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Empirical Relationships between Species Richness, Evenness, and Proportional Diversity

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ABSTRACT: Diversity (or biodiversity) is typically measured by a species count (richness) and sometimes with an evenness index; it may also be measured by a proportional statistic that combines both measures (e.g., Shannon-Weiner index or H'). These diversity measures are hypothesized to be positively and strongly correlated, but this null hypothesis has not been tested empirically. We used the results of Caswell's neutral model to generate null relationships between richness (S), evenness (J'), and proportional diversity (H'). We tested predictions of the null model against empirical relationships describing data in a literature survey and in four individual studies conducted across various scales. Empirical relationships between log S or J' and H' differed from the null model when <10 species were tested and in plants, vertebrates, and fungi. The empirical relationships were similar to the null model when >10 and <100 species were tested and in invertebrates. If >100 species were used to estimate diversity, the relation between log S and H' was negative. The strongest predictive models included log S and J'. A path analysis indicated that log S and J' were always negatively related, that empirical observations could not be explained without including indirect effects, and that differences between the partials may indicate ecological effects, which suggests that S and J' act like diversity components or that diversity should be measured using a compound statistic.

Keywords: diversity, biodiversity, evenness, richness, path analysis, species density.

Diversity is a community attribute related to stability, productivity, trophic structure (McIntosh 1967; McNaughton 1977; Tilman 1996), and migration (Wisheu and Keddy 1996; Caley and Schluter 1997; Colwell and Lees 2000). However, the way we measure diversity presumes the importance of species richness compared to species relative abundance, the nature of relationships between richness and abundance, and possibly whether communities are open or closed.

Species richness, or the number of species, is currently the most widely used diversity measure. Relative species abundance in a community is another factor that affects diversity (Whittaker 1965; Hurlbert 1971). It is measured with a standardized index of species abundance (evenness or equitability) that is typically on a scale ranging from near 0, which indicates low evenness or high single-species dominance, to 1, which indicates equal abundance of all species or maximum evenness (Routledge 1980; Alatalo 1981). Finally, proportional abundance indices such as the Shannon-Weiner index sum species weighted by their relative abundance (Magurran 1988). These indices depend on both species richness and evenness, although they weight rare species differently (Hill 1973). Diversity can be measured in other ways (Magurran 1988), but authors have long argued that species abundance and proportional diversity are simply and directly related to species richness (Sanders 1968; Johnson and Raven 1970; Fager 1972; Hill 1973; Alatalo 1981; Schluter and Ricklefs 1993; Huston 1994).

Analytic arguments, mathematical models, and simulations indicate that relationships between species richness, evenness, and proportional diversity are simple, positive, and strong. De Benedictis (1973) first argued that mathematical relationships constrain correlations between species richness (S), an evenness measure (J'), and proportional abundance (measured by the Shannon-Weiner index H') to be positive and strong. De Benedictis pointed out that these mathematical relationships are the null model, against which the influence of empirical, biological effects should be tested. Hill (1973) extended this idea by arguing that diversity is fundamentally the number of species in a community and that other diversity measures comprise a related, higher-order series. Furthermore, May (1975) derived positive relationships between S, J', and H' while assuming species abundance was either log normal or log-series distributed. Patterns of species abundance were regularly observed to follow these distributions (May 1975; Magurran 1988), which suggests that species richness is a common cause of...
variation in relative abundance and diversity. Consequently, it does not seem remarkable that species richness is currently used as the sole measure of diversity in many reviews (e.g., Ricklefs and Schluter 1993; Harper and Hawksworth 1994; Barthlott and Winiger 1998; McKinney and Drake 1998) and the independent variable in experimental diversity studies (e.g., Naeem et al. 1994; Tilman 1996; Allison 1999; Hector et al. 1999), even though other studies indicate that richness and evenness may be independent.

Simulations suggest that some evenness indices may be independent of species richness across a range of values (Sheldon 1969; Smith and Wilson 1996). Furthermore, diversity indices do vary independently of species richness in the laboratory (Hairston et al. 1968; Rainey and Travisano 1998) and in field experiments (McNaughton 1977; Wilsey and Potvin 2000). These studies indicate that diversity can change with key ecological processes such as competition, predation, and succession, each of which alter proportional diversity through changes in evenness without any change in species richness. Consequently, many authors suggest that we should treat richness and evenness separately (Whittaker 1965; Tramer 1969; Hurlbert 1971; Magurran 1988; Legendre and Legendre 1998; Weiher and Keddy 1999). This separation does provide meaningful insight into community function (McNaughton 1977) and may address critical assumptions in experimental analyses of diversity change (Huston 1997; Wilsey and Potvin 2000), but it assumes that factor interrelations are unimportant.

