Conflict between Local and Global Changes in Plant Diversity through Geological Time

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Reliable measurement of the original diversity of paleovegetation must account for many influences: the amount of time and space represented by the sample, the number of plant parts in the sample, the stature of the paleovegetation in relation to sample area, and the preservational quality of the sample, as well as the number of species in the source community and their relative abundances. Plant compression fossil assemblages from river or delta floodplain environments generally have undergone minimal time and space averaging, which allows species richness to be measured and compared at a variety of temporal and spatial scales. Comparison of late Paleozoic and early Cenozoic wet floodplain vegetation reveals little difference in species richness or diversity at the smallest measurable spatial scale, based on samples of a few square meters representing 0.1–0.5 hectares of source vegetation. Outcrop transects several hundred meters to several kilometers long that sample across minor variations in wet floodplain habitat also show similar levels of diversity in the Paleozoic and Cenozoic, with the exception of one Cenozoic transect with very high diversity. Diversity differences between Paleozoic and Cenozoic sites and transects are far less than would be expected based on global species richness curves for the Devonian through Pleistocene. The small differences in the diversity of wet floodplain vegetation probably relate to several factors, including the number of trees that can coexist in a small area, difficult edaphic conditions on wet floodplains, and perhaps the geologically early colonization and saturation of these habitats. The difficulty of making reliable measures of plant diversity in the fossil record, and the absence of change observed with relatively high quality data, suggest that biological explanations for changes in global species richness through geological time are premature.

INTRODUCTION

Most of the work on plant richness and diversity through geological time has focused on global or continental scale patterns (Knoll et al., 1979; Niklas et al., 1980, 1983, 1985; Tiffney, 1981; Niklas, 1988; Niklas and Tiffney, 1994). These studies have shown a dramatic, essentially monotonic increase in the number of plant species from the Devonian to the early Cenozoic, with major upturns following the evolution of seed plants in the Early Carboniferous and angiosperms in the Late Cretaceous. The pattern of change in Late Cretaceous plant richness has been worked out in further detail by Lidgard and Crane (1990), who documented even more dramatic increases in species number associated with the radiation of flowering plants.

The number of plant species on the Earth is the result of richness accrued at lower spatial scales. Higher within community richness, greater heterogeneity of species composition across local environmental gradients, and greater provinciality of floras at regional or continental scales will all increase the global number of plant species. However, the increase in global richness over geological time generally has been interpreted to result from innovations in the reproductive biology of plants. The argument has been made that more sophisticated methods of fertilization and dispersal allow higher levels of niche differentiation, and therefore more species to coexist in the same community (Niklas et al., 1980).

This explanation for global richness increase implies strongly that richness at the community level also should have increased through time. Data to test this prediction were collected by Niklas et al. (1980), and further analyzed by Knoll (1986). These authors used the number of species per published flora as a rough proxy for community richness, acknowledging that the published lists do not necessarily represent equivalent sampling efforts, time intervals, or areas. The overall pattern at the "community" scale was congruent with that observed at the global scale,
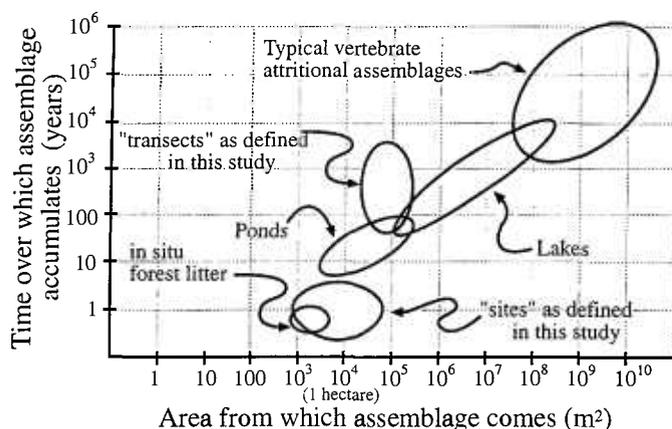
FIGURE 1—Spatial and temporal dimensions of plant compression fossil assemblages. The fossils from a typical wet floodplain site, as defined in the text, are derived from a small area and over a short amount of time. Transects, as defined in the text, increase the spatial and temporal dimensions of the sample, but are still much less time and space averaged than typical vertebrate and invertebrate attritional assemblages.

with major increases in mean number of species per flora occurring in the Early Carboniferous and Late Cretaceous.

In this paper we examine the effect that sampling effort, depositional environment, and sample area can have on the richness and diversity of plant fossil assemblages, and reconsider the issue of plant community diversity through time in light of Paleozoic and Cenozoic samples that have been matched for these factors.

