = 0.0258$. ○ = continental streams, ● = island streams.

regression showed that maximum Ephemeroptera ($p < 0.001$), Trichoptera ($p < 0.001$), and combined EPT genera richness ($p < 0.001$) decreased with elevation, whereas Plecoptera genera richness increased with elevation ($p < 0.001$). The LOWESS results were generally and qualitatively similar to the quantile regression results but identified two trends in the data not detected by quantile regression. First, the relationships between elevation and maximum richness in Ephemeroptera, Plecoptera, and combined EPT genera richness were nonlinear with a more steep decline in richness at elevations $>2000$–2500 m than observed between 0 and 2000 m. Second, Plecoptera richness appeared to be similar between ca 300 and 2500 m with a steep decline in richness above 2500 m.

### Productivity – disturbance patterns

Both quantile regression and LOWESS showed that richness generally increased over the range of NDVI values (Fig. 7a). Quantile regression detected a significant linear relationship with richness for Plecoptera ($p<0.001$), Trichoptera ($p<0.001$), and combined EPT ($p<0.001$), but not Ephemeroptera ($p=0.166$). However, the LOWESS results implied strong positive relationships between richness and NDVI values with a more marked decrease in richness below NDVI values of ca 0.20–0.35.

Richness of all taxa groups generally declined with increasing CV in monthly precipitation for all orders (Fig. 7b). Quantile regression detected a significant linear decline in richness with CV in precipitation for Plecoptera ($p<0.01$), Trichoptera ($p<0.001$), and combined EPT ($p<0.01$), but not for Ephemeroptera ($p=0.6321$). The LOWESS analyses also revealed negative relationships, but indicated a marked decline in richness for all 3 orders at CV's $>100\%$.

### Variation among biogeographical realms and biomes

Two-factor ANOVAs showed that richness was significantly associated with both biogeographic realm and biome, but the significant interaction term implied that the effect of one was dependent on the other (Table 2). However, F-values for the main effects (realm and biome) were always highest for biome and usually lowest for the interaction term. We interpret this result to mean that although the effects of the two factors cannot be completely separated, regional ecological conditions affected richness more strongly than biogeographic history. Together, biome and realm explained 32–39% of the variation in local stream insect genera richness worldwide, but the amount of variation associated with biome was 47–71% higher than that associated with realm (comparison of mean square terms in Table 2).

Although the multiple range tests revealed few distinct differences between pairs of realms or biomes, some general trends in the mean values were apparent (Table 3). Richness of the three orders generally did not vary similarly across either biogeographical realms or biomes. For example, excluding island faunas, highest Ephemeroptera richness was observed in the Africotropical realm, whereas the lowest richness occurred in the Antarctic (New Zealand) realm. For Plecoptera, highest richness occurred in Neartic streams and lowest richness in Neotropical and Africotropical streams. For Trichoptera, richness was highest in the Australian realm and lowest in the Africotropical realm. Differences among realms in combined EPT richness were subsequently less distinct than for individual orders. All data from the Oceanian realm were from islands, and richness was 2–4 × lower than that on mainland sites for all taxa groups, except Plecoptera, which were completely absent from islands.

Individual sites with high genera richness could be found in all biogeographical realms, but the location of the richest sites varied slightly among orders. Ephemeroptera diversity was highest in Malaysia, Venezuela, central and eastern United States, Brazil, and Poland. Plecoptera diversity was highest in the mountainous regions of the United States, New Zealand, and Japan. Trichoptera diversity was highest in Australia, the Appalachian Mountains of the United States, Malaysia, Venezuela, and England. Combined EPT genera richness was highest in Malaysia, montane regions of the United States, Australia, Japan, and Venezuela.

Patterns were more consistent among the orders across biomes, and there appeared to be a strong association between higher richness and forested landscapes. Streams flowing through broadleaf evergreen forests supported 8–189% more Ephemeroptera, Trichoptera, or combined EPT taxa than did streams flowing through other forested biomes, and streams in desert and tundra streams had between 40 and 85% fewer genera than forested biomes. Variation in Plecoptera genera richness across biomes differed from other orders. In contrast to mayflies and caddisflies, stonefly richness was highest in temperate broadleaf deciduous forests, although stonefly richness was lowest in desert and tundra streams as observed in the other two orders.

## Discussion

### Caveats regarding data and analyses

The interpretation of descriptive and comparative studies is almost always constrained to some extent by problems associated with either the completeness of data or the adequacy of methods used to analyze the data. This study was no exception, in spite of the fact that we compiled a much larger data set than previously examined by others, and we used those statistical models that best fit the distributional properties of the data. The most significant limitation in the data we