The sign and strength of relationships between different diversity measures are assumptions that are largely based on simulations, models, and analytical work. In the following study, our objective is to test whether or not empirical estimates of richness, evenness, and proportional diversity are strongly, positively, and highly interrelated. Alternatively, species richness and evenness may be independent, or variation in significant relationships may be due to ecological effects. It may not be possible to specify exact, expected values for $S$, $J$, and $H$ (De Benedictis 1973), but a null model can be used as a benchmark against which empirical parameters can be tested. We use the published values of Caswell’s (1976) neutral model to provide expected (null) relationships between $S$, $J$, and $H$ (De Benedictis 1973). In the neutral model, migration (species richness) largely governs $J$ and $H$, whereas scale (e.g., alpha, beta, or gamma diversities) and biotic interactions (e.g., competition or predation) do not affect these variables.

Methods

The Neutral Model as a Null Hypothesis

The number of species depends on time available for immigration in the neutral model. Species population size is the result of a stochastic process in which the expected birth rate equals the expected death rate (Caswell 1976). Thus, model values are generated in the absence of environmental effects, biotic interactions, spatial or temporal variation, or higher-order complexity (Caswell 1976). Caswell’s published results were used to generate the expected univariate relationships and the multiple-regression model. Since our diversity estimates come from a range of communities with different genetic backgrounds and because these communities are under different environmental constraints and sampled with different strategies or effort, empirical trends should regress to averages generated by Caswell’s neutral model if these variables are constrained to be strongly and positively related.

Caswell’s (1976) neutral model generates strong positive correlations between species richness ($S$), evenness ($J$), and proportional diversity ($H$); this is similar to the results obtained by De Benedictis (1973). We log transformed $S$ so that it was on the same scale as $H$ and $J$ (Alatalo 1981). These log-transformed, first-order models account for the same proportion of variation explained by corresponding second-order (polynomial) regressions that use the non-transformed values of $S$. More importantly, extrapolation from a first-order model is not as uncertain as extrapolation from a second-order model. The first-order predictive models relating log-transformed species richness ($\log S$) or $J$ to $H$ are positive, highly significant, and explain most of the variation in $H'$ ($H' = 0.96 + 0.75 \times \log S$; $r^2 = 0.96$, $F = 475.9$, df = 1, 22, $P < .0001$; $H' = -2.56 + 6.62 \times J$; $r^2 = 0.91$, $F = 222.6$, df = 1, 22, $P < .0001$). Finally, the slope of the regression of $H'$ on $\log S$ (mean ± SE; $0.75 \pm 0.04$) should be the same as the average value of $J$ ($J' = H'/H'_{\text{max}} = H'/\log S$). The 95% confidence limits of the slope enclose the mean value of $J$ ($0.73 \pm 0.03$), which indicates that results of the neutral model also fit the analytic expectation that $\log S$, $H'$, and $J'$ are positively and directly related. The multiple-regression model (which uses $\log S$ and $J'$ as independent variables) is highly significant and explains almost all of the variation in $H'$ ($H' = -1.8 + 2.83 \times J' + 0.47 \times \log S$; $R^2 = 0.99$, $F = 1,185.94$, df = 2, 21, $P < .0001$). Although the residual distribution of this model is not significantly different from normal (Shapiro-Wilk $W$-test = 0.92, $P = .08$), it is U-shaped with a minimum near $H' = 2$ and a maximum at the lowest and highest values of $H'$. This distribution suggests a bias in the model, so both $J'$ and $\log S$ were transformed (squared), and the model was recalculated. There was no evidence of a bias in the distribution of residuals in the model with the independent parameters squared, and both multiple-regression models had similar multiple coefficients of determination (parameters squared: $H' = -0.03 + 2.05 \times J' + 0.06 \times \log S^2$; $R^2 = 0.99$, $F = 8166.6$, df = 2, 21, $P > .0001$).
used this transformed model even though bias indicated by the residual variation did not appear to have a strong effect on the model strength. Evenness \( J' \) and log \( S \) are highly correlated \( (r = 0.89, P < .0001) \), which suggests that these parameters may be collinear, but we could not detect related variance inflation.

**Data Sources**

We compiled diversity estimates from a computer literature search (1994–1997). To be included in the search, articles had to have the words “evenness” or “equitability” and “species number,” “richness,” or their derivatives in the title, abstract, or keywords. We compiled these statistics from journals in the collections of the Smithsonian Tropical Research Institute (Balboa, Panama) and McGill University (table 1).

A second data set was analyzed based on individual articles chosen from older, published data sets. To be included, data either had to have had a different species number range or they had to have been collected over different scales (e.g., local, regional, biogeographical, or temporal).

**Tests**

We performed two tests on the first data set (size range and taxonomic categories). First, if diversity components are simply and positively related to the number of species \( (S) \), we would expect that these relationships would be consistent across the range of species numbers used to estimate diversity. To estimate diversity, we divided the data set into three groups: low \( (\leq 10) \), intermediate \( (10 < S < 100) \), and high \( (S \geq 100) \) numbers of species. Each group was then tested against the null model. Second, while diversity is measured using different numbers of species, it is generally estimated within guilds, functional groups, or trophic levels. Consequently, we recast the survey data into four broad taxonomic categories and reran the analysis with the expectation that relationships within taxa, between \( S, J', \) and \( H' \), would be similar to the null model, assuming mathematical relationships between these variables constrained them to be positively and strongly related.

