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The Quantification of Plant Biodiversity through Time

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The quantification of plant biodiversity through time

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SUMMARY

Existing quantitative summaries of the taxonomic diversification of vascular plants are not in numerical agreement, although they permit similar broad evolutionary interpretations of the history of land plants. We examine three aspects of the collection and analysis of such data which demonstrate that quantitative studies are still in their infancy.

Comparisons among diversification patterns reflected in two data sets reveal that comparatively minor taxonomic and stratigraphic revisions result in statistically significant quantitative changes as well as qualitative differences in the patterns of diversity change over geological time. Two mathematical models based on three data sets are used to estimate the 'unsampled' diversity of fossil plant species. These techniques indicate that considerably more data need to be collected before disparities among vascular plant diversification patterns obtained by different authors can be brought to closure.

The question of what constitutes the smallest sampling unit of morphological diversity (i.e. the taxonomic level that yields statistically independent observations) remains unresolved for vascular plants. Nested analysis of the percent distribution of variance for three plant morphological variables (height, tracheid diameter, and xylem cross-sectional area) indicate that the taxonomic level at which major evolutionary innovations become apparent has shifted from the species–genus level to higher taxonomic levels during the early radiation of pteridophytes. Such shifts may have occurred during the taxonomic radiation of other broadly defined plant groups (gymnosperms and angiosperms), and thus may have altered the taxonomic level on which selection pressures have operated. This may influence our interpretation of the mechanisms of diversity response to environmental variation.

1. INTRODUCTION

Numerous papers have adduced vascular plant diversification patterns based on species-level compilations of originations and extinctions (Knoll *et al.* 1979; Niklas *et al.* 1980, 1983, 1985; Tiffney 1981; Niklas 1988; Knoll 1984, 1986; Lidgard & Crane 1988, 1990; Crane & Lidgard 1989; Kovach & Batten 1993). Most broadly concur with the patterns of vascular plant diversification proposed by Niklas *et al.* (1980): (i) a Silurian–Early Devonian proliferation of early macrophytes characterized by comparatively simple morphology and anatomy; (ii) a Late Devonian–Carboniferous radiation of pteridophytes and gymnosperms; (iii) a gymnosperm-dominated early–mid Mesozoic flora of comparatively stable diversity, despite significant changes in the composition of subordinate taxa; and (iv) a mid-late Cretaceous through Tertiary ascent in species numbers primarily due to the radiation of angiosperms which dominate Late Tertiary and Recent floras. Nonetheless, these papers often disagree on particular aspects of plant diversification. The rates at which angiosperms diversified during the Cretaceous (Crane & Lidgard 1989), and the pattern of Mesozoic diversification of lycopsid taxa (Kovach & Batten 1993) are the most recent to emerge in the literature. These apparent discrepancies are due to a variety of factors, among which the inclination of different authors to split or lump fossil species, the choice of organs examined, the over- and under-representation of various stratigraphic intervals, and the influence of preservational biases among the parts of closely related taxa doubtless play significant roles. These and other biases involved in the collection and analysis of data are discussed in detail by Raup (1979), Niklas *et al.* (1980), and Tiffney (1981) among others.

Differences of opinion regarding quantitative features of diversification patterns likely also result when authors make comparisons among data sets

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published at different times (e.g. Niklas *et al.* 1980; Crane & Lidgard 1989; Kovach & Batten 1993). Individual compilations cannot be complete, and, despite the best of intentions, critical citations may be missed or intentionally ignored for one reason or another (Grant 1980; Signor 1990). For these and other reasons, the diversification pattern evinced by a particular data set invariably reflects some degree of idiosyncrasy resulting from random and non-random sampling effects. Interpretation is further confounded by the fact that supraspecific taxa are as susceptible to taxonomic revision as fossil species (Patterson & Smith 1987; Smith & Patterson 1988; Maxwell & Benton 1990) and that diversification patterns typically become progressively more coarse-grained (and arguably less informative) at higher taxonomic levels (Niklas 1988). Thus, a cautious use of supraspecific-level fossil data to infer species-level diversification patterns seems warranted (Sepkoski *et al.* 1981; Valentine 1985).

Although differences clearly exist among data sets, the important question is whether such deviations invalidate interpretations made from diversity patterns, or simply reflect variation around a common pattern. A numerical assessment of the degree to which diversification patterns disagree is the first logical step to answer this question. The existing papers which address how changes in the palaeontological data base affect our perception of diversification patterns treat the diversification of animals based on family-level compilations. Provided that the data set is sufficiently large, these papers indicate that the basic signature of a macroevolutionary pattern is comparatively insensitive to the discovery of new taxa, taxonomic revision, or the correction and enhancement of the stratigraphic ranges of taxa (Sepkoski 1993; see also Bujak & Williams 1979; Maxwell & Benton 1990). This makes intuitive sense because diversity is a cumulative variable whose fidelity increases as the square root of sample size. Because published data sets for fossil plant species are comparatively small, a lack of precise agreement among the diversification patterns is hardly surprising, and it is appropriate to try and estimate how much more sampling is required to raise them to the trustworthiness of the invertebrate data bases.

There is a second potential bias within compilations of diversity which would compromise their interpretation. From a comparative organismic perspective, measurements of taxonomic diversity are crude reflections of the diversity of important morphological, anatomical, or reproductive biological variables (see Bambach 1977; Knoll *et al.* 1979). Species nested in genera, genera nested in families, and so forth share biological features as a consequence of common ancestry, rather than of independent (adaptive) evolutionary change and therefore may not provide statistically independent observations (Pagel & Harvey 1988). Efforts to determine extinction patterns traditionally have viewed 'biodiversity' and 'taxonomic diversity' as equivalent. Different supraspecific taxa, however, may obtain the same evolutionary fate as a consequence of selection pressures against features shared by common ancestry. If so, then the 'mass' extinction of many closely related taxa may constitute a single biological as well as a statistical event.