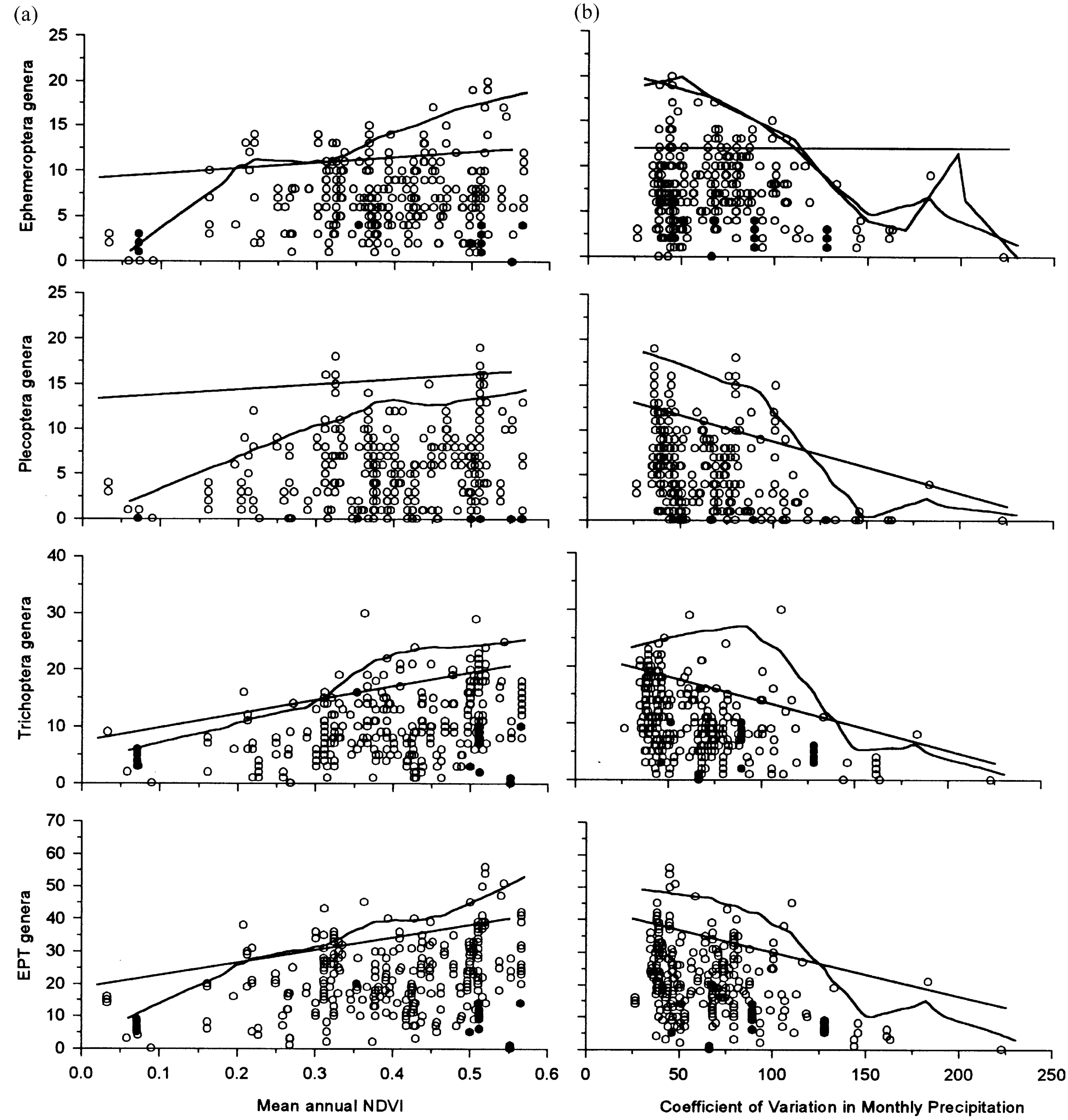

Fig. 7. Relationship between productivity (a) and disturbance (b) and local Ephemeroptera, Plecoptera, Trichoptera, and combined EPT genera richness. Productivity was estimated using mean annual NDVI values and disturbance was estimated using coefficients of variation in monthly precipitation (see text for details). Straight lines are 90th quantile regression estimates for genera as functions of NDVI values or coefficients of variation in monthly precipitation. Curved lines were fitted with LOWESS regression (tension = 0.5) through maximum genera richness values at 0.03 and 20% intervals in NDVI values and coefficients of variation in monthly precipitation. For 90th quantile regressions: Ephemeroptera genera richness = 6.0 + 9.1 × NDVI, n = 360, $p = 0.1656$, Plecoptera genera richness = 5.7 + 13.3 × NDVI, n = 424, $p = 0.0004$, Trichoptera genera richness = 24.3 + 7.4 × NDVI, n = 329, $p < 0.0001$, EPT genera richness = 38.7 + 19.0 × NDVI, n = 307, $p < 0.0001$, Ephemeroptera genera richness = 12.0 – 0.0 × CV precipitation, n = 360, $p = 0.6321$, Plecoptera genera richness = 14.6 + 0.1 × CV precipitation, n = 424, $p = 0.013$, Trichoptera genera richness = 22.5 – 0.1 × CV precipitation, n = 329, $p = 0.0012$, EPT genera richness = 43.8 – 0.1 × CV precipitation, n = 307, $p = 0.0031$. ○ = continental streams, ● = island streams.

Table 2. Results of two-way Type III ANOVA of the effects of biogeographical realm and biome on local continental Ephemeroptera, Plecoptera, Trichoptera and combined EPT genera richness. EPT = Ephemeroptera + Plecoptera + Trichoptera.

| Source | DF | SS | MS | F | p |
|---|---|---|---|---|---|
| Ephemeroptera | | | | | |
| Model | 28 | 1433.22 | 51.19 | 5.61 | 0.0001 |
| Error | 331 | 3018.90 | 9.12 | | |
| Corrected total | 359 | 4452.12 | | | |
| Biogeographical realm | 6 | 228.63 | 38.11 | 4.18 | 0.0005 |
| Biome | 8 | 576.71 | 72.09 | 7.9 | 0.0001 |
| Biogeographical realm × biome | 14 | 284.06 | 20.29 | 2.22 | 0.0069 |
| $R^2 = 0.32$ | | | | | |
| Plecoptera | | | | | |
| Model | 29 | 2386.61 | 82.30 | 7.15 | 0.0001 |
| Error | 394 | 4537.92 | 11.52 | | |
| Corrected total | 423 | 6924.53 | | | |
| Biogeographical realm | 6 | 122.47 | 20.41 | 1.77 | 0.1035 |
| Biome | 8 | 552.84 | 69.11 | 6 | 0.0001 |
| Biogeographical realm × biome | 15 | 846.88 | 56.46 | 4.9 | 0.0001 |
| $R^2 = 0.34$ | | | | | |
| Trichoptera | | | | | |
| Model | 27 | 3936.94 | 145.81 | 6.39 | 0.0001 |
| Error | 301 | 6866.04 | 22.81 | | |
| Corrected total | 328 | 10 802.98 | | | |
| Biogeographical realm | 6 | 792.62 | 132.10 | 5.79 | 0.0001 |
| Biome | 8 | 1999.78 | 249.97 | 10.96 | 0.0001 |
| Biogeographical realm × biome | 13 | 929.73 | 71.52 | 3.14 | 0.0002 |
| $R^2 = 0.36$ | | | | | |
| EPT | | | | | |
| Model | 27 | 13 078.04 | 484.37 | 6.51 | 0.0001 |
| Error | 279 | 20 754.54 | 74.39 | | |
| Corrected total | 306 | 33 832.58 | | | |
| Biogeographical realm | 6 | 2423.87 | 403.98 | 5.43 | 0.0001 |
| Biome | 8 | 7635.47 | 954.43 | 12.83 | 0.0001 |
| Biogeographical realm × biome | 13 | 3190.29 | 245.41 | 3.3 | 0.0001 |
| $R^2 = 0.39$ | | | | | |