TAPHONOMY AND DIVERSITY OF PLANT FOSSIL ASSEMBLAGES

A variety of factors make it difficult to measure richness and diversity even in living communities: variation in size of sampling quadrats relative to the organisms being studied, variations in sampling effort, the size of the area sampled, and the evenness of abundances of species in the community. These factors affect measurements of diversity in fossil assemblages as well, but fossil assemblages present additional problems that generally are not present in the analysis of living communities. Chief among these are the mixing of organisms from more than one community type, which artificially increases richness, and the failure of some species to be preserved, which artificially decreases richness. Mixing commonly occurs both through time-averaging and transport of remains and has the largest effect on assemblages of hard parts such as bones, shells, or woody plant parts (Burnham, 1990; Behrensmeyer and Hook et al., 1992; Kidwell and Behrensmeyer, 1993). Differential preservation is most likely to be a problem when species or organs vary widely in their susceptibility to decay and transport (e.g., the rarity of flowers in volcanic mudflows).

Most plant tissues are more susceptible to decay and mechanical destruction than shell or bone, so there is less

potential for transport and time averaging in plant fossil assemblages (Behrensmeyer and Hook et al., 1992). Taphonomic time-averaging is a relatively minor influence on parautochthonous leaf assemblages because leaves decay rapidly near the soil surface (Golley, 1983; Ferguson, 1985), and buried leaves will not survive reworking. Actualistic studies show that leaf litter at any one point is derived largely from the surrounding 1000 to 3000 square meters of vegetation, even in a forest setting (Burnham et al., 1992; Burnham, 1993). The difference between the temporal and spatial "scope" of parautochthonous leaf fossil assemblages and other kinds of fossil assemblages is illustrated in Figure 1.

The extremely local nature of leaf compression fossil assemblages in floodplain sediments is a mixed blessing. The advantage is that parautochthonous leaf assemblages in such environments are nearly free from the effects of time and space averaging that are ubiquitous in most other kinds of fossil assemblages. They are "snapshots" of vegetation at an instant in time, and consequently they are more or less equivalent to one another and to ecological samples of living vegetation. The disadvantage is that such samples are limited in the area of the source vegetation they represent, so limited that many penecontemporaneous samples are required to represent the composition and richness of even the local vegetation.

PLANT DIVERSITY IN THE LATE PALEOZOIC AND EARLY CENOZOIC

Study Sites

All of the fossil assemblages used in this study were derived from low-gradient, fluvial or fluvio-deltaic settings, and are parautochthonous in the sense that there is no evidence for transport of remains outside of the vegetation type recorded by the assemblage. Sediments bearing the plant fossils are dominantly fine-grained (clay/silt), lack primary stratification that would indicate current flow, and contain plant parts of various sizes and hydrodynamic properties. Most of the assemblages were probably deposited on wet, but subaerial, distal floodplains, in small ponds formed by channel abandonment or flooding of areas distal to the channel, or in distal levee or crevasse-splay events.

Almost all of the Cenozoic assemblages were deposited on floodplains. Most plant fossils occur in laterally extensive, poorly laminated, organic shales (5% to 80% carbon by weight). The zones preserving identifiable megafossils are localized within the shales, usually are less than 20 cm thick, and have less organic matter than most of the deposit. These plant fossil bearing lenses probably represent individual sedimentation events on the wet floodplain, with the intervening organic shale representing periods when leaves decayed before burial could occur. If the preservational intervals represent single flood events, then the fossil assemblages they contain probably represent less than one year, and certainly less than a ten-year period. Leaf compressions are dense, but do not occur in discrete mats that would indicate more than one episode of accu-

mulation. Many of the leaves are overlapped by other specimens, and some are incomplete, perhaps reflecting minor transport or decay in the litter prior to deposition. Details of venation are well-preserved by the fine-grained sediments, even in taxa with living relatives that have high rates of decay (e.g., *Alnus*).

About fifteen of the 116 early Cenozoic assemblages are preserved in siltstone or very fine sandstone in which organic layers are interlaminated with slightly coarser clastic sediment. These are probably crevasse-splay or levee deposits, but the preservation of leaves and the distinct composition of the flora are consistent with parautochthonous deposition. The derivation of levee leaf assemblages from the immediately surrounding vegetation has been demonstrated in actualistic studies (Burnham, 1989). Four of the Cenozoic floras come from flat-laminated siltstones that represent deposition in floodplain ponds or segments of abandoned channel. More detailed descriptions of the sedimentary environments of the Cenozoic assemblages are found in Wing (1984), and Bown et al. (1994).

The Paleozoic samples are from delta plain environments nearer to paleocoastlines, and represent a somewhat broader spectrum of depositional settings than the Cenozoic samples. Middle Pennsylvanian samples from Indiana (Chinook and Roaring Crk.) are drawn from delta plain swamp and crevasse-splay or interdistributary settings. The Late Pennsylvanian New Castle samples from Texas were collected from organic shales and wet floodplain deposits most analogous to the Cenozoic samples from Wyoming. Early Permian assemblages from the mouth of Brushy Crk. in Texas were deposited in a pond or small lake that formed as part of an abandoned channel or splay. All of the Paleozoic samples are from fine-grained deposits and represent parautochthonous assemblages, but the thickness of the fossil-bearing units, in some places up to 1 meter, suggests that some of the assemblages could have accumulated over periods of 10 to 100 years.