**Results**

**Overall Relationships**

In the 5-yr literature survey, there were 486 estimates of \( S \) and \( H' \); however, we could verify estimates of \( J' \) in only 339 of these cases. There were estimates for all three indices in 323 of these cases. Consequently, for the following multivariate analyses, the sample size was smaller than the sample size used for the univariate tests. However, we compared the univariate coefficients generated using the multivariate data set as an internal check on the sensitivity of the univariate relationship between log \( S \) or \( J' \) and \( H' \) to differences in sample size. For the entire data set \( (n = 486; \) hereafter “complete”), the average \( H' \) estimate was \( 1.95 \pm 0.05 \), and the average number of species was \( 31 \pm 2.01 \). The mean \( H' \) of the restricted data set \( (n =

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<table>
<thead>
<tr>
<th>Data set</th>
<th>Taxa</th>
<th>Study</th>
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<tbody>
<tr>
<td>1</td>
<td>Plants</td>
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</tr>
<tr>
<td>2</td>
<td>Invertebrates</td>
<td>Greenberg and Thomas (1995)</td>
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<tr>
<td>3</td>
<td>Fungi</td>
<td>Hendrix et al. (1995)</td>
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<td>4</td>
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<td>Nunnex-Olivera et al. (1995)</td>
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<td>Savage and Beaumont (1997)</td>
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<td>Coleman et al. (1997)</td>
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<td>Pinca and Dallot (1997)</td>
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<td>43</td>
<td>Invertebrates</td>
<td>Cutter et al. (1994)</td>
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</table>
323; hereafter “restricted”) was not significantly different (1.91 ± 0.07), and the average number of species did not change significantly (31.6 ± 2.1).

We entered log S and J’ into the multiple-regression model developed above (H’ = log S + J’ + e) to evaluate the combined influence of both diversity components on H’. In the null model, squaring the independent parameters reduced the bias indicated by the U-shaped residual distribution but did not affect the parameter or model significance (H’ = −0.24 + 2.2J’2 + 0.06 × log S). Both S and J’ had highly significant univariate effects on H’ in the restricted data set (table 2). The multiple coefficient of determination was highly significant overall and was higher than either univariate model (table 2). Log S and J’ were significantly intercorrelated, but this correlation was not high (table 2), which suggests that they were at least partially independent (Slinker and Glantz 1985; Neter et al. 1996). As in the null model, the empirical multiple-regression model explained most variation in H’. However, in contrast to the null model, there was a much larger difference between the multiple coefficient of determination (R2) of the empirical data and the proportion of variation explained by the univariate relationship between log S and H’ (table 2).

Species-Richness Range

Low-Group Univariate Relationships. Relationships between log S or J’ and H’ were very different from what we expected. We calculated the regression of H’ on log S (<10) with and without the high-diversity outliers (fig. 1A). The outliers did not have a significant effect on this relationship, so they were removed and were analyzed separately. The relationship between log S and H’ is significant, although the slope is close to 0 (fig. 1A; r2 = 0.08, F = 20.44, df = 1, 219, P < .01). The outliers have a similar slope (fig. 1A). The relationship does not change significantly when S = 2 is removed from the data (H’ = 0.26 + 0.39 × log S), which suggests that this relationship is robust. The slope of the empirical data was significantly different from what we expected (sequential ANCOVA; slope: F = 7.6, df = 1, 240, P = .006). Figure 1A’ indicates that the empirical relationship between J’ and H’ is positive over the low-species-number range but that it also increases at a much lower rate than the null model predicts. Consequently, it crosses the line predicted by the null model near 10 species. The r2 value of the ordinary linear regression (H’ on J’) was so high (r2 = 0.87, P < .0001) that the slope of the reduced major axis, or geometric mean regression (GMR), was not very different from the linear regression (Ricker 1984). Finally, in contrast to the null model, the slope (0.31 ± 0.08) of the empirical relationship between H’ and log S did not provide a good estimate of the average value of J’ (0.62 ± 0.02).

Intermediate-Group Univariate Relationships. Univariate relationships in the intermediate group (>10 and <100) were more similar to what we expected (fig. 1B, 1B’). However, they were in the low group. Proportional diversity (H’) increased with log S at a similar rate as in the null model, but average values of H’ were smaller than what might otherwise be expected (sequential ANCOVA; slope: F = 0.16, df = 1, 248, P = .69; intercept: F = 342.51, df = 1, 248, P < .0001; fig. 1B). The difference between slopes of empirical and expected relationships (H’ on J’) was marginally significant (ANCOVA; slope: F = 5.08, df = 1, 178, P = .056). The slope of the GMR (5.62 ± 0.05) was closer than the ordinary regression (5.0 ± 0.02; fig. 1B) to the slope of the null relationship (6.62), but it was still significantly different. Finally, in this species number range, the slope of the relationship between log S and H’ (0.81 ± 0.05) was also significantly different from the average value of J’, in contrast to the analytic expectation (J’ = H’/log S).