Table 3. Local continental least square mean Ephemeroptera, Plecoptera, Trichoptera and combined EPT genera richness in different geographical regions. Significantly different means among continental (non-island) locations determined by the Ryan-Einot-Gabriel-Welsch test (Anon. 1988, $p < 0.0125$) and are identified by different letters. Sample sizes are given in Table 1.

| Factor | Genera richness | | | |
|---|---|---|---|---|
| | Ephemeroptera | Plecoptera | Trichoptera | EPT |
| Biogeographical realm | | | | |
| Africotropical | 9.50 a | 1.00 c | 7.57 b | 18.07 a |
| Antarctica | 2.69 c | 3.81 abc | 9.19 ab | 15.69 a |
| Australian | 6.10 b | 6.04 ab | 14.12 a | 25.94 a |
| Indomalayan | 8.93 ab | 3.88 abc | 10.00 ab | 23.17 a |
| Nearctic | 7.79 ab | 7.12 a | 9.01 ab | 23.12 a |
| Neotropical | 7.44 ab | 2.82 bc | 10.58 ab | 17.83 a |
| Palaearctic | 6.81 ab | 5.72 ab | 10.46 ab | 21.57 a |
| Oceanian, all islands | 1.50 | 0.00 | 5.00 | 6.50 |
| Biome | | | | |
| Broadleaf evergreen forest | 11.06 a | 3.63 ab | 15.38 a | 30.06 a |
| Broadleaf deciduous forest and woodland | 8.67 ab | 8.15 a | 11.03 ab | 27.85 a |
| Mixed coniferous and broadleaf forests | 7.43 abc | 7.25 ab | 10.02 ab | 23.42 a |
| Coniferous forest and woodland | 3.84 bcd | 5.11 ab | 7.10 ab | 16.05 ab |
| Wooded grasslands | 7.08 abc | 4.64 ab | 12.05 ab | 23.00 a |
| Grasslands | 8.49 ab | 6.25 ab | 8.23 ab | 22.88 a |
| Cultivated lands | 6.41 abc | 5.16 ab | 9.14 ab | 18.92 ab |
| Desert shrubs and bare ground | 2.29 cd | 1.19 ab | 2.29 b | 4.57 b |
| Tundra | 0.00 d | 1.00 b | 3.00 b | 4.00 b |

compiled was the paucity of information for streams either near the equator or the poles and for certain biomes. For those regions with low numbers of samples, we are therefore not confident that we adequately characterized either the mean or maximum richness of streams in these areas. This problem also potentially affects any type of "gradient analysis", regardless of the analytical method used, in that real trends can be either obscured or artifactual trends created by the influence of data values that do not adequately describe the real conditions in a region. Problems of interpretation are further constrained by the fact that no statistical models are perfectly suited to the analysis of complex, non-linear trends. Interpretation of analyses must therefore be tempered with these issues in mind.

Although it is clear that certain regions have been understudied, we believe our analyses have provided important insight regarding patterns of global richness in stream insect faunas that have, as yet, not been well described. Below, we offer interpretations of the patterns that emerged from our analyses. Note, that we consider all interpretations as working hypotheses to be further scrutinized and tested as additional data emerges from the understudied regions of the earth. We also point out that one extremely important result of our study is that we have explicitly identified those regions most in need of additional study. Recognition of how little information is available in some regions will hopefully accelerate future work devoted to filling these critical gaps in our knowledge of the earth's stream insect faunas.

## Latitudinal trends

Previous latitudinal comparisons of stream invertebrate assemblages have reported contradictory results with some (Bishop 1973, Stout and Vandermeer 1975, Lake et al. 1986, 1994, Pearson et al. 1986, Benson and Pearson 1987, Jacobsen et al. 1997) reporting higher and others (Hubendick 1962, Patrick 1966, Illies 1969, Stanford and Ward 1983, Zwick 1986, Arthington 1990, Flowers 1991) either lower or similar benthic invertebrate richness in tropical as compared to temperate streams. However, none of these studies was as extensive as this one for latitudinal range, breadth of stream types sampled, or the number of samples collected per richness estimate. Our results show that a simple, monotonic latitudinal gradient does not exist for mayflies, stoneflies, and caddisflies in local maximum richness, except at latitudes > 30° (Fig. 5). The lower richness values near 20–30° and peaks in richness near 30–40°N latitude that we observed (Fig. 5), were remarkably similar to the patterns described for North American regional mammalian and amphibian species richness by Currie (1991), who did not offer an explanation for this pattern. We suggest the overall nonlinear trends that we observed in richness across the latitudinal gradient are likely caused by 2 different climatic phenomena: 1) highly variable hydrologic conditions between 10 and 30°N latitude (Fig. 3) and 2) progressively increasing climatic severity at latitudes > 40°. CV in monthly precipitation may integrate several elements of disturbance or harshness in stream ecosystems, such as frequency and intensity of both flooding and drought (Finlayson and McMahon 1988, Hughes and James 1989, Poff and Ward 1989, Poff 1996, Stanley et al. 1997). If CV in monthly precipitation is a general approximation of disturbance regimes, in terms of both potential high and low water events acting on stream organisms, these results are consistent with most previous descriptive and experimental manipulations in streams that have shown taxa richness to be inversely related to disturbance (Vinson and Hawkins 1998). Shorter ice-free periods and progressively decreasing mean stream temperatures at latitudes > 40° impose increasingly severe constraints on both habitat and food availability, 2 factors that strongly influence the richness of stream invertebrates (Vinson and Hawkins 1998). The tendency for Trichoptera richness to be less variable across latitudes than Plecoptera or Ephemeroptera is likely related to their greater habitat and trophic diversity compared to other aquatic insects (Wiggins and Mackay 1978).