This paper explores three issues: the similitude among diversification patterns obtained from different data sets; the relative completeness of existing data sets; and the extent to which subordinate taxa constitute independent observations of changes in biodiversity. Our objective is not to affirm the preeminence of one pattern or taxon among the many possible alternatives but rather to highlight problems of interpretation and methodology.

2. SIMILITUDE AMONG DATA SETS

Figure 1 plots the number of vascular plant species for three data sets against 29 geologic epochs that, for convenience, have been numerically encoded (e.g. 1 = Upper Silurian, 29 = Upper Pleistocene; see figure legend for details; inasmuch as this paper does not concern itself with origination and extinction rates and the same time intervals are used in all cases, the fact that time intervals vary in length is of no consequence in the present paper). The raw data for all three sets were collected from the primary literature (see Niklas *et al.* 1985). None of the data sets present a complete census of the literature (new records could be added with further library research), although the stability of patterns observed between the 1980 and 1985 iterations suggests that little further insight would be gained into the broadest patterns of land plant evolution. The oldest of the three data sets, which contains 6096 fossil vascular species, was taken from Niklas *et al.* (1980). The 1985 data set contains 8349 species (data from Niklas *et al.* 1985), whereas the 1990 data set contains 8688 vascular species and is a revision of the original compilations (K. J. Niklas, unpublished data). The 1990 revision involved the correction or enhancement of the stratigraphic ranges of roughly 560 species (roughly 10% of the original 1980 data set), the deletion of approximately 250 species (roughly 4% of the original), and a net gain of 2592 species (roughly 43% more than the 1980 data set). The consequences of these revisions on the apparent pattern of species diversification are evident both from visual inspection of the plots of species number against geologic age (lower panel) as well as from the plot of percent change in the 1980 data set against geological age (upper panel). In general qualitative terms, the diversification pattern evinced by the 1990 revision differs from that of the 1980 data set in two principal ways: the Permo-Triassic deflection appears magnified (code numbers 8–9), and the signature for the Middle Eocene diversification curve is 'spiked' with regard to the Upper Eocene (code numbers 20 and 21). In quantitative terms, the mean percent change in species numbers across all geologic epochs is $14.0 \pm 9.6\%$; the least revised time intervals are the Upper Silurian–Upper Devonian (code numbers 1–4; average change = $1.58 \pm 0.35\%$) and the Upper Cretaceous–Upper Paleocene (code numbers 16–18; average change = $3.96 \pm 0.60\%$);

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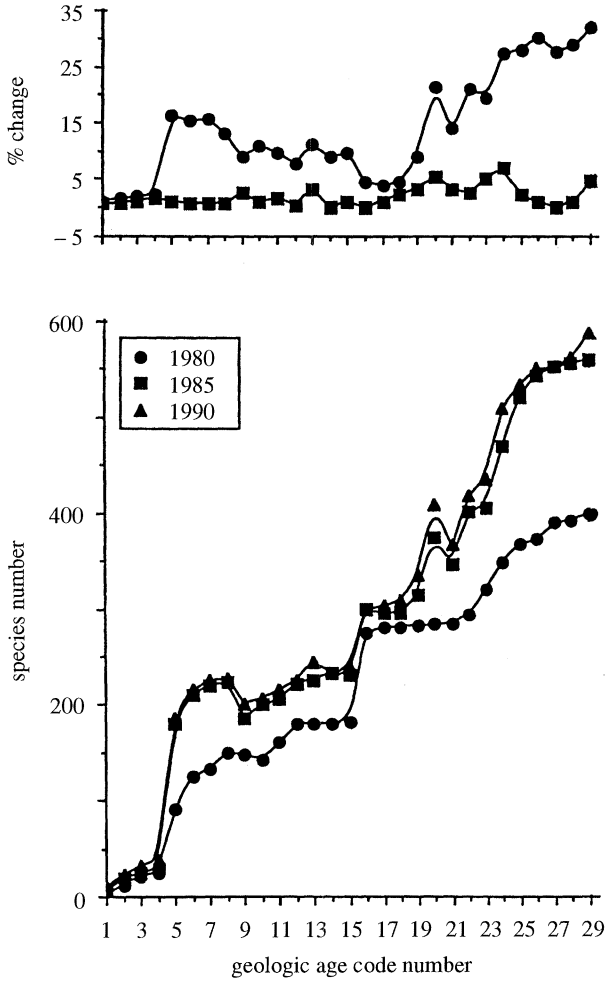

Figure 1. Percent change (relative to peak diversity in Upper Pleistocene) and absolute difference in species numbers obtained from three compilations of fossil vascular plant species (Niklas *et al.* 1980, 1985; Niklas, unpublished revision 1990) plotted against geologic time. Geologic age code numbers are as follows: 1 = U. Silurian, 2 = L. Devonian, 3 = M. Devonian, 4 = U. Devonian, 5 = L. Carboniferous, 6 = U. Carboniferous, 7 = L. Permian, 8 = U. Permian, 9 = L. Triassic, 10 = M. Triassic, 11 = U. Triassic, 12 = L. Jurassic, 13 = M. Jurassic, 14 = U. Jurassic, 15 = L. Cretaceous, 16 = U. Cretaceous, 17 = L. Paleocene, 18 = U. Paleocene, 19 = L. Eocene, 20 = M. Eocene, 21 = U. Eocene, 22 = L. Oligocene, 23 = U. Oligocene, 24 = L. Miocene, 25 = U. Miocene, 26 = L. Pliocene, 27 = U. Pliocene, 28 = L. Pleistocene, 29 = U. Pleistocene.