High-Group Univariate Relationships. In contrast to the intermediate group, the relationship between log S and H’ in the high group (≥100) was negative (fig. 1C; r2 =

<table>
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<td>Evenness</td>
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<td>.94***</td>
<td>.92***</td>
<td>.94***</td>
<td>.98***</td>
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<tr>
<td>Richness-evenness</td>
<td>r</td>
<td>.35***</td>
<td>.23*</td>
<td>.64***</td>
<td>−.15</td>
</tr>
</tbody>
</table>

Note: Proportional diversity is the dependent variable, and species richness and evenness are the independent variables.

* P < .05.

** P < .01.

*** P < .001.
0.31, $F = 12.4$, df = 1, 28, $P = .002$). Variation in $H'$ was positively and strongly related to variation in $J'$ (fig. 1C; $r^2 = 0.93$, $F = 241.2$, df = 1, 17, $P < .0001$). However, $r^2 = 0.02$, $P = .11$ for invertebrates, and $r^2 = 0.05$, $P < .0001$ for plants. The slope of the invertebrate ($H'$ on $J'$) relationship was not significantly different from the null model (ANCOVA; slope: $F = 0.003$, df = 1, 39, $P = .96$; intercept: $F = 211.22$, df = 1, 40, $P < .0001$).

**Taxonomic Categories**

Univariate relationships ($H'$ on $J'$) varied between groups and also differed with respect to the expected (null model) trend lines (fig. 2). The relationships between $H'$ and $J'$ were positive in fungi, invertebrates, and vertebrates, but in plants, the relationship was not significant ($r^2 = 0.02$, $P = .11$). The slope of the invertebrate ($H'$ on $J'$) relationship was not significantly different from the null model (ANCOVA; $F = 0.97$, df = 1, 270, $P = .33$), whereas the other empirical relationships were significantly different from the expected line (ANCOVA; $F = 8.15$, df = 1, 168, $P < .0001$; fungi: $F = 4.64$, df = 1, 136, $P = .04$).

Finally, above $H'$, the relationship between $H'$ and $J'$ for invertebrates was also similar to the expected null line (ANCOVA; $F = 1.36$, df = 1, 190, $P = .25$), although figure $2C$ indicates that there are two
Figure 2: Univariate relationships between log-transformed species richness (log$_S$; A, B, C) or evenness ($J'$; A', B', C') and proportional diversity ($H'$) for different taxa (fungi: A, A'; plants: B, B'; invertebrates: C, C'; vertebrates: D, D'). The dashed line indicates the null-regression line; the solid line indicates the best fit to the empirical data.

clusters of data. Based on our analysis of the number of species used to estimate diversity (fig. 1), we confirmed that these clusters represent either low or intermediate and high number of species measured. The other empirical relationships between $J'$ and $H'$ were significantly different from the null model (ANCOVA; vertebrates: $F = 8.61$, df = 1, 81, $P = .004$; plants: $F = 60.18$, df = 1, 96, $P < .0001$; fungi: $F = 45.33$, df = 1, 36, $P < .0001$). There is also evidence of different data clusters in the $H'$ on $J'$ plots, resembling clusters that differed between three species-richness groups (fig. 1).

The multiple-regression model for each taxonomic group used the restricted data set and transformed (squared) independent variables ($\log_S$, $S^2$ and $J''$). The correlation between richness and evenness was positive in animals (vertebrates and invertebrates) and negative in plants, although it was not very strong in any taxonomic category (table 3). The univariate coefficients of determination for $\log_S$, $S^2$ and
for the restricted data set were all significant. But their magnitudes differed across taxonomic categories, and neither variable consistently explained more of the variation across the taxonomic categories (table 3). When both evenness and richness were in the multivariate model, the multiple coefficient of determination was very high in each taxonomic group (≥0.94; table 3), which is similar to the analyses of data grouped by number of species (invertebrates: $H^' = -0.13 + 2.17 \times J' + 0.06 \times \log S$; vertebrates: $H^' = -0.33 + 2.51 \times J' + 0.05 \times \log S$; plants: $H^' = -0.28 + 2.01 \times J' + 0.06 \times \log S$; fungi: $H^' = -0.38 + 1.40 \times J' + 0.12 \times \log S$).