We suspect the contradictory findings of previous studies of latitudinal gradients in aquatic insects are related to small sample sizes, the large variation in within-latitude richness observed here (Fig. 5) and elsewhere (Flowers 1991), and to differences in trends among insect groups. For example, the diversity within aquatic beetles (Coleoptera) (Brown 1981) and dragonflies (Odonata) (Bishop 1973, Williams and Feltmate 1992) appears to be clearly higher in the tropics than temperate regions, whereas Plecoptera diversity appears higher in temperate streams (Fig. 5, also see Illies 1965). Other stream biota, show both higher (fish, Allan and Flecker 1993) and lower (Unionidae: molluscs, Bogan 1993) diversity in the tropics compared with temperate streams. These patterns appear to have less to do with biogeographic dynamics than with environmental tolerances and habitat requirements characteristic of taxa in different groups.

## Elevational trends

Our results support the idea that species richness decreases with increasing elevation (see reviews by Huston 1994, Rahbek 1995). We found little evidence for diversity peaks at intermediate elevations (Rosenzweig 1995, Rahbek 1997, and Lomolino 2001). We suspect that the same factors that cause a decrease in richness at higher latitudes also cause the decline with elevation. Short ice-free periods, low allochthonous inputs, and generally severe habitat conditions at elevations $> 3000$ m limit the number of taxa that can persist at higher elevations (Ward 1994). A slight increase (or lack of decrease) in richness up to 2500 m for Plecoptera supports the generalization that stoneflies are cool water stenotherms, restricted to cooler mountain streams (Hynes 1976, 1988, Baumann 1979, Brittain 1990). However, the precipitous drop in richness at elevations $> 2500$ m implies that many genera in this order are also unable to cope with the severe habitat conditions that occur at the highest elevations.

The high within-elevation variation in richness that we observed is not surprising, because at a global scale, differences in latitude, distance inland from a coastline, and general climate patterns can ameliorate the influence elevation has on habitat factors such as water temperature (Huston 1994, Vinson and Hawkins 1998). Cool streams can be found in higher elevations at low latitudes and at lower elevations at high latitudes. Even within individual basins, abrupt changes in stream insect richness have been observed along elevational gradients as streams cross biomes (Donald and Anderson 1977, Brewin et al. 1995, Carter et al. 1996), zones of hydraulic transition (Statzner and Higler 1986, Petersen and Sangfors 1991), or regions of different land use (Brewin et al. 1995, Carter et al. 1996).

## Productivity-disturbance patterns

Ecosystem productivity, as estimated by a variety of measures such as solar radiation, evapotranspiration, NPP, and precipitation, has frequently explained much of the variance in regional species richness patterns in a number of ecosystems (Wright 1983, Currie and Paquin 1987, Turner et al. 1988, Currie 1991, Wright et al. 1993). At global scales, regional richness typically increases monotonically with measures of energy or productivity (Currie 1991), whereas at regional to local scales, local richness appears more likely to peak at intermediate levels of energy or productivity (Rosenzweig 1992, Wright et al. 1993).

The data we compiled showed that maximum Ephemeroptera, Trichoptera, and combined EPT genera richness increased monotonically with a measure of terrestrial NPP (Fig. 7) with little indication of leveling off, whereas Plecoptera genera richness increased smoothly initially and then appeared to reach a threshold, implying that at higher NPP sites richness was limited by something other than NPP. A threshold energy-richness relationship was observed in North American mammals (Kerr and Packer 1997) and southern Africa's woody flora (O'Brien 1993). Likewise, Guegan et al. (1998) found that broad-scale patterns in local riverine fish diversity were best explained by both energy and habitat complexity. Fish species richness increased with energy, and in areas with similar energy, richness was highest in more heterogenous habitats. These results are generally consistent with our analyses that showed local genera richness increased with NPP, but that large variations in genera richness existed within similar NPP levels, suggesting that other factors, such as local habitat structure, history, or disturbance regime also limit richness in these areas. The lack of an increase in Plecoptera richness at higher NPP levels may be related to their generally overall lower richness in tropical areas where the highest levels of NPP were observed.

Previous work on the effect of disturbance in streams has emphasized the importance of matching disturbance measures to the organisms concerned (Muotka and Vitranen 1995, Poff and Allan 1995, Townsend et al. 1997b). For example, the most appropriate disturbance measure for benthic stream invertebrates is thought to be stream bed movement (Death and Winterbourn 1995, Townsend et al. 1997b), whereas measures of streamflow variability are likely more appropriate for fishes (Horowitz 1978, Poff and Allan 1995). Why local genera richness declined sharply and consistently throughout the range of CV in monthly precipitation is interesting and its explanation is not likely straightforward, especially in light of the fact that mean genera richness in Australia for combined EPT genera was similar to or greater than that observed in the rest of the world, despite the fact that CVs in seasonal and annual streamflow in Australia are about twice that of the rest of the world (Finlayson and McMahon 1988).

If CV in monthly precipitation is a general approximation of disturbance regimes acting on stream invertebrate assemblages, such as flood frequency and intensity and drying aspects of stream ecosystems (Stanley et al. 1997), these results are consistent with most previous descriptive and experimental manipulations in streams that have shown disturbances (defined in a variety of ways) lower stream biota taxa richness (Hoopes 1974, Horowitz 1978, McElravy et al. 1982, Boulton and Suter 1986, Robinson and Minshall 1986, Englund 1991, Reice 1991, Scarsbrook and Townsend 1993, Death and Winterbourn 1995, Erman and Erman 1995, Townsend et al. 1997b). For example, Horowitz (1978) found fish species richness in 15 North American prairie rivers to be strongly and negatively correlated with CV in daily streamflow ($r^2 = 0.84$). Likewise, Death and Winterbourn (1995) found stream invertebrate species richness to be highly negatively correlated ($r^2 = 0.78$) with a multivariate stream habitat stability measure, which included a temporal measure of water current velocity. Conversely, Clausen and Biggs (1997) found the opposite for stream invertebrates in 62 stream sites throughout New Zealand, i.e., they found taxa richness increased with increasing CV in streamflow although the relationship was weak (Spearman correlation coefficient $= 0.28$, $p < 0.05$) and appeared confounded with stream size.