Paleoclimate for both the late Paleozoic and early Cenozoic sample sets is thought to have been wet or seasonally wet, and warm (frost-free or essentially frost-free). The Paleozoic localities from Illinois and Texas were within 10 degrees of the paleo-equator at the time of deposition, the Cenozoic ones were at about 45 degrees N latitude during a period of Earth history when latitudinal gradients of temperature were quite shallow (Zachos et al., 1993).

Methods

The basic unit of sampling for all levels is the *site,* or quarry, a term that has a specific meaning in this context. At each *site* 4–6 square meters of the fossiliferous horizon was dug up and sampled. If more than one plant-bearing lithology was present, collections were made and quantified separately. The thickness of fossil bearing rock sampled at each site was generally between 5 and 20 centimeters, but up to a meter in some of the thicker organic shale deposits.

Relative abundances of species were determined by two methods. For the Cenozoic samples approximately 400

leaves were identified to species level and counted for each site. Relative abundances were calculated based on the proportion of specimens assigned to each taxon. Only half leaves or larger fragments were counted to assure that separate pieces of the same leaf were not counted more than once. Only foliar material was counted in the census. Leaf number and leaf mass have been shown to be highly correlated with basal area in living temperate forests (Burnham et al., 1992).

Relative abundances for the Paleozoic samples were determined by a method in which each block of fossiliferous matrix was treated as a separate quadrat (Pfefferkorn et al., 1975). Any taxon occurring on the block was scored as present, and relative abundances were calculated as the proportion of quadrats on which a given taxon was present. This method of censusing is more appropriate than leaf counting for Paleozoic floras because ferns and pteridosperms have highly divided leaves, stems are the major identifiable organ type of lycopsids and calamites, and the size of an identifiable fragment can vary greatly between species. Counting each of these fragments as an "individual" would bias the census in favor of species that can be identified by small fragments.

Comparisons of different methods of estimating the abundances of species in compression assemblages have shown that both methods estimate similar species richness and rank order abundance (Lamboy and Lesnikowska, 1988; DiMichele et al., 1991). Consequently, variations within sample sets can be compared and evaluated regardless of the technique used in quantification. However, the results of the leaf count and quadrat methods cannot be compared directly. The quadrat method underestimates the abundance of common forms, producing more even abundance distributions than the leaf counting method. The rarest species, however, will be recorded as having the same abundance level in both methods: they will occur as single specimens in a count and will occur only once in the quadrat method.

Data

Site Diversity

Floral lists for all Paleozoic sites are given in Appendix 1; lists for Cenozoic sites are given in Wing et al. (1995). The small number of species believed to have had a floating aquatic habit were removed from the lists because we are comparing the diversity of terrestrial vegetation. Species lists from both time periods include small-statured species, for example herbaceous ferns, as well as arborescent ones. There are a total of 151 sites at which we have measured the number of species, 35 Paleozoic and 116 Cenozoic (Table 1). In aggregate these sites have yielded 308 species, 73 Paleozoic and 235 Cenozoic. Relative abundances of species were quantified at 16 of the Paleozoic sites and 30 of the Cenozoic sites, and for these sites we have calculated indices of diversity (H' = Shannon, D_{Mg} = Margalef's, D = 1/Simpson's dominance) and a non-parametric estimator of species number, Chao1 (Table 2; Chao, 1984; Magurran, 1988; Colwell and Coddington, 1994).

TABLE 1—Mean richness for 151 Paleozoic and Cenozoic plant sites.

	Paleozoic (35 sites)	Cenozoic (116 sites)
Censused sites	n = 16; range = 3–23; mean = 12.0; SD = 5.6	n = 30; range = 6–18; mean = 10.4; SD = 3.1
Sites not censused	n = 19; range = 3–15; mean = 8.7; SD = 2.9	n = 86; range = 2–38; mean = 9.5; SD = 5.9
Grand mean	10.2	9.7
Total species	73	235

Transect Diversity

As discussed above, individual paleobotanical samples of parautochthonous leaf assemblages represent an extremely small area of vegetation, probably between one-tenth and one-half hectare. Differences in species richness and diversity between vegetation types may not be expressed clearly at such a small spatial scale. To increase the spatial scale of our analysis we developed transects at nine levels, four Paleozoic and five Cenozoic, where it was possible to sample parautochthonous leaf assemblages at multiple locations along thin fossiliferous intervals. These transects, comprising from four to 26 samples, are spread across distances ranging from hundreds of meters to nearly ten kilometers, and give a better indication of wet floodplain forest diversity than can be obtained from single samples. They may also include samples that were deposited hundreds of years apart.