Individual Diversity Studies

Data reported in individual studies are typically more restricted. It could be argued that results based on a survey of unrelated studies may not apply to more restricted taxonomic categories measured at different scales (e.g., across transects in a community, within communities across years, between local communities, or between communities in geographically distinct locations). We used Loya’s (1972) coral diversity data, which comprised 84 transect estimates of coral diversity at Eilat in the Red Sea (diversity variation within a community). We dropped seven transects that had numbers of species that were <10, so the number of species ranged from 10 to 30. Harrel et al.’s (1967) data on fish diversity (two to 13 species) are from intermittent Oklahoma streams of several different orders ($H^'$ in different local communities). Karr (1971) reported bird diversities in different habitats located in Illinois and Panama (diversity changes between geographically distinct locations). We dropped the community with the lowest number of species (11) and used the other 10 estimates that ranged from middle to high species numbers (47–165). Finally, Patrick (1968) reported the diversity of freshwater diatom communities measured over 2 yr; all her species counts were >100 (diversity variation within a community and over time).

If the species number was <50 (Harrel et al. 1967; Loya 1972), slopes of the relationships between $\log S$ and $H^'$ were not significantly different from the null model, which is unlike the results obtained from the literature-compiled data set. However, when species numbers were >100, the slopes were negative (table 4). The first-order regression for Karr’s (1971) data was not significantly different from the null model (table 4), but the second-order coefficient was negative and highly significant ($R^2 = 0.98$, $\log S^2$: $t = -5.5$, $P = .0009$, $H^' = -22.4 + 7.5 \times \log S - 0.53 \times \log S^2$). The shape of the curve suggests there is a maximum between $\log S = 6.5$ and $\log S = 7.0$. This is the same range in which there was a negative relationship between $S$ and $H^'$ in Patrick’s (1968) data ($H^' = 9.4 - 0.06 \times \log S$) and in the larger data set compiled from the literature review (fig. 1C).

Slopes of relationships between $J'$ and $H^'$ were highly significant (table 4) and crossed the expected line in the two studies having lower species numbers (Harrel et al. 1967: $H^' = -0.14 + 3.3 \times J'$; Loya 1972: $H^' = 0.82 + 3.8 \times J'$). Studies with higher species numbers had regressions with slopes similar to the null model but with significantly higher intercepts (Karr 1971: $H^' = -1.3 + 8.9 \times J'$; Patrick 1968: $H^' = 0.07 + 6.5 \times J'$; table 4). Although the slope of the relationship between $J'$ and $H^'$ for Patrick’s data was significantly different from the null model (table 4), there was very little variation around the empirical line, and the two slopes were almost identical (slope for Patrick’s data = 6.5; slope for the null model = 6.6). These results were also similar to the large, literature-compiled data set.

As was the case in the large, literature-compiled data set (tables 2, 3), neither the magnitude nor the sign of the correlation between evenness and richness was consistent in the individual studies (table 5). When the correlation between richness and evenness was low (not significant) or negative (table 5), species richness was not as highly related to $H^'$ as it was when the correlation was high. This pattern is similar to variation between the number of species groups (table 2) and different taxonomic categories (table 3). With both diversity components in the multivariate model ($\log S, S^2$ and $J^2$), the predictive relationships were much

### Table 3: Relationships among the survey data

<table>
<thead>
<tr>
<th>Test</th>
<th>Variable</th>
<th>Fungi</th>
<th>Plants</th>
<th>Vertebrates</th>
<th>Invertebrates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample size</td>
<td>$n$</td>
<td>16</td>
<td>76</td>
<td>61</td>
<td>170</td>
</tr>
<tr>
<td>Richness</td>
<td>$r^2$</td>
<td>.43***</td>
<td>.06*</td>
<td>.75***</td>
<td>.82***</td>
</tr>
<tr>
<td>Evenness</td>
<td>$r^2$</td>
<td>.27*</td>
<td>.53***</td>
<td>.69***</td>
<td>.58***</td>
</tr>
<tr>
<td>Multivariate model</td>
<td>$R^2$</td>
<td>.96***</td>
<td>.93***</td>
<td>.94***</td>
<td>.94***</td>
</tr>
<tr>
<td>Richness-evenness</td>
<td>$r$</td>
<td>-.28</td>
<td>-.43***</td>
<td>.54***</td>
<td>.51***</td>
</tr>
</tbody>
</table>

Note: Relationships are broadly grouped by taxonomic differences. Proportional diversity is the dependent variable, and species richness and evenness are the independent variables.

* $P < .05$
** $P < .01$
*** $P < .001$
stronger. Each multivariate model explains >90% of the variation in \( H' \) (table 5). This is, once again, similar to the results of the large literature-compiled data set analyses (tables 2, 3). In summary, individual studies differ from the null model in much the same ways as do different size range groups or taxonomic categories in the other data set.

Other Explanations for Deviations from the Null Model

In contrast to derived or simulated relationships (De Benedictis 1973; May 1975), empirical univariate relationships of \( \log S \) or \( J' \) on \( H' \) were consistent neither in their magnitude nor in their sign. This was not merely a property of unrelated empirical data because we saw similar patterns both within taxa in general and in individual data sets in particular. These results also indicate that scale dependence is not a plausible, alternative explanation. The magnitude of the correlation between \( \log S \) and \( J' \) varied across different groups of diversity estimates, and the sign of this correlation was not always positive, nor were these variables generally independent. But when they were combined in a multivariate relationship, most variation in \( H' \) was explained.