Maximum taxa richness declined consistently throughout the range of CV in monthly precipitation, but there was considerable variation in genera richness within similar disturbance regimes (Fig. 7). The mechanisms underlying different biotic assemblage responses to increasing environmental variability are likely related to local adaptations of the organisms and to differences in how channels respond during floods (Angradi 1996) or low water periods (Stanley et al. 1997). Aquatic invertebrate adaptations to frequently or unpredictably disturbed environments include rapid growth and development, lack of diapause or resting stages, small size, flexible life histories, high adult mobility and longevity, and the near year-around presence of adults available for post-flood oviposition (Gray 1981, Fisher et al. 1982, Lake et al. 1986, Williams and Feltmate 1992, Townsend et al. 1997a, b). Stream insects in Australia appear to have overcome unpredictable environments by having more flexible life histories than northern hemisphere species (Lake et al. 1986).

Nearly all of the streams with the highest CVs in precipitation were located in the desert biome. In addition to having highly variable discharge regimes, desert streams also tend to be isolated and few in number, which may limit colonization by aquatic insects that have poor dispersal abilities in arid landscapes (Andrews and Minshall 1979, Palmer et al. 1996). The data we compiled from sites classified as deserts were truly dry, desolate, and drought-prone places with high CVs in monthly precipitation, such as the southern Sahara in Africa (CVs = 223% and EPT genera = 0) and central Australia (CV = 162% and EPT genera = 6). For comparison, two streams located within the Sonoran Desert, USA, were classified as being in a grassland biome and had CVs in monthly precipitation of 78 and 98% and had 17 and 19 EPT genera.

## Relative importance of historical and ecological factors

If historical factors are largely responsible for the number of taxa observed at a site, then more variation in richness should be associated with biogeographic realm than with differences in environmental conditions occurring within a realm (e.g., biome). Alternatively, if ecological factors largely constrain richness, then the opposite trend should be true and we should observe convergence in community characteristics in geographically isolated streams within similar environmental settings (Schluter and Ricklefs 1993). Biogeographic history is clearly important in structuring the composition of regional species pools for a number of diverse plant and animal groups including stream insects (Ross 1967, Edmunds 1972, Hynes 1988, Wooton 1988), and we found that mayflies, stoneflies, and caddisflies clearly differed in terms of which realm supported the most genera (Fig. 1, Table 3). This result implies that the 3 orders have either been differentially successful at exploiting environmental conditions found in each realm or that they have different biogeographic histories and centers of adaptive radiation. However, the tendency for richness in all 3 orders to be more strongly associated with biome than biogeographical realm implies that local ecological factors may be more important than historical factors in determining local insect richness in streams.

These results also support the idea that the fundamental mechanisms regulating biotic richness are similar across streams (Recher 1969, Fuentes 1976, Cody and Mooney 1978, Ricklefs 1987, Tonn et al. 1990, Ricklefs and Latham 1993). Streams within similar biomes supported similar numbers of taxa without regard to biogeographic realm. This observed similarity in richness among streams worldwide implies that the physical and biological environment of streams has been a strong selective force on stream insects and the adaptive response of stream organisms to those environmental conditions have been similar wherever they occur. This idea is consistent with the observations of well-traveled stream ecologists who have been struck by the remarkable global similarity of streams and stream communities (Hynes 1970).

Describing local and broad-scale biodiversity patterns is critical to determining and understanding the origins and maintenance of biotic diversity, the extent to which results may be generalized to less-studied areas of the world, and the scale at which ecosystems need to be protected and preserved. Our analyses provide a strong empirical foundation on which to base future research that is needed to fill in existing data gaps. Although our analyses resolved some questions regarding how patterns of local richness vary at a global scale, we do not know much about patterns of regional richness in stream insects. Future studies should focus on elucidating the connections between regional and local richness of stream insects and the relative importance of the various mechanisms controlling richness at each spatial scale.

*Acknowledgements* – This work benefited greatly from the generosity of Claudia Cressa, Alex Flecker, Chris Humphrey, Björn Malmqvist, Richard Pearson, and Adriano Sanches Melo who supplied references and unpublished data from out-of-the-way places. Ted Angradi, Todd Crowl, and Jim MacMahon delivered sage guidance throughout and Susan Durham provided statistical consultation. Financial support was provided by the Utah State Univ. Ecology Center.

## References

Allan, J. D. and Flecker, A. S. 1993. Biodiversity conservation in running waters. – Bioscience 43: 32–43.

Andrews, D. A. and Minshall, G. W. 1979. Longitudinal and seasonal distribution of benthic invertebrates in the Little Lost river, Idaho. – Am. Midl. Nat. 102: 225–236.

Angradi, T. R. 1996. Inter-habitat variation in benthic community structure, function, and organic matter storage in 3 Appalachian headwater streams. – J. North Am. Benthol. Soc. 15: 42–63.

Anon. 1988. SAS/STAT user's guide. Release 6.03 ed. – SAS Inst. Cary, NC.

Anon. 1993. Preliminary 1987/88 continental precipitation data sets for ISLSCP on a 1 degree grid based on precipitation gauge measurements. – Global Precipitation Climatology Centre, Offenbach, Germany.

Arthington, A. H. 1990. Latitudinal gradients in insect species richness of Australian lotic systems: a selective review. – Trop. Freshw. Biol. 2: 179–196.

Barnard, P. C. and Biggs, J. 1988. Macroinvertebrates in the catchment streams of Lake Naivasha, Kenya. – Rev. Hydrobiol. Trop. 21: 127–134.

Baumann, R. W. 1979. Nearctic stonefly genera as indicators of ecological parameters (Plecoptera: Insecta). – Great Basin Nat. 39: 241–244.

Benson, L. J. and Pearson, R. G. 1987. Drift and upstream movement in Yuccabine Creek, an Australian tropical stream. – Hydrobiologia 153: 225–239.

Bishop, J. E. 1973. Limnology of a small Malayan river Sungai Gombak. – Dr. W. Junk, The Hague.