Table 3 presents dominance indices and observed and estimated richness for quantitatively collected sites in each of the transects, as well as estimated species richness for each transect as a whole. It is difficult to compare transects having different numbers of sites because longer transects with more sites are more likely to encounter rare or patchily distributed species. Thus transects with more sites will on average record more species unless the vegetation is completely homogeneous at the spatial scale of the larger transect. In order to make appropriate comparisons of transects with different numbers of sites we have statistically subsampled (bootstrapped) the larger transects. The bootstrapped richness values in Table 3 (S_b) were calculated for each transect by randomly drawing a sample of sites (1 ... n) from the full number (n) in the transect, without replacement, 500 times. This permitted the calculation of a mean richness for each number of sites 1 ... n, and allows us to compare transects with different numbers of sites on an equal basis. In Table 3 we report the mean richness for four sites because this is the number in the smallest transects.

Another approach to comparing species richness of different transects is to use an estimator that takes into ac-

count the number of species that occur at only one site ("uniques"). Uniques are presumed to be rare species unlikely to be found in any sample, and the presence of large numbers of uniques implies the existence of other rare species that have not been sampled. Here we use the Chao2 statistic to estimate the number of species in each transect (Chao, 1984; Colwell and Coddington, 1994).

DISCUSSION

Site Diversity

The most striking feature of our plant diversity data for the Paleozoic and Cenozoic is its relative uniformity. A t-test comparing observed site richness (S_o) of the Paleozoic and Cenozoic sample sets (Table 1) shows that the means are statistically indistinguishable (T = 0.55, DF = 64, P = 0.59). The validity of this result might be questioned because, although the Paleozoic and Cenozoic sites are of similar size, a higher proportion of the Paleozoic sites were censused (46% vs. 26%). Sites that have been censused presumably have been studied more intensively than those that have not, and sampling intensity is well known to affect observed richness (Fisher et al., 1943).

To examine the possible effect of censusing on observed richness we compared the mean richness of censused vs. uncensused sites within each time period (Table 1). There is no significant difference between censused and uncensused Cenozoic sites (T = 1.03, DF = 97.8, P = 0.31), but within the Paleozoic sample set censused sites do have significantly higher richness than uncensused sites (T = 2.10, DF = 21.5, P = 0.05). However, a t-test of the uncensused sites shows no significant difference in mean observed richness between the Paleozoic and Cenozoic (T = −0.83, DF = 56.7, P = 0.41), and a two-way ANOVA of the data summarized in Table 1 shows no significant effects of time period or censusing on observed site richness (P = 0.10 for censused vs. non-censused sites, and P = 0.84 for time period). Thus, although a higher proportion of Paleozoic sites were censused, and censused Paleozoic sites are slightly richer than uncensused Paleozoic sites, this effect does not explain the similarity in observed site richness between the Paleozoic and Cenozoic data sets.

Another approach to comparing Paleozoic with Cenozoic site richness is to consider only the 46 censused sites (Table 2). Just as with the full data set, a t-test of site richness at the censused localities reveals no significant difference between the Paleozoic and Cenozoic (T = 1.08, DF = 19.8, P = 0.29). Once again questions of sampling intensity must be addressed. Direct comparison of sampling effort ("N" in Table 2) between the Paleozoic and Cenozoic data sets indicates a greater value for the Paleozoic sites. (The difference is marginally significant, with P = 0.053 in a Kruskal-Wallis test. We have used a nonparametric test because the distribution of n in the Paleozoic data set is not normal. All other parameters had distributions close to normal.) The higher value of N for the Paleozoic samples is caused by the one site where leaves were counted instead of oc-

TABLE 2—Diversity measures, observed and estimated richness for 46 censused Paleozoic and Cenozoic plant sites.

	Paleozoic (16 sites)				Cenozoic (30 sites)			
	Mean	SD	Min	Max	Mean	SD	Min	Max
N	320.63	553.14	16.00	2327.00	280.60	101.69	103.00	464.00
S_o	12.00	5.63	3.00	23.00	10.37	3.05	6.00	18.00
Sing	2.69	1.35	0.00	5.00	2.33	1.71	0.00	7.00
H'	1.71	0.55	0.60	2.57	1.54	0.26	0.93	1.93
D_{mg}	1.44	0.49	0.50	2.51	1.16	0.34	0.65	1.92
D	4.63	2.19	1.47	8.81	3.69	0.97	2.13	5.46
Chao1	15.84	6.83	3.50	27.50	17.77	12.68	6.50	65.00

N = Number of observations or specimens; S_o = Observed number of species; Sing = Number of singletons in sample; H' = Shannon-Wiener index = $-\Sigma p_i \ln p_i$, where p_i = proportional abundance of the ith species; D_{mg} = Margalef's index = $(S_o - 1)\ln N$; D = the inverse of Simpson's index = $1/\Sigma(((n_i(n_i - 1))/(N(N - 1)))$, where n_i = number of observations of the ith species; Chao1 = Chao's estimator of richness = S_o + (Sing^2/2(number of doubletons)).