the most revised time intervals are the Lower Carboniferous–Middle Triassic (code numbers 5–10; average change = 15.1 ± 1.78%) and the Middle Eocene–Upper Pleistocene (code numbers 20–29; average change = 26.3 ± 3.3%). By comparison, few (if any) qualitative or quantitative changes in the 1985 diversification pattern were effected by the 1990 revisions. The mean percent change in species numbers across all geologic epochs is 1.94 ± 1.79%. The most significant % change in species number was for the Middle Eocene (code number 20).

Bivariate regression and correlation analyses of the data shown in figure 1 provide additional quantitative information regarding the effects of the 1990 revision on previously determined diversification patterns of vascular plant species. Figure 2 plots the normalized and absolute species numbers for the 1985 and 1990 data sets versus those of the original 1980 compilation. The normalized data-points were obtained from the quotient of the absolute species number in each geologic epoch and the Upper Pleistocene species number in each data set (i.e. the 'peak' in each diversification pattern; code number 29, see figure 1). Data-points exceeding the upper and lower 95% confidence intervals (i.e. L_2 and L_1) for each reduced major axis regression curve are identified by their respective geological age code numbers. Reduced

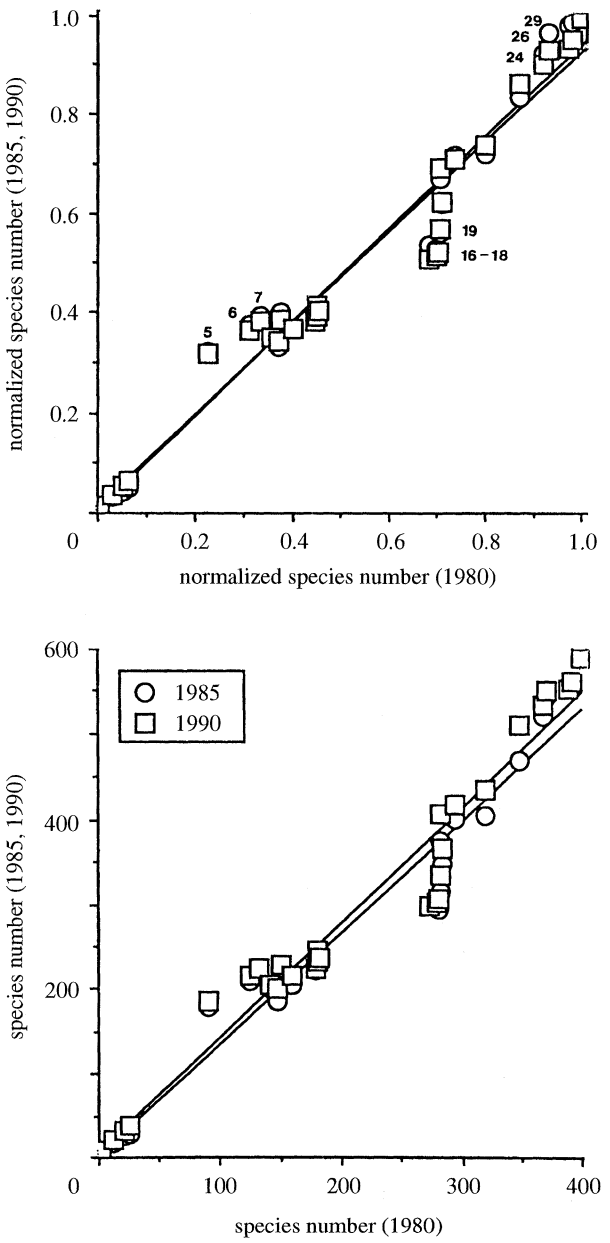

Figure 2. Normalized and absolute species numbers from the 1985 and 1990 compilations plotted against normalized and absolute species numbers from the 1980 data set. Regression curves obtained from reduced major axis regression analysis. Data points outlying upper and lower 95% confidence intervals are flanked by geologic age code numbers (see figure 1).

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major axis regression (Model II type regression) rather than ordinary least squares regression (Model I type regression) was used to determine the slope m of the linear regression curve because neither data set constitutes a legitimate 'independent variable' (see Sokal & Rohlf 1981). The bivariate plots for normalized data evince highly significant coefficients of correlation ($r^2 = 0.952$, $p < 0.001$, for 1985 versus 1980; $r^2 = 0.954$, $p < 0.001$, for 1990 versus 1980). As expected, regression analysis indicates that the normalized data obtain slopes that do not statistically differ from unity ($m = 0.965 \pm 0.041$, $L_2 - L_1 = 1.1 - 0.88$, for 1985 versus 1980; $m = 0.941 \pm 0.039$, $L_2 - L_1 = 1.0 - 0.86$, for 1990 versus 1980), indicating that, on the average, the 1990 revisions have not altered the overall signatures for diversification evinced by the two previous diversification patterns. The most informative feature of the bivariate plots is the geologic ages of data-point outliers. Outliers falling above the regression curves in figure 2 denote geologic epochs for which the 1990 revision has disproportionately increased species diversity (code numbers 5–7, 24, 26; 29) whereas for those data-point outliers falling below regression curves the 1990 revision has had the opposite effect (code numbers 16–19; 21). Regression of normalized species numbers for the 1990 data set versus those of the 1985 data set (not shown) indicates that the most recent revisions have disproportionately increased the species numbers for the Middle Eocene, Upper Oligocene, and Lower Miocene (code numbers 20, 23, 24) relative to those reported in 1985.