Bogan, A. E. 1993. Freshwater bivalve extinctions (Mollusca: Unionoida): a search for causes. – Am. Zool. 33: 599–609.

Boulton, A. J. and Suter, P. J. 1986. Ecology of temporary streams – an Australian perspective. – In: DeDeckker, P. and Williams, W. D. (eds), Limnology in Australia. CSIRO and Dr. W. Junk, Melbourne and Dordrecht, pp. 311–327.

Box, E. O., Holben, B. N. and Kalb, V. L. 1989. Accuracy of a vegetation index as predictor of biomass, primary production, and net CO2 flux. – Vegatatio 80: 71–89.

Brewin, P. A., Newman, T. M. L. and Ormerod, S. J. 1995. Patterns of macroinvertebrate distribution in relation to altitude, habitat structure and land use in streams of the Nepalese Himalaya. – Arch. Hydrobiol. 135: 79–100.

Brittain, J. E. 1990. Life history strategies in Ephemeroptera and Plecoptera. – In: Campbell, J. C. (ed.), Mayflies and stoneflies. Kluwer, pp. 1–12.

Brown, H. P. 1981. A distributional survey of the world genera of aquatic dryopoid beetles (Coleoptera: Dryopidae, Elmidae, and Psephenidae sens. LAT.). – Pan-Pac. Entomol. 57: 133–148.

Brown, J. H. and Gibson, A. C. 1983. Biogeography. – C.V. Mosby, St. Louis, MO, USA.

Cade, B. S., Terrell, J. W. and Schroeder, R. L. 1999. Estimating effects of limiting factors with regression quantiles. – Ecology 80: 311–323.

Caley, M. J. and Schluter, D. 1997. The relationship between local and regional diversity. – Ecology 78: 70–80.

Carter, J. L., Fend, S. V. and Kennelly, S. S. 1996. The relationships among three habitat scales and stream benthic invertebrate community structure. – Freshw. Biol. 35: 109–124.

Clausen, B. and Biggs, B. J. F. 1997. Relationships between benthic biota and hydrological indices in New Zealand streams. – Freshw. Biol. 38: 327–342.

Cleveland, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. – J. Am. Stat. Assoc. 74: 829–836.

Cody, M. L. and Mooney, H. A. 1978. Convergence versus nonconvergence in Mediterranean-climate ecosystems. – Annu. Rev. Ecol. Syst. 9: 265–321.

Colwell, R. K. 1974. Predictability, constancy, and contingency of periodic phenomena. – Ecology 55: 1148–1153.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. – Science 199: 1302–1310.

Cornell, H. V. 1993. Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities. Univ. of Chicago Press, pp. 243–252.

Cornell, H. V. and Lawton, J. H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. – J. Anim. Ecol. 61: 1–12.

Cornell, H. V. and Karlson, R. H. 1996. Species richness of reef-building corals determined by local and regional processes. – J. Anim. Ecol. 65: 233–241.

Covich, A. P. 1988. Geographical and historical comparisons of neotropical streams: biotic diversity and detrital processing in highly variable habitats. – J. North Am. Benthol. Soc. 7: 361–386.

Currie, D. J. 1991. Energy and large patterns of animal- and plant-species richness. – Am. Nat. 137: 27–49.

Currie, D. J. and Paquin, V. 1987. Large-scale biogeographical patterns of species richness of trees. – Nature 329: 326–327.

Death, R. G. and Winterbourn, M. J. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. – Ecology 76: 1446–1460.

Defries, R. S. and Townshend, J. R. G. 1994. NDVI-derived land cover classifications at a global scale. – Int. J. Rem. Sens. 15: 3567–3586.

Dodds, W. K. 1997. Distribution of runoff and rivers related to vegetative characteristics, latitude, slope: a global perspective. – J. North Am. Benthol. Soc. 16: 162–168.

Donald, D. B. and Anderson, R. S. 1977. Distribution of the stoneflies (Plecoptera) of the Waterton River drainage, Alberta, Canada. – Syesis 10: 111–120.

Edmunds Jr, G. F. 1972. Biogeography and evolution of Ephemeroptera. – Annu. Rev. Entomol. 17: 21–42.

Englund, G. 1991. Effects of disturbance on stream moss and invertebrate community structure. – J. North Am. Benthol. Soc. 10: 143–153.

Erman, N. A. and Erman, D. C. 1995. Spring permanence, Trichoptera species richness, and the role of drought. – J. Kans. Entomol. Soc. 68: 50–64.

Finlayson, B. L. and McMahon, T. A. 1988. Australia v. the world: a comparative analysis of streamflow characteristics. – In: Warner, R. F. (ed.), Fluvial geomorphology of Australia. Academic Press, pp. 17–40.

Fisher, S. G. et al. 1982. Temporal succession in a desert stream ecosystem following flash flooding. – Ecol. Monogr. 52: 93–110.

Flowers, R. W. 1991. Diversity of stream-living insects in northwestern Panama. – J. North Am. Benthol. Soc. 10: 322–334.

Fuentes, E. R. 1976. Ecological convergence of lizard communities in Chile and California. – Ecology 57: 3–17.

Goward, S. N. and Dye, D. G. 1987. Evaluating North American net primary productivity with satellite observations. – Adv. Space Res. 7: 165–174.

Gray, L. J. 1981. Species composition and life histories of aquatic insects in a lowland Sonoran desert stream. – Am. Midl. Nat. 106: 229–242.

Guegan, J. F., Lek, S. and Oberdorff, T. 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. – Nature 391: 382–384.

Hoopes, R. L. 1974. Flooding, as the result of hurricane Agnes, and its effect on a macrobenthic community in an infertile headwater stream in central Pennsylvania. – Limnnol. Oceanogr. 19: 853–857.

Horowitz, R. J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. – Ecol. Monogr. 48: 307–321.

Hubendick, B. 1962. Aspects on the diversity of the fresh-water fauna. – Oikos 13: 249–261.

Hughes, J. M. R. and James, B. 1989. A hydrological regionalization of streams in Victoria, Australia, with implications for stream ecology. – Aust. J. Mar. Freshwat. Res. 40: 303–326.

Hugueny, B. et al. 1997. The relationship between local and regional species richness: comparing biotas with different evolutionary histories. – Oikos 80: 583–587.