This suggests that indirect relationships between \( S, J', \) and \( H' \) may contribute to direct (univariate) relationships between richness, evenness, and proportional diversity. In order to test this hypothesis, we calculated standardized partial coefficients of determination and used a path analysis to decompose relationships between richness (\( S \)), evenness (\( J' \)), and proportional diversity (\( H' \)). We used this analysis to test whether causal models that included indirect effects were consistent with the observed results (Li 1975). Another advantage of this analysis is that standardized partial-regression coefficients of \( S \) and \( J' \) can be compared since they are both on the same scale.

There are several ways that three variables can be related. The simplest causal model is a chain of uncorrelated causes (Li 1975). The hypothesis that \( S \) governs evenness and, in turn, proportional diversity is a (causal) chain model. This model can be rejected since correlations between \( H' \) and \( \log S \) do not equal the products of the other two correlations, which they should if were is a causally dependent path. Next, \( S \) may be considered to be the common cause of both \( H' \) and \( J' \) (which are uncorrelated) or uncorrelated joint causes of \( H' \), but these models can also be rejected for the same reason as the chain model (Li 1975).

There are two other models with a (small) residual effect, two other direct effects, and an intercorrelated effect that are consistent with the observed correlations: ecological relationships (ecological model) and mathematical relationships (mathematical model). The ecological model assumes there are direct effects of \( S \) and \( J' \) on \( H' \) in addition to the intercorrelated effects of \( \log S \) and \( J' \) on \( H' \) (fig. 3). The mathematical model assumes a different path with a direct effect of \( S \) and \( H' \) on \( J' \) (\( H'/\log S = J' \)), in addition to the intercorrelated effects of \( \log S \) and \( H' \) on \( J' \) (fig. 3).

In the ecological model, table 6 indicates that the direct effect of \( \log S \) on \( H' \) is lower than the effect of \( J' \) on \( H' \) in the low (\( \leq 10 \)), medium (\( >10 \) and \( <100 \)), and high groups (\( \geq 100 \)). However, the difference between the direct effect of \( \log S \) and \( J' \) did not have a consistent direction when the data were put into taxonomic categories (table 6). Direct effects of both \( \log S \) and \( J' \) on \( H' \) were always positive in the ecological model, whereas the correlation between them was either positive or negative. However, \( \log S \) had a consistently direct negative effect on \( J' \) in the mathematical model. This effect was remarkably similar to the size of \( \log S \) on \( H' \) in the ecological model in the low, medium, and high species number groups. This was not the case in the taxonomic categories (table 6).

Table 4: Significance tests of univariate coefficients (intercept and slope) of relationships in four studies and the null model described in the text

<table>
<thead>
<tr>
<th>Study</th>
<th>Intercept F-test</th>
<th>Slope F-test</th>
<th>Intercept F-test</th>
<th>Slope F-test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Harrel et al. (1967)</td>
<td>187.2***</td>
<td>.12 NS</td>
<td>119.1***</td>
<td>21.5***</td>
</tr>
<tr>
<td>Loya (1972)</td>
<td>67.8***</td>
<td>.03 NS</td>
<td>31.8***</td>
<td>26.8***</td>
</tr>
<tr>
<td>Karr (1971)</td>
<td>58.04***</td>
<td>2.46 NS</td>
<td>299.8***</td>
<td>.26 NS</td>
</tr>
<tr>
<td>Patrick (1968)</td>
<td>***</td>
<td>*** (negative)</td>
<td>661.8***</td>
<td>11.8**</td>
</tr>
</tbody>
</table>

Note: NS indicates a nonsignificant F-test.
* \( P \leq .05 \).
** \( P \leq .01 \).
*** \( P \leq .001 \).
positively and highly correlated. If all these indices are related, why collect abundance data, particularly when there are logistical problems in just making a detailed species inventory (e.g., Lawton et al. 1998) and when most communities appear to be open, or unsaturated, rather than closed (Ricklefs and Schluter 1993; Caley and Schluter 1997; Colwell and Lees 2000; Gaston 2000)? Yet, a species count as the sole index of diversity has long seemed to be intuitively dissatisfying. That is, a community with evenly distributed species abundance appears more diverse than a community with the same number of species that is dominated by a few species (Hurlbert 1971; Magurran 1988; Purvis and Hector 2000).