Although additional analyses would be instructive, as for example regression of the number of originations or extinctions (see Sepkoski 1993, figure 5), the preceding comparisons among the three data sets for fossil plant species sufficiently illustrate that relatively modest revisions of a numerically small data set obtain statistically significant differences in a palaeontological diversification pattern. However, although these differences are statistically significant, the overall pattern of diversification remains the same among all three data sets, particularly the 1985 and 1990 sets, and therefore the most recent 1990 revisions do not require alteration of previous interpretations of process made from these patterns.

That the 1990 revisions are statistically significant is not surprising because, all other things being equal, the measurement error of a cumulative variable (such as species diversity) is proportional to the square root of the sample size (= number of species per geologic stratum) and therefore proportionally increases as the number of observations decreases (Guiaşu 1977; Sokal & Rohlf 1981). In theory, therefore, the 'signal' of a diversification pattern can be enhanced by either increasing the sample size or diminishing the number of revisions (an analogous and numerically rigorous conclusion for the astronomical sciences is drawn by Harwit (1981)).

3. PATTERN CLOSURE

Continued revision of a small palaeontological data base raises a very practical question: What evidence suffices to show that a diversification pattern has been brought to closure? We suggest two approaches.

First, it is important to recognize that a decline in the variance in the species number obtained by the same authors is not sufficient evidence. For example, although the 1985 and 1990 diversification patterns do not significantly differ, neither does the percent change in species number between the 1985 and 1990 data sets. Thus, a diversification pattern can give the appearance of being brought to closure in the absence of significant revisions. This emphasizes that a 'true' difference δ between the numerical values for a given sampling unit (e.g. upper Devonian, code number 4) in any two iterations of a diversity compilation (observations) can only be demonstrated when there is a statistically appropriate number of new records added in the second iteration. It is evident that prior knowledge of the variation in species number per time interval is required because the number of iterations of the data set (N) required to show that δ is statistically meaningful at a specified significance level α with a probability p that the significance will be found depends upon the true variation σ in species number reported for each time-period: e.g.

$$N \geqslant 2\left(\frac{\sigma}{\delta}\right)^2 \{t_{\alpha[\nu]} + t_{2(1-p[\nu])}\}^2, \qquad (1)$$

where ν is the degrees of freedom of the sample standard deviation (see Sokal & Rohlf 1981, p. 263). The numerical value of σ need not be known exactly because the value of N depends upon the ratio of σ to δ. Because $\nu = n(N-1)$, where n is the number of data sets from which σ is estimated, equation (1) must be solved reiteratively. For example, the variation of species number reported for the Upper Devonian is roughly 5% based on the 1990 and 1980 data sets (i.e. $\sigma = 5\%$ and $n = 2$). To estimate the number N of observations required to be 90% certain of detecting a 5% difference between any two reported species numbers at the 1% level (i.e. $p = 0.90$, $\delta = 5\%$ and $\alpha = 0.01$), we may arbitrarily specify $N = 13$, such that $\nu = 2(13-1) = 24$. Thus, equation (1) becomes

$$N \geqslant 2\left(\frac{0.05}{0.05}\right)^2 \{t_{0.01[24]} + t_{2(1-0.90[24])}\}^2$$

$$= 2\{2.797 + 1.318\}^2 = 33.87.$$

When $N = 16$, equation (1) obtains $N \geqslant 2\{2.750 + 1.310\}^2 = 32.96$. A conservative estimate, therefore, is that 35 observations are required to detect a 5% difference at the 90% probability level between any two reported values for Upper Devonian species number. Relaxing δ to 10%, equation (1) indicates that $N \geqslant 8.467 \approx 8.5$. That is, a conservative estimate for the requisite number of data sets reporting species number for the Upper Devonian is 10. Importantly, given that the variance in reported species numbers differs among geologic time-intervals, the number of observations required to detect a difference among species numbers likewise will vary among stratigraphic intervals. Figure 3, for example, plots N required to detect a 10% difference in species number

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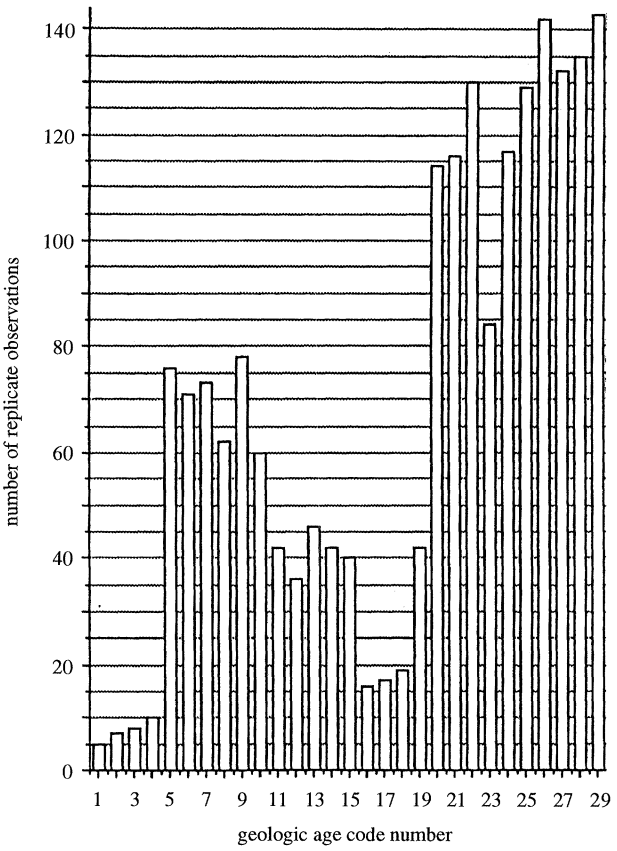