Huston, M. A. 1994. Species diversity: the coexistence of species on changing landscapes. – Cambridge Univ. Press.

Hynes, H. B. N. 1970. The ecology of running waters. – Univ. of Toronto Press.

Hynes, H. B. N. 1976. Biology of Plecoptera. – Annu. Rev. Entomol. 21: 135–153.

Hynes, H. B. N. 1988. Biogeography and origins of the North American stoneflies (Plecoptera). – Mem. Entomol. Soc. Can. 144: 31–37.

Hynes, H. B. N. and Williams, T. R. 1962. The effect of DDT on the fauna of a central African stream. – Ann. Trop. Med. Parisitol. 56: 78–91.

Hynes, J. D. 1975. Annual cycles of macro-invertebrates of a river in southern Ghana. – Freshw. Biol. 5: 71–83.

Illies, J. 1964. The invertebrate fauna of the Huallaga, a Peruvian tributary of the Amazon River, from the sources down to Tingo Maria. – Int. Vereinigung fur Theoretische und Angewandte Limnol. 15: 1077–1083.

Illies, J. 1965. Phylogeny and zoogeography of the Plecoptera. – Annu. Rev. Entomol. 10: 117–140.

Illies, J. 1969. Biogeography and ecology of neotropical freshwater insects, especially those from running waters. – In: Fittkau, E. J. et al. (eds), Biogeography and ecology in South America. Dr. W. Junk, The Hague, pp. 685–708.

Jacobsen, D., Schultz, R. and Encalada, A. 1997. Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. – Freshw. Biol. 38: 247–261.

Karlson, R. H. and Cornell, H. V. 1998. Scale-dependent variation in local vs. regional effects on coral species richness. – Ecol. Monogr. 68: 259–274.

Kerr, J. T. and Packer, L. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy areas. – Nature 385: 252–254.

Lake, P. S. et al. 1986. Australian streams and Northern Hemisphere stream ecology: comparisons and problems. – Proc. Ecol. Soc. Aust. 14: 61–82.

Lake, P. S. et al. 1994. Species richness in streams: patterns over time, with stream size and with latitude. – Int. Vereinigung fur Theoretische und Angewandte Limnol. 25: 1822–1826.

Latham, R. E. and Ricklefs, R. E. 1993. Continental comparisons of temperate-zone tree species diversity. – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities. Univ. of Chicago Press, pp. 294–314.

Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. – Global Ecol. Biogeogr. 10: 3–13.

Los, S. O., Justice, C. O. and Tucker, C. J. 1994. A global $1 \times 1$ degree NDVI data set for climate studies derived from the GIMMS continental NDVI data. – Int. J. Rem. Sens. 15: 3493–3518.

Lugo, A. E. and Brown, S. 1991. Comparing tropical and temperate forests. – In: Cole, J. J. et al. (eds), Comparative analyses of ecosystems: patterns, mechanisms, and theories. Springer.

MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. – Am. Nat. 98: 387–397.

McElravy, E. P., Wolda, H. and Resh, V. H. 1982. Seasonality and annual variability of caddisfly adults (Trichoptera) in a "non-seasonal" tropical environment. – Arch. Hydrobiol. 94: 302–317.

McGowan, J. A. and Walker, P. W. 1993. Pelagic diversity patterns. – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities. Univ. of Chicago Press, pp. 203–214.

Meeson, B. W. et al. 1995. ISLSCP Initiative 1 – Global data sets for land-atmosphere models, 1987-1988. Vol. 1-5. – Published on CD by NASA.

Minshall, G. W. 1988. Stream ecosystem theory: a global perspective. – J. North Am. Benthol. Soc. 7: 263–288.

Muotka, T. and Vitranen, R. 1995. The stream as a habitat templet for bryophytes: species' distributions along gradients in disturbance and substratum heterogeneity. – Freshw. Biol. 33: 141–160.

Oberdorff, T., Guegan, J. F. and Hugueny, B. 1995. Global species patterns of fish species richness in rivers. – Ecography 18: 345–352.

Oberdorff, T., Guegan, J. F. and Hugueny, B. 1997. Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between western Europe and North America. – J. Biogeogr. 24: 461–467.

O'Brien, E. M. 1993. Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. – J. Biogeogr. 20: 181–198.

Paine, R. T. 1966. Food web complexity and species diversity. – Am. Nat. 100: 65–75.

Palmer, M. A., Allan, J. D. and Butman, C. A. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. – Trends Ecol. Evol. 11: 322–326.

Patrick, R. 1966. The Catherwood foundation Peruvian-Amazon expedition. – Monogr. Acad. Nat. Sci. Philadelphia 14: 5–40.

Pearson, R. G., Benson, L. J. and Smith, R. E. W. 1986. Diversity and abundance of the fauna in Yuccabine creek, a tropical rainforest stream. – In: DeDeckker, P. and Williams, W. D. (eds), Limnology in Australia. CSIRO and Dr. W. Junk, Melbourne and Dordrecht, pp. 329–342.

Perry, J. A. and Schaeffer, D. A. 1987. The longitudinal distribution of riverine benthos: a river dis-continuum? – Hydrobiologia 148: 257–268.

Petersen Jr, R. C. and Sangfors, O. 1991. An extreme example of the role of fluvial hydraulics and the structure of large river ecosystems: the Rio Bio Bio, Chile. – Int. Vereinigung fur Theoretische und Angewandte Limnol. 24: 2086–2090.

Poff, N. L. 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. – Freshw. Biol. 36: 71–91.

Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. – J. North Am. Benthol. Soc. 16: 391–409.

Poff, N. L. and Ward, J. V. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. – Can. J. Fish Aquat. Sci. 46: 1805–1818.

Poff, N. L. and Allan, J. D. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. – Ecology 76: 606–627.

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? – Ecography 18: 200–205.

Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in neotropical birds. – Am. Nat. 149: 875–902.

Recher, H. F. 1969. Bird species diversity and habitat diversity in Australia and North America. – Am. Nat. 103: 75–80.