TABLE 3—Observed and estimated richness of nine transects.

Transect	Age	# Sites	Mean S_o/site	Mean S_o/census	S_o transect	S_b (4 sites)	Chao2 transect
RC	Penn	7	9.3	no census	27	21	36
AXCHIN	Penn	7	8.9	no census	21	17	35
NEWCAS	Penn	8	8.8	8.4	27	20	32
MBRCK	Perm	5	7.8	no census	15	14	33
112m	Eoc	15	9.2	8.2	29	19	33
621m	Eoc	26	10.4	11.4	67	25	187
y98	Eoc	4	8.8	no census	14	14	14.4
tat	Eoc	9	6.4	7.7	22	17	28
dcf	Eoc	4	5.3	1 census	13	13	53.5

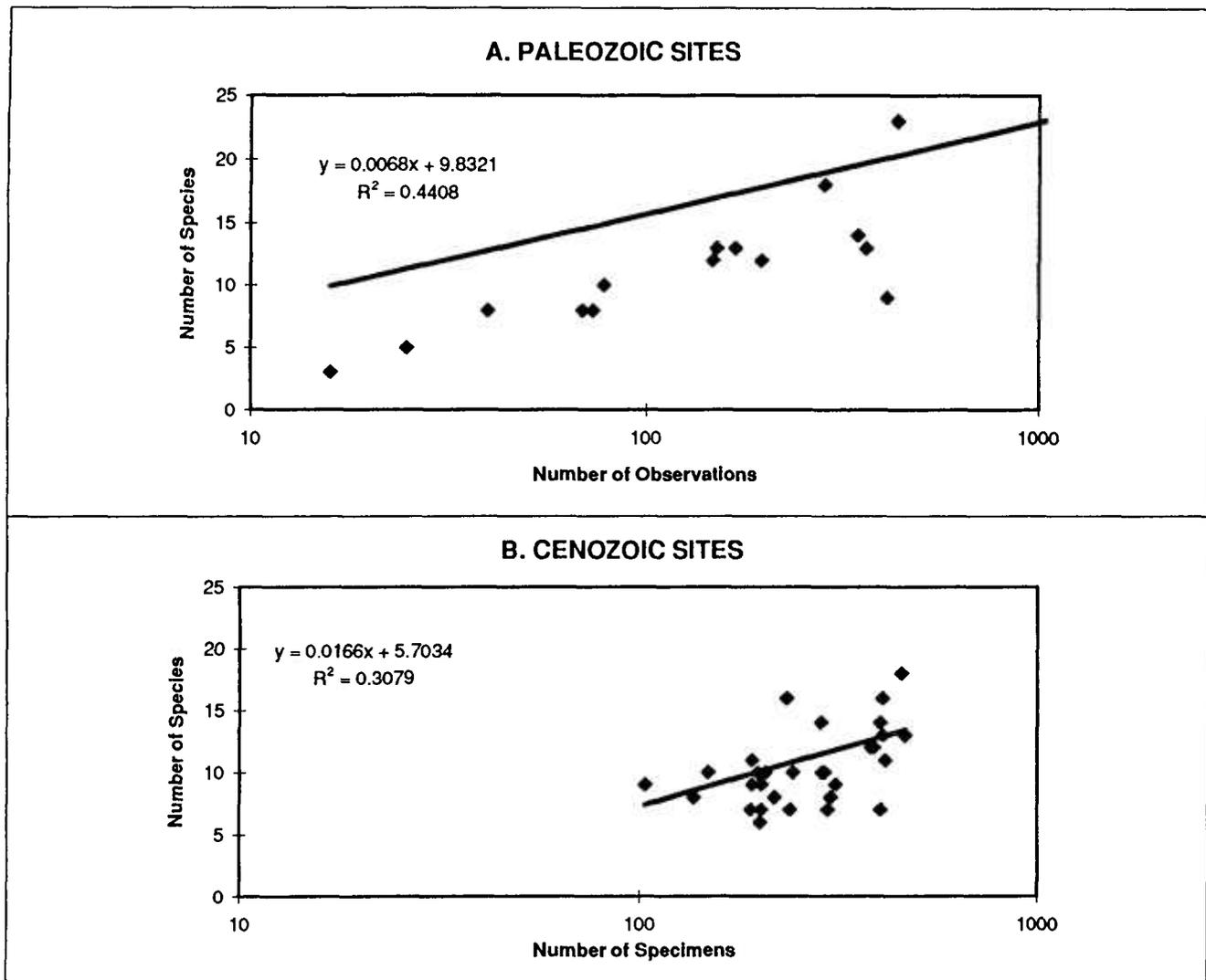S_b = bootstrapped estimate of number of species recovered at four sites. Chao2 = $S_{o(transect)}$ + ((# species occurring at only 1 site)^2/2(number of species occurring at 2 sites)).

currences (n = 2327), but in general the sample sizes are similar.