Figure 3. Histogram of number of replicate observations N (i.e. reported species numbers in each of 29 geologic time-intervals) plotted against geologic time (see figure 1). Values for N were computed on the basis of equation 1 (see text) to detect a 10% difference in species number at the 1% level, based on the variance in species number per geologic time interval obtained among three data sets for vascular plant species (Niklas *et al.* 1980, 1985; Niklas, unpublished results 1990).

at the 1% level for the 29 stratigraphic units. These values were computed on the basis of the variance in species number per geologic time interval obtained among three data sets ($n = 3$) for vascular plant species (Niklas *et al.* 1980, 1985; Niklas, unpublished data 1990). Estimated values for N would have been appreciably higher had variance in species numbers been calculated on the data sets of different authors, rather than one three data sets from the same authors in these computations. The data in figure 3 provide neither a precise requirement for the number of future samples to be gathered, nor 'prove' that existing data sets are 'wrong' in the patterns they evince. This exercise only shows that we clearly have an insufficient number of observations to adduce whether the diversification pattern has been brought to closure.

A second method of inferring the quality of existing diversity data sets is to estimate the number of geologically contemporaneous taxa based on the number of taxa already discovered. Several workers have noted the similarity between palaeontological studies of taxonomic diversity and demographic studies of populations (Van Valen 1973; Raup 1975, 1978; Stanley 1979; Nichols & Pollock 1983). In both types of study, essentially random samples are drawn from a population (i.e. the fossil record and an extant population) and diversity is estimated based on the probability of capture. Nichols & Pollock (1983) have emphasized the relevancy of capture–recapture models, particularly the Jolly-Seber model, when the objective is to estimate total diversity on the basis of repeated sampling of a particular series of strata (Jolly, 1965; Seber, 1965, 1973). In the case of extant populations, a population is repeatedly sampled and the number of times the same individual (or taxon) is captured in each sample is recorded and used to estimate the true numerical abundance of organisms within (or taxonomic diversity of) the population. Likewise, the number of times different fossil taxa are observed in different samples drawn from the same geologic time interval may be used to estimate the palaeodiversity yet to be disclosed. Although the limitations of capture–recapture models are numerous (e.g. for the Jolly-Seber model, every taxon is assumed to have the same probability of being captured; see Nichols & Pollock 1983, pp. 153–157), these models have considerable merit. Surprisingly, they have yet to be applied to the plant fossil record and have received scant attention among palaeozoologists. In part this may reflect the fact that modern species generally are recognized on the basis of the morphology and anatomy of the entire organism, whereas fossil species are recognized on the basis of the morphology and anatomy of a single organ. This distinction may have considerable consequence on the application of any method derived from the study of living species to the interpretation of palaeontological data, although we suspect that such is not the case here.

We sampled each of the 29 stratigraphic intervals a minimum of seven times. Each 'sample' consisted of a paper or papers embracing a 'flora', a fossil assemblage from one geographical and temporal point. The results (based on the Jolly-Seber model) are presented in figure 4 as estimated species number versus geologic time, along with the patterns obtained from the 1980, 1985, and 1990 data sets. The total estimated species number for the Phanerozoic is 8688 and therefore adds a mere 826 species to the 1990 data set (roughly a 9% increase). The average change in species number per interval resulting from the application of this approach is roughly 4%, which likely is symptomatic of the comparatively small numbers of replicate samples for each geologic time-interval, and of the incomplete literature base we used. Further, the literature 'samples' used here are drawn from the same literature base used to assemble the 1980–1990 data sets. Thus, it is not surprising that the overall estimated diversification pattern bears a striking similarity to that shown for the 1990 data set despite notable increases in species numbers predicted for the Upper Silurian to Upper Devonian (code numbers 1–4) and for the Upper Miocene to Upper Pleistocene (code numbers 25–29). With these caveats in mind, the resulting prediction must be accepted as very crude, and is presented here only to illustrate how a particular approach could be used to evaluate

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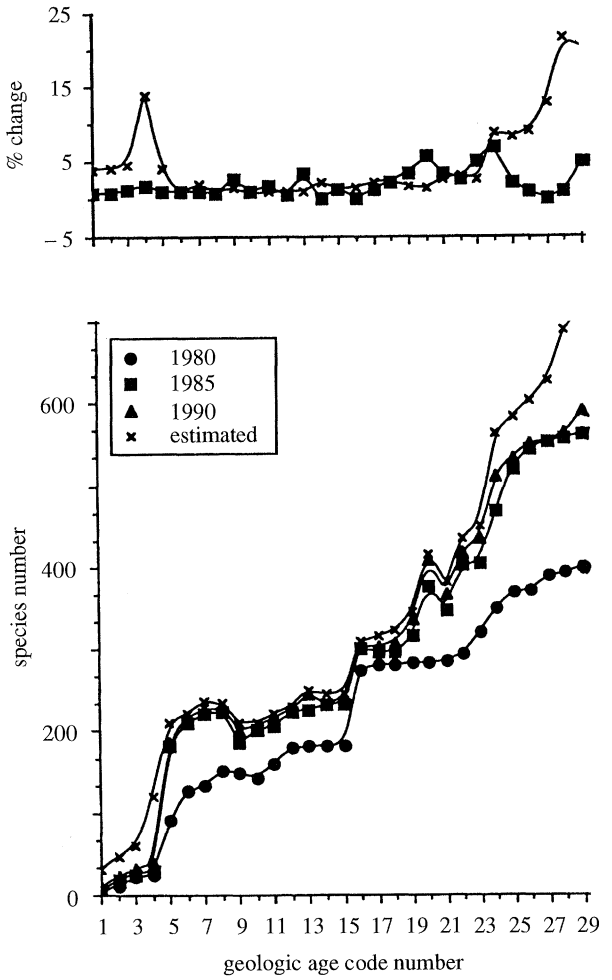