Reice, S. R. 1991. Effects of experimental spates on benthic community structure in New Hope Creek, North Carolina, USA. – Int. Vereinigung fur Theoretische und Angewandte Limnol. 24: 1691–1693.

Ricklefs, R. E. 1980. Latitudinal patterns in seasonality and year-to-year variation in climate. – Caribbean J. Sci. 15: 183–197.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. – Science 235: 167–171.

Ricklefs, R. E. and Latham, R. E. 1993. Global diversity patterns in mangrove floras. – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities. Univ. of Chicago Press, pp. 215–219.

Ricklefs, R. E. and Schluter, D. (eds) 1993a. Species diversity in ecological communities. – Univ. of Chicago Press.

Ricklefs, R. E. and Schluter, D. 1993b. Species diversity: regional and historical influences. – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities. Univ. of Chicago Press, pp. 350–363.

Robinson, C. T. and Minshall, G. W. 1986. Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. – J. North Am. Benthol. Soc. 5: 237–248.

Rosenzweig, M. L. 1992. Species diversity gradients: we know more and less than we thought. – J. Mammal. 73: 715–730.

Rosenzweig, M. L. 1995. Species diversity in space and time. – Cambridge Univ. Press.

Rosenzweig, M. L. and Abramsky, Z. 1993. How are diversity and productivity related? – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities. Univ. of Chicago Press, pp. 52–65.

Ross, H. H. 1967. The evolution and past dispersal of the Trichoptera. – Annu. Rev. Entomol. 12: 169–206.

Scarsbrook, M. R. and Townsend, C. R. 1993. Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. – Freshw. Biol. 29: 395–410.

Schluter, D. 1986. Tests for similarity and convergence of finch communities. – Ecology 67: 1073–1085.

Schluter, D. and Ricklefs, R. E. 1993. Convergence and the regional component of species diversity. – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities. Univ. of Chicago Press, pp. 230–240.

Sellers, P. J. 1985. Canopy reflectance, photosynthesis and transpiration. – Int. J. Rem. Sens. 6: 1335–1372.

Sellers, P. J. et al. 1994. A global 1 by 1 NDVI data set for climate studies. Part 2: the generation of global fields of terrestrial biophysical parameters from NDVI. – Int. J. Rem. Sens. 17: 3519–3545.

Sellers, P. J. et al. 1995. An overview of ISLSCP initiative 1 – global data sets. ISLSCP initiative I global data sets for land-atmosphere models, 1987–88. Vol. 1-5. – Published on CD by NASA.

Sellers, P. J. et al. 1996. A revised land surface parameterization (SiB2) for atmospheric GCMs. Part II: the generation of global fields of terrestrial biophysical parameters from satellite data. – J. Clim. 9: 706–737.

Stanford, J. A. and Ward, J. V. 1983. Insect species diversity as a function of environmental variability and disturbance in stream systems. – In: Barnes, J. R. and Minshall, G. W. (eds), Stream ecology: application and testing of general ecological theory. Plenum Press, pp. 265–278.

Stanley, E. H., Fisher, S. G. and Grimm, N. B. 1997. Ecosystem expansion and contraction in streams. – Bioscience 47: 427–435.

Statzner, B. and Higler, B. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. – Freshw. Biol. 16: 127–139.

Stout, J. and Vandermeer, J. 1975. Comparison of species richness for stream-inhabiting insects in tropical and mid-latitude streams. – Am. Nat. 109: 263–280.

Thomson, J. D. et al. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. – Ecology 77: 1698–1715.

Tonn, W. M. 1990. Climate change and fish communities: a conceptual framework. – Trans. Am. Fish. Soc. 119: 337–352.

Tonn, W. M. et al. 1990. Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. – Am. Nat. 136: 345–375.

Townsend, C. R., Doledec, S. and Scarsbrooks, M. R. 1997a. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. – Freshw. Biol. 37: 367–387.

Townsend, C. R., Scarsbrook, M. R. and Doledec, S. 1997b. Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. – J. North Am. Benthol. Soc. 16: 531–544.

Trexler, J. C. and Travis, J. 1993. Nontraditional regression analyses. – Ecology 74: 1629–1637.

Tucker, C. J. et al. 1986. The relationship of global green leaf area biomass to atmospheric CO2 concentration. – Nature 319: 195–199.

Turner, J. R. G., Lennon, J. J. and Lawerson, J. A. 1988. British bird species distributions and the energy theory. – Nature 335: 539–541.

Udvardy, M. D. F. 1975. A classification of the biogeographical provinces of the world. – Int. Union for Conserv. of Nature and Natural Resour. Occas. Pap. No. 18, Morges, Switzerland.

Vinson, M. R. 1998. Global patterns in stream insect taxa richness. – Ph.D. thesis, Utah State Univ.

Vinson, M. R. and Hawkins, C. P. 1998. Biodiversity of stream insects: variation at local, basin, and regional scales. – Annu. Rev. Entomol. 43: 271–293.

Wallace, A. R. 1876. The geographical distribution of animals. Vol. 2. – Macmillian.

Ward, J. V. 1994. Ecology of alpine streams. – Freshw. Biol. 32: 277–294.

Wiggins, G. B. and Mackay, R. J. 1978. Some relationships between systematics and trophic ecology in nearctic aquatic insects, with special reference to Trichoptera. – Ecology 59: 1211–1220.

Williams, D. D. and Feltmate, B. W. 1992. Aquatic insects. – CAB International, Wallingford, U.K.

Williams, T. R. and Hynes, H. B. N. 1971. A survey of the fauna of streams on Mount Elgon, East Africa, with special reference to Simuliidae (Diptera). – Freshw. Biol. 1: 227–248.

Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. – Oikos 41: 496–506.

Wright, D. H., Currie, D. J. and Maurer, B. A. 1993. Energy supply and patterns of species richness on local and regional scales. – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities. Univ. of Chicago Press, pp. 66–74.

Wooton, R. J. 1988. The historical ecology of aquatic insects: an overview. – Paleogeogr. Paleoclimatol. Paleoecol. 62: 477–492.

Zwick, P. 1986. The Bornean species of the stonefly genus Neoperla (Plecoptera:Perlidae). – Aquat. Insects 8: 1–53.