As discussed above, however, Paleozoic and Cenozoic floras were quantified using different methods; n symbolizes the number of observations for the Paleozoic sites, but the number of leaf specimens for the Cenozoic sites. Within each data set there is a loose but statistically significant positive correlation between sample size and richness (Fig. 2a, b). The stronger correlation between sampling effort and site richness observed in the Paleozoic data set largely reflects the low numbers of species recovered at sites where only 10–100 observations were made. Sampling effort was more uniform among the Cenozoic sites. Among the majority of the sites, where n is 200–500, there is little correlation between n and observed richness. Collecting curves for individual sites also show that richness rises very slowly if at all with more than 200–300 observations or specimens (Fig. 3). Because site richness

plateaus at a level of sampling that was exceeded at most sites, and because sample size does not have a strong effect on richness within either data set, it is likely that the censuses adequately sample the preserved species. Similar site richness in the Paleozoic and Cenozoic data sets does not reflect lower sampling effort at the Cenozoic sites.

The relationship between sampling effort and site richness depends in part on the distribution of relative abundances—where there are more rare species, sampling will have to be more intense to recover the same proportion of total species as at sites with fewer rare forms. Since it has been hypothesized that flowering plants are better able to persist as rare populations than earlier evolved groups (e.g., Hickey and Doyle, 1977; Crepet, 1984), it is important to determine if there are more rare species present in the Cenozoic samples. This can be done by comparing measures of evenness. Evenness cannot be compared easily between the Paleozoic and Cenozoic data sets because the

A. PALEOZOIC SITES

$$y = 0.0068x + 9.8321$$
$$R^2 = 0.4408$$

Number of Species (y-axis: 0, 5, 10, 15, 20, 25)
Number of Observations (x-axis: 10, 100, 1000)

B. CENOZOIC SITES

$$y = 0.0166x + 5.7034$$
$$R^2 = 0.3079$$

Number of Species (y-axis: 0, 5, 10, 15, 20, 25)
Number of Specimens (x-axis: 10, 100, 1000)

FIGURE 2a and 2b—Sampling effort vs. number of species observed, S_o, for: a) Paleozoic sites, and b) Cenozoic sites. For Paleozoic sites sampling effort is measured by the number of observations made using a quadrat based method. For Cenozoic sites sampling effort is the number of leaves counted. See text for discussion of sampling methods.

quadrat method of quantification increases the apparent evenness of the sample relative to the leaf counting method (see Methods).

In spite of this bias, the diversity indices calculated in Table 2 show little difference between Paleozoic and Cenozoic sites. Only Margalef's diversity index (D_{mg}) is significantly higher for the Paleozoic censuses (T = -2.07, DF = 22.7, P = 0.05), probably because the natural log of N is used in calculating D_{mg}, and as we have discussed, there is a difference in N between the two sets of samples. The Shannon index (H′), which is strongly correlated with richness, and Simpson's dominance (D), which is more sensitive to abundances of the common species, are nearly identical for the Paleozoic and Cenozoic data sets. No evenness index captures all aspects of abundance distri-

butions, so we have plotted rank order abundance curves at the same scale for each data set to facilitate visual comparison (Fig. 4a, b). It should be noted that the two highest curves on the Paleozoic graph (Fig. 4a) are derived from censuses of the same site; the higher of the two curves is based on count data, the lower on quadrat data.

Since the difference between the quadrat and leaf count methods of quantification will affect the abundance of rare species least, the number of singletons may be the most robust point of comparison between the two data sets. As with the other measures there is no significant difference in the mean number of singletons in the Paleozoic vs. Cenozoic data sets (T = -0.77, DF = 37.4, P = 0.45). There is no evidence that Cenozoic sites in general have abundance distributions with long "tails" of rare species. This

impression is also confirmed by comparing the Chao1 richness estimates for the Paleozoic and Cenozoic samples. Chao1 is extremely sensitive to rare species because the square of the number of singletons is used in estimating the number of species that were present in the sampling area. Although the difference in Chao1 estimates for the Paleozoic and Cenozoic sites is not significant (T = 0.67, DF = 44.0, P = 0.51), the five highest Chao1 estimates are all for Cenozoic sites.