Figure 4. Percent change (relative to peak diversity in U. Pleistocene) and absolute difference in species numbers obtained from a Jolly-Seber capture–recapture model as well as data obtained from three compilations of fossil vascular plant species (Niklas *et al.* 1980, 1985; Niklas, unpublished revision 1990) plotted against geologic time (see figure 1).

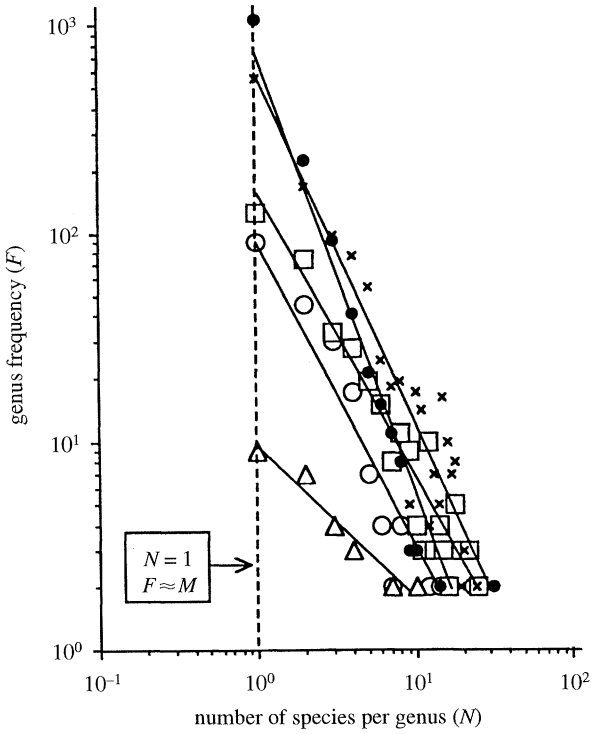

Figure 5. Log_{10}–log_{10} plot of genus-frequency F (i.e. number of genera containing N number of species) versus number of species per genus N. Data based on taxonomic checklists for extant marine algae (open circles; Farlow 1881), mosses (squares; Grout 1936–1939), pteridophytes (triangles; Mickel 1979), angiosperms (crosses; Gleason 1968), and protozoa (filled circles; Kudo 1966). Vertical dashed line denotes $N = 1$. Regression curves have the mathematical form $F = \beta N^{-\alpha}$.

whether a diversification pattern has been brought to closure.

This discussion affords an opportunity to share a curious observation perhaps useful to those interested in the diversity of extant organisms. As first noted by Willis (1992), the frequency of taxa with different numbers of subordinate taxa (i.e. species nested within genera, genera nested within families, and so forth) graphs as a hollow curve with a negative slope, indicating that a very large number of taxa contain one or a very few subtaxa (e.g. monospecific genera far outnumber genera containing two or three species; see Lotka 1956, pp. 311–317; Anderson 1975; Dial & Marzluff 1989; Burlando 1990; Nee & Moorers 1992). Specifically, the number of genera F containing N number of species obtains the relation $F = \beta N^{-\alpha}$, where β is the Y-intercept and α is the slope of the regression curve for the log_{10}-transformed data. Figure 5, for example, provides log_{10}–log_{10} frequency distributions of genera reported in randomly sampled published checklists for extant North American pteridophytes, marine algae, mosses, and angiosperms as well as a world-wide compendium for extant protozoa. Note that, when the number of species per genus equals one, the value of F is the total number of monospecific genera in each of the five data sets. Thus, the value of the Y-intercept obtained by regression of the log_{10}-transformed data roughly equals the number of monospecific genera (i.e. $\beta \approx M$). More important is that reduced major axis regression analysis of diversity data from a total of 21 checklists shows that β is highly correlated with the total numbers of species S, genera G, and monospecific genera M within each checklist (figure 6): $S = 14.7\beta^{1.00}$ ($r^2 = 0.831$); $G = 4.13\beta^{0.896}$ ($r^2 = 0.978$); and $M = 1.28\beta^{0.971}$ ($r^2 = 0.978$). We have not tested whether the number of monospecific genera (β value) in a fossil assemblage can be used to crudely estimate S and G. It also would be interesting to examine the changes in the genus-frequency distribution patterns occurring over geological time within individual lineages since these changes could be used to compare rates of origination among different taxonomic ranks.