Our analysis of empirical data indicates that this intuitive dissatisfaction with $S$ as the index of diversity is justified. The empirical relationship between species number ($\log S$) and $J'$ or $H'$ is not consistent in statistical strength, coefficient magnitude, or sign over the three orders of species numbers we used to estimate diversity. Furthermore, simple linear relationships vary in strength and magnitude across four broad taxonomic categories and among four individual studies. These results indicate that the assumption that mathematical relationships constrain empirical richness, evenness, and proportional diversity to be strongly and positively related may not be correct. Indeed, the mathematical path model (table 6) indicates that $S$ and $J'$ are always negatively related, which provides clear evidence of a systematic empirical effect that differs from analytic expectations, simulation results, and the null model (De Benedictis 1973; Hill 1973; May 1975; Caswell 1976).

At the same time, we observed correspondence between the results generated by Caswell’s (1976) neutral model and some of the empirical results. Our results show the utility of this altogether too infrequently used null model. It provided a test for differences in simple relationships between taxonomic groups and, within these groups, marks where these trends may change across the number of species used to measure diversity (fig. 2). Furthermore, the multivariate coefficient for $\log S$ in the null model (0.06) is remarkably similar to most empirical coefficients. However, the null model generally predicts neither the sign nor the magnitude of univariate, empirical coefficients relating $\log S$, $J'$, and $H'$, nor does empirical species richness explain most variation in $H'$. In other words, $S$ is not generally the common cause of variation in either $H'$ or $J'$, nor are these three variables generally independent from each other. Thus, they seem to be acting as diversity components that may reflect different ecological processes.

**Diversity Models**

We used a path-analytic approach to test whether or not indirect effects between these variables were a necessary

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**Table 5:** Regression statistics for four diversity studies that differed in the scale at which diversity was estimated and the number of species used to estimate proportional diversity

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample size</td>
<td>$n$</td>
<td>34</td>
<td>77</td>
<td>10</td>
<td>12</td>
</tr>
<tr>
<td>Richness</td>
<td>$r^2$</td>
<td>.52***</td>
<td>.75***</td>
<td>.87***</td>
<td>.46*</td>
</tr>
<tr>
<td>Evenness</td>
<td>$r^2$</td>
<td>.58***</td>
<td>.61***</td>
<td>.89***</td>
<td>.99***</td>
</tr>
<tr>
<td>Multivariate model</td>
<td>$R^2$</td>
<td>.96***</td>
<td>.94***</td>
<td>.99***</td>
<td>.99***</td>
</tr>
<tr>
<td>Richness-evenness</td>
<td>$r$</td>
<td>.13</td>
<td>.42***</td>
<td>.77***</td>
<td>-.68*</td>
</tr>
</tbody>
</table>

* $P < .05$.
** $P < .01$.
*** $P < .001$. 

---
part of an empirical diversity statistic. Neither the common cause (i.e., $S$ governs $H'$ and $J'$ directly), nor the independent joint cause (both directly affect $H'$), nor the chain of uncorrelated causes ($S$ governs $H'$ and $J'$ in sequence) are sufficient models because they do not take correlations between diversity components into account. However, these models underlie assumptions that diversity factors are strongly, positively, and fundamentally related to $S$, on the one hand, or that $S$ and $J'$ are independent, on the other. These models also underlie some explanatory models of empirical trends. For example, it has been argued that an increasing number of species (i.e., through migration) must have a positive but diminishing effect on (increasing) proportional diversity because of an increasing positive effect of evenness (Monk 1967; Sager and Hasler 1969). What is observed at high species numbers is a very systematically insensitive to rare species (Sager and Hasler 1969). What is observed at high species numbers is a very close positive relationship between $J'$ and $H'$, and none of the evenness values for the literature-compiled data or individual data sets are remarkably low. This result provides no indication that guilds with higher species richness generally have low evenness (see Weiher and Keddy 1999), even though the standardized partial-regression coefficients indicate that the direct relationship between these two parameters is always negative. We suggest that these results cannot be rationalized unless indirect or intercorrelated effects between richness and evenness are considered to be meaningful and direct effects of both factors are compared on the same scale.

At the outset of this analysis, we suggested that significant deviations from the null model may suggest the importance of ecological issues on diversity. Currently, an ecological issue is whether communities are closed or open, that is, whether communities are structured by biotic interactions or are open to migration (Ricklefs and Schluter 1993; Caley and Schluter 1997; Colwell and Lees 2000; Gaston 2000). Immigration is the only biological effect in Caswell’s (1976) neutral model; otherwise, abundance is governed by a stochastic process. In this respect, the null model may be regarded as a test of whether or not migration regulates local diversity (measured by $H'$). Alternatively, biotic interactions affecting abundance (e.g., competition, predation) may govern diversity. Our results indicate that univariate relationships between $S$ or $J'$ and $H'$ are very similar to the null model in invertebrates but differ significantly in other taxonomic categories (fig. 2). It has been widely reported that terrestrial and aquatic invertebrate communities often consist of a large proportion of rare species (Williams 1964; Hughes 1984), and