The similarity in site richness between the Paleozoic and Cenozoic may in part relate to the physical size of the organisms being sampled, i.e., only so many large trees can grow in the 1000–2000 square meter area that contributes leaves to a site. There is substantial direct evidence for the size of the Paleozoic trees. Arborescent lycopsids were large organisms—of similar size to extant angiosperm trees (e.g., Thomas and Watson, 1976; DiMichele and DeMaris, 1987; Gastaldo, 1986). Pteridosperms were moderate-sized trees (Wnuk and Pfefferkorn, 1987; Pfefferkorn et al., 1984), as were Marratiales (Morgan, 1959), and some Cordaitales (Trivett and Rothwell, 1985). Size estimates of the Cenozoic trees are based on in situ trunks of Taxodiaceae, which have diameters ranging from 20 cm to a meter or more (e.g., Kraus, 1988; Basinger et al., 1994), and on the assumption that fossil leaves belonging to extant arborescent families such as Juglandaceae and Betulaceae represent extinct plants of tree size. The available evidence indicates a range of sizes from small to large trees in both the Paleozoic and Cenozoic vegetation. It seems unlikely that the size of the organisms being sampled had a major effect on the number of species recovered at the sites. This could be an important point, however, in extending comparisons to Early Devonian sites, or to fossil assemblages of in situ herbaceous vegetation (Raymond and Metz, 1995).
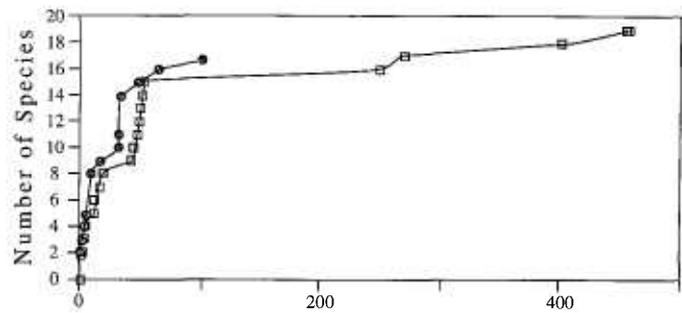

FIGURE 3—Collecting curve for a typical Cenozoic and typical Paleozoic site showing that few species are added at higher sampling effort. Shaded circles are for the Paleozoic site, open boxes for the Cenozoic site.

species, and a higher rate of species increase with additional sites than any other transect. The high diversity of the 621-meter level transect is not a result of higher richness of individual sites, nor does it appear to be a result of its length. Sixteen of the twenty-six sites are concentrated in a central area only 400 meters long, and these sites contain 56 (84%) of the species. The proximate "cause" of high species number at the 621-meter level is the presence of 38 species (57% of the total) that are unique to single sites. The source of this heterogeneity in species composition is not clear—there is no sedimentological evidence that this layer represents a more heterogeneous environment than any of the others. It is possible that the warm, seasonally dry climate that prevailed at the time of deposition of this layer accentuated minor differences in wet floodplain topography, thus creating small-scale heterogeneity in edaphic conditions that is not detectable by field examination of the sediments (Wing et al., 1995).

Transect Diversity

As with the site data discussed above, the transect data, which index richness at a larger spatial scale, show little difference between the Paleozoic and the Cenozoic (Table 3). Although on average the Cenozoic transects have higher richness than the Paleozoic ones (29 vs. 22.5 species), they also have more sites on average (11.6 vs. 6.8). The number of species in a transect is highly correlated with the number of sites ($R^2 = 0.91$, P < 0.001). In order to make meaningful comparisons of species richness among transects we must compensate for differences in numbers of sites, which has been done by randomly resampling, or bootstrapping, each transect.

The bootstrapped curves for the transects show a wide variation in the rate at which new species are added with additional sites, but none of them have an asymptotic shape that would suggest that the backswamp forests have been adequately sampled for species at this spatial scale. There are no apparent group differences between the Paleozoic and Cenozoic transects (Table 3, Figs. 5 and 6). The one transect that is clearly different is from the 621-meter level of the Willwood Fm.; it is longer (6.5 km as opposed to <1 km for most others), has more sites, more

Comparison with Previous Results

Previous work on plant diversity at approximately the spatial scales discussed here has been presented by Niklas et al. (1980) and Knoll (1986). These papers indicate a 50% increase in mean diversity of published floras between the late Paleozoic and the early Cenozoic, which has been interpreted as reflecting increased "alpha" (within habitat) diversity permitted by evolutionary innovations in plant reproductive biology (evolution of heterospory, seeds, insect pollination). Published floras are non-equivalent units, however, representing highly variable numbers of collecting sites, depositional environments, taphonomic and preservational settings, and amounts of time and space. All these factors are known to have effects on richness. Minimally the effect of non-equivalent sampling units will be to make the true pattern of alpha-diversity change through time more difficult to detect.