4. THE SMALLEST SAMPLING UNIT

Pagel & Harvey (1988) emphasize that subordinate taxa (e.g. species within genera, genera within families, etc.) share biological features as a consequence of

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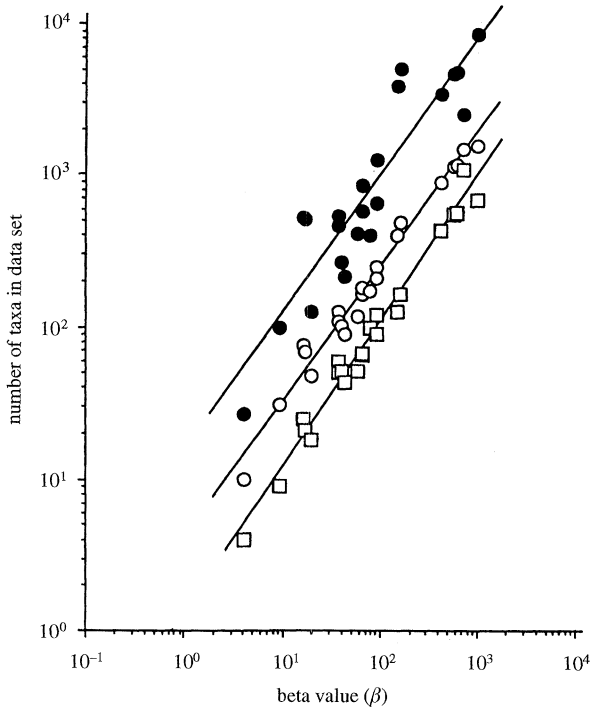

Figure 6. Log_{10}–log_{10} plot of number of taxa versus beta value (see figure 5) computed for each of 21 plant taxonomic checklists. Filled circles, total number of species (S); open circles, total number of genera (G); squares, number of monospecific genera (M).

common ancestry as well as because of evolutionary adaptive changes. Therefore, data from subtaxa may not represent statistically independent observations (i.e. they may not be the smallest statistical sampling unit when interpreting evolutionary patterns dependent on features shared by common ancestry).

This possibility has important implications to the analysis of extinction patterns. Mass extinction events (i.e. statistical outliers from background extinction levels) document the extirpation of many lower taxa. Although each mass extinction event includes the annihilation of phyletically and ecologically dissimilar taxa, it is possible that equally large numbers of species are lost due not to individually distinct traits but to characters based on common ancestry. Because the magnitude of a 'mass' extinction event predetermines whether the event is a statistical outlier (see Raup & Sepkoski 1984), the distribution of variance for biological features among taxonomic levels should never be neglected. This is not to deny the importance of the extinction of individual species, which can give distinctive insight into the dynamics of specific groups and ecosystems. Rather, it is to suggest that one needs to suit the analysis of data to the particular question at hand.

The determination of the smallest sampling unit also bears on the estimation and quantification of phenotypic diversity. This measure of diversity typically is depicted as the trajectory of morphological or anatomical variance against geological time and is calculated on the basis of the morphological or anatomical extremes evinced by the particular subordinate taxon selected for analysis (see Foote 1992). It is evident, therefore, that without prior knowledge of the percent distribution of the variance in phenotypic features among different taxonomic levels, we have no *a priori* reason to assume that the extremes evinced by the chosen subtaxon obtain the greatest measure of variance. Consequently, the study of adaptive evolution is susceptible to misinterpretation when the statistical artifact of data-point inflation resulting from taxonomic interdependence in addition to convergent evolution are not recognized and minimized.

Nested analysis of variance provides a simple and convenient method to determine the manner in which the total variation in a continuous biological variable is distributed among data-classification levels, even when sample sizes are unequal (Sokal & Rohlf 1981, pp. 293–308). From the distribution of percent variance, the particular subordinate level of data-classification obtaining reasonably independent data-points can be determined. This approach has been used to evaluate the percent variance distribution of a variety of biological variables. When applied to mammals, nested analysis of variance has shown that species and genera generally should not be used as taxonomic units of analysis involving several important life history and size variables as they typically contribute only 10–20% of the total variance of many of these characters (e.g. Clutton-Brock & Harvey 1977; Harvey & Mace 1982; Harvey & Clutton-Brock 1985; see Pagel & Harvey 1988, pp. 421–422, table 1). Although mammalian species and genera do not add substantial variance independent of phylogenetic association, the mean value for many mammalian life history and size variables obtained for the family level is a poor predictor for the values of other families nested within the same order. Thus, the mean family values of these characters are statistically independent observations. It is problematic whether these results hold true for every kind of animal or plant since 'species', 'genus', 'family', etc., arguably may hold different meanings for different kinds of organisms. Similarly, different characters may become statistically significant at different systematic levels in different clades, reflecting their independent biological features and historical trajectories.

Although it is tempting to speculate that, within each clade, characters shared by virtue of common ancestry steadily accumulate over time at progressively higher taxonomic levels, the extent to which the distribution of variance for biological variables among taxa changes over evolutionary time must be appraised for each particular group of organisms. Ideally, this appraisal should focus on the group's initial radiation, as for example that of vascular land plants during the early Palaeozoic. To a limited extent, data for Silurian and Devonian tracheophytes are sufficient to exercise the required nested analysis of variance for three morphological and anatomical biological variables, each of which has undergone considerable evolutionary modification during the early adaptive radiation of vascular land plants: plant height, the diameter of primary tracheids, and the cross-sectional area of xylem in plant stems. It is

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well known that the height of extant plants is highly variable among and within taxa, as well as for each individual plant, as a consequence of indeterminate stem-growth. Also, the fragmented nature of fossil remains in most cases precludes the direct measurement of overall plant height. Fortunately, the scaling relation for plant height in terms of stem diameter has been empirically determined for a variety of plant clades and anatomical clades (Niklas 1993). This scaling relation permits a crude estimate of the variance in height based on the largest stem diameter reported for each fossil taxon. Tracheid diameter and xylem cross-sectional area also vary among and within taxa as well as within each individual plant. However, the variance for each of these anatomical variables can be estimated from compilations of their values reported in the primary literature (Niklas 1984, 1985). These data for plant height, tracheid diameter, and xylem cross-section are limited in two additional and very important respects.