### Table 6: Standardized partial-regression coefficients and correlations for two path models

<table>
<thead>
<tr>
<th>Source</th>
<th>Ecological model</th>
<th>Mathematical model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{S}$</td>
<td>$p_{w'S}$</td>
</tr>
<tr>
<td>Overall</td>
<td>31.9</td>
<td>.67</td>
</tr>
<tr>
<td>≤10 species</td>
<td>7.4</td>
<td>.29</td>
</tr>
<tr>
<td>&gt;10 and &lt;100 species</td>
<td>39.1</td>
<td>.43</td>
</tr>
<tr>
<td>≥100 species</td>
<td>165.5</td>
<td>.18</td>
</tr>
<tr>
<td>Plants (2–168)</td>
<td>17.0</td>
<td>.69</td>
</tr>
<tr>
<td>Vertebrates (2–488)</td>
<td>47.6</td>
<td>.59</td>
</tr>
<tr>
<td>Invertebrates (3–187)</td>
<td>37.8</td>
<td>.70</td>
</tr>
<tr>
<td>Fungi (3–10)</td>
<td>8.0</td>
<td>.87</td>
</tr>
</tbody>
</table>

**Note:** The subscripts on the standardized partial-regression coefficients ($p$) indicate the direction of the direct effect (from the right). Correlations ($r$) are between the subscripted variables; $\bar{S}$ is the average number of species in each source listed in the left hand column. For a diagram of the models, see figure 3.
long-term monitoring indicates that the numbers of insect species at collecting stations continue to increase with time (Rosenzweig 1998). Assuming that correspondence with the null model indicates that migration governs invertebrate community diversity and that the partials reflect direct ecological effects, we would expect that the richness partial coefficient on $H'$ in invertebrate communities would be higher than evenness in the ecological model (table 6). Following this logic, we note that plant communities do not have a significant relationship (fig. 2B), which suggests that the evenness partial should have a larger direct effect than richness. Finally, the difference between vertebrate richness and evenness should be between invertebrates and plants. Differences between the richness and evenness partials listed in table 6 are consistent with the hypothesis that the richness partial indicates the direct effect of migration and that the evenness partial indicates the direct effects of biotic interactions on diversity. Thus, both components affect diversity, but taxonomic differences in the strength of these effects may weight empirical trends across the range of species number or standardized abundance (fig. 1).

**We Measure Diversity in Many Ways, but What Is It?**

Hurlburt (1971) argued that diversity had been defined in so many ways that it risked becoming a nonconcept, but he also advised taking both richness and evenness into account when measuring diversity. We treated $H'$ as the dependent variable because it takes both factors into account and is widely used. Proportional diversity ($H'$) is sensitive to both species richness and evenness (Pielou 1966; Peet 1974) and is the best measure of their joint influence (Fager 1972; De Beneedectis 1973). However, the information-theoretic relevance of $H'$ to ecological diversity is dubious (Hastinon et al. 1968; Hurlburt 1971), so it may be most usefully thought of as a measure of the uncertainty in predicting the species of an individual (Hastinon et al. 1968; Fager 1972). Sample estimates of $H'$ are normally distributed (Magurran 1988). Proportional diversity as measured by $H'$ is not strongly affected by rare species, and it has a broader region of sensitivity than the Simpson’s index (Fager 1972). Proportional diversity ($H'$) is also relatively sample-size independent (Sanders 1968). For our purposes, $H'$ is a useful measure of proportional diversity because it is widely reported and has been developed as a test statistic for a model that is neutral with respect to physical, functional, and biotic interactions (Caswell 1976). However, the use of the $H'$ statistic has been dismissed because it is not intuitively related to ecological diversity (Hurlburt 1971), it is insensitive to different species abundance distribution (May 1975), it is descriptive (Ghilarov 1996), and it has a small-sample bias (Routledge 1980). Other indices may have a better ability to discriminate (Taylor et al. 1976) or may have better statistical properties (Lande 1996; but see Magnussen and Boyle 1995). Nonetheless, $H'$ remains the most useful empirical statistic because it is more widely used, even though its performance and meaning are controversial.

In addition to questioning the sampling, statistical, and measurement issues involved in choosing a diversity estimator, Kempton and Taylor (1974) also questioned whether, in practice, the diversity of species should be separated into its components (richness and evenness). A division can provide insight into community function (McNaughton 1977; Wilsey and Potvin 2000) and, possibly, into systematic biological effects (Caley and Schluter 1997; Gaston 2000). However, neither richness nor evenness are reliable independent measures of differences in diversity compared with the performance of the combined statistic (Kempton and Taylor 1974). Our analysis of disparate empirical data indicates that diversity reflects effects of evenness and richness components along with their intercorrelations.

Species abundance plots represent this integration graphically, but they are inconvenient statistically (Weiler and Keddy 1999). Consequently, we believe that to measure diversity empirically or to test the outcome of multi-species interactions using diversity as a community attribute, species abundance also has to be measured in a species inventory and both components have to be integrated within a compound statistical measure. However, the compound diversity measure that best integrates evenness and richness, that has the desired statistical properties, and that makes the most ecological sense is another issue.

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