1. The percentage distribution of variance for each variable in these early plants can only be partitioned into the variance contributed by species and genera, on the one hand, and the variance contributed by families and higher taxonomic levels, on the other. This is because, in our estimation, the taxonomic structure of early Palaeozoic plants above the family level and below the genus level is presently not well enough well understood to permit confidence in a higher degree of resolution.

2. The Upper Silurian to Upper Devonian time interval can only be partitioned into four broad time intervals (Upper Silurian and Lower, Middle and Upper Devonian) because too few taxa are present to allow tabulation by stratigraphic stage. This is a severe limitation since the manner in which the percent variance of each variable is re-distributed over time can only be evaluated on the basis of four data-points. Clearly, this precludes legitimate regression analysis.

Figure 7 plots the percent variance in plant height, tracheid diameter, and xylem cross-sectional area at the species and genera level versus geologic time. In purely qualitative terms, the percent variances of tracheid diameter and xylem cross-sectional area, on the average, decline during the Late Silurian and the Devonian, suggesting that the taxonomic level in which evolutionary variance in these characters is expressed has progressively shifted from the species and genera level to the family (and higher) taxonomic level. This may be an artefact resulting from: (i) the capacity for greater taxonomic 'resolution' with decreasing geological age: younger plant remains tend to be more morphologically and anatomically complex and therefore offer more numerous characters with which to distinguish subordinate taxa; or (ii) the manner in which 'species', 'genus', 'family' shift meaning as palaeontologists classify progressively younger fossil remains. These possibilities cannot be ignored. However, the temporal pattern of the percent variance of plant height at the species and genus level is less prone to these two potential artefacts. Although the species and genera level variance in plant height

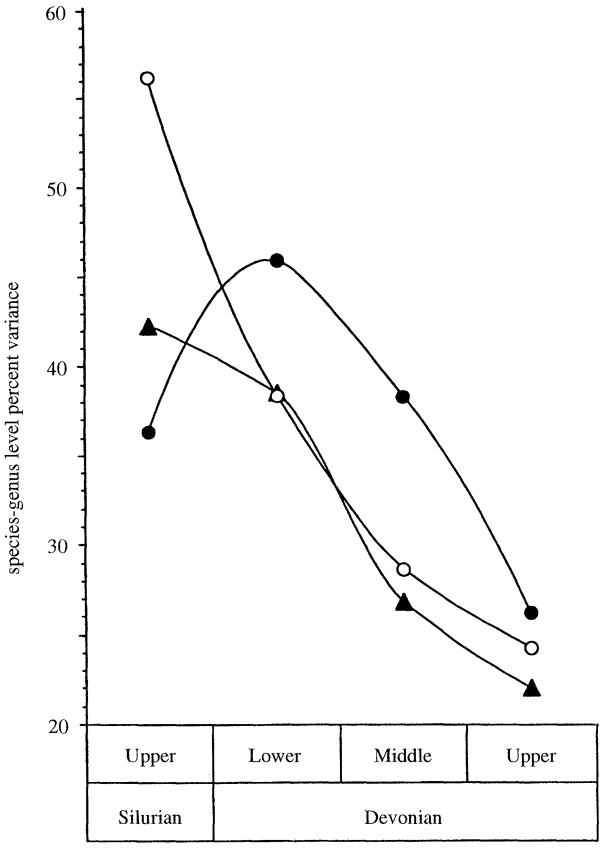

Figure 7. Percent variance of early Palaeozoic plant height (filled circles), tracheid diameter (triangles), and xylem cross-sectional area (open circles) contributed by the species and genera taxonomic levels plotted against geologic stages. Abscissa is not in absolute geologic time; interpolated lines connecting data-points are provided to assess qualitative trends and have no mathematical or statistical relevancy.

evinces much less 'directionality' across the Silurian–Devonian, it nonetheless declines throughout the Devonian, suggesting that, in general terms, evolutionary changes in plant height initially manifest at subordinate levels progressively became canalized in higher taxa.

Although a sceptical attitude is warranted given the numerous limitations imposed by the fossil record on evolutionary changes in the percent distribution of variance among taxonomic levels of early Palaeozoic vascular plants, the suggestion that the variance in prominent biological variables has shifted from lower to higher taxonomic levels within these clades over geologic time should be considered. It raises the intriguing possibility that similar shifts in the variance of characters may have been associated with subsequent taxonomic radiation events, as for example the diversification and subsequent 'canalization' of gymnosperms and angiosperms. If so, then the long-noted evolutionary procession of palaeofloras dominated by pteridophytes, then gymnosperms and most recently angiosperms may be coarsely explicable in terms of selection pressures against features shared as a consequence of common ancestry at progressively higher taxonomic levels within each of these three

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broad groups of plants. Shifts in the variance of characters to higher taxonomic levels must be an ongoing evolutionary process. New characters continually arise within populations and species, and when successful, underwrite radiations that lead to the incorporation of the characters in groups of increasing size and ultimately higher rank. Therefore, the level at which character variance resides is not fixed but depends upon the character as well as the evolutionary phase being considered. Thus, features which might be profitably analysed at the species level in one point of a clade's history may be better analysed at a higher taxonomic level at a subsequent evolutionary time.

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