If the variation in sampling intensity or taphonomic effects changes through time, then a spurious pattern of temporal change in alpha diversity could be generated. Many middle Mesozoic floras, particularly from North America, are preserved in red-bed sequences that may not preserve plants as well as coal-rich strata, therefore pre-

A. Rank Abundance Plot of Paleozoic Sites

B. Rank Abundance Plot of Cenozoic Sites
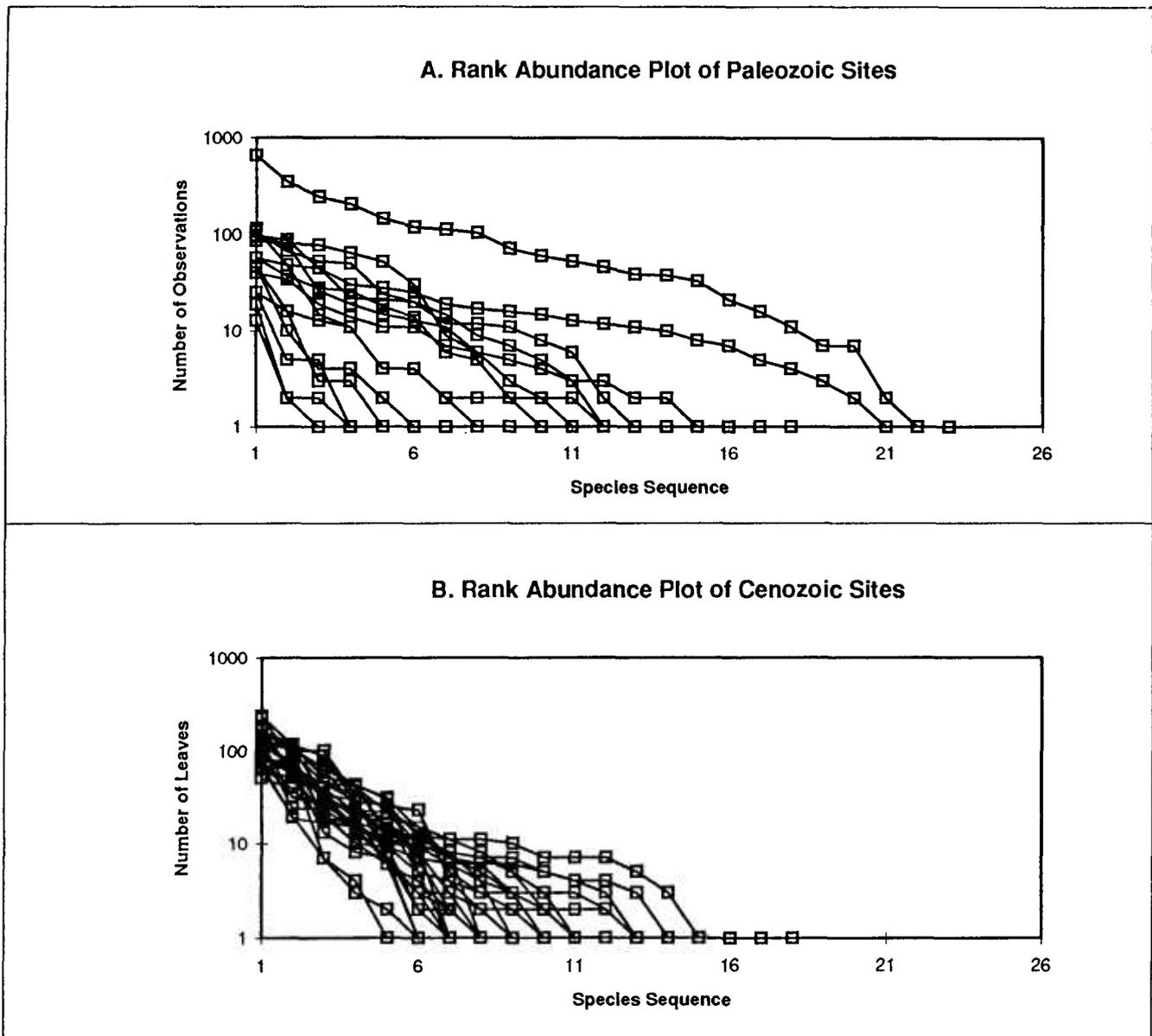
FIGURE 4a and 4b—Rank abundance plots for: a) Paleozoic sites, and b) Cenozoic sites, showing similar distribution of relative abundances of species regardless of geologic age.

serving lower levels of alpha diversity. (Admittedly this is not true of the transect reported here from the Mouth of Brushy Creek in Texas, a Permian red-bed flora similar in richness to the transects of Carboniferous floras from coal-bearing sequences in the mid-continent.) Also consider that the maximum diversity of Carboniferous floras is almost the same as the maximum diversity of Cretaceous ones (Knoll, 1986, Table 7.1). If biology placed limits on the ability of plants to partition niches and exist in hyperdispersed populations, then how can Carboniferous floras have attained maximum levels of species richness comparable to Cretaceous floras? Either biotic thresholds were

passed much earlier in plant evolution than is generally thought, or the major controls on local plant diversity are related to abiotic rather than biotic factors.

Comparison of Fossil Site Richness with Living Forests

Data compiled by Gentry (1988) for one-tenth hectare (1000 sq. m) plots are comparable in spatial scale to the individual site data we have assembled. The exclusion of plants with dbh <2.5 cm from Gentry's data makes them even more similar to paleobotanical data, where there is a diminished likelihood of preservation for herbs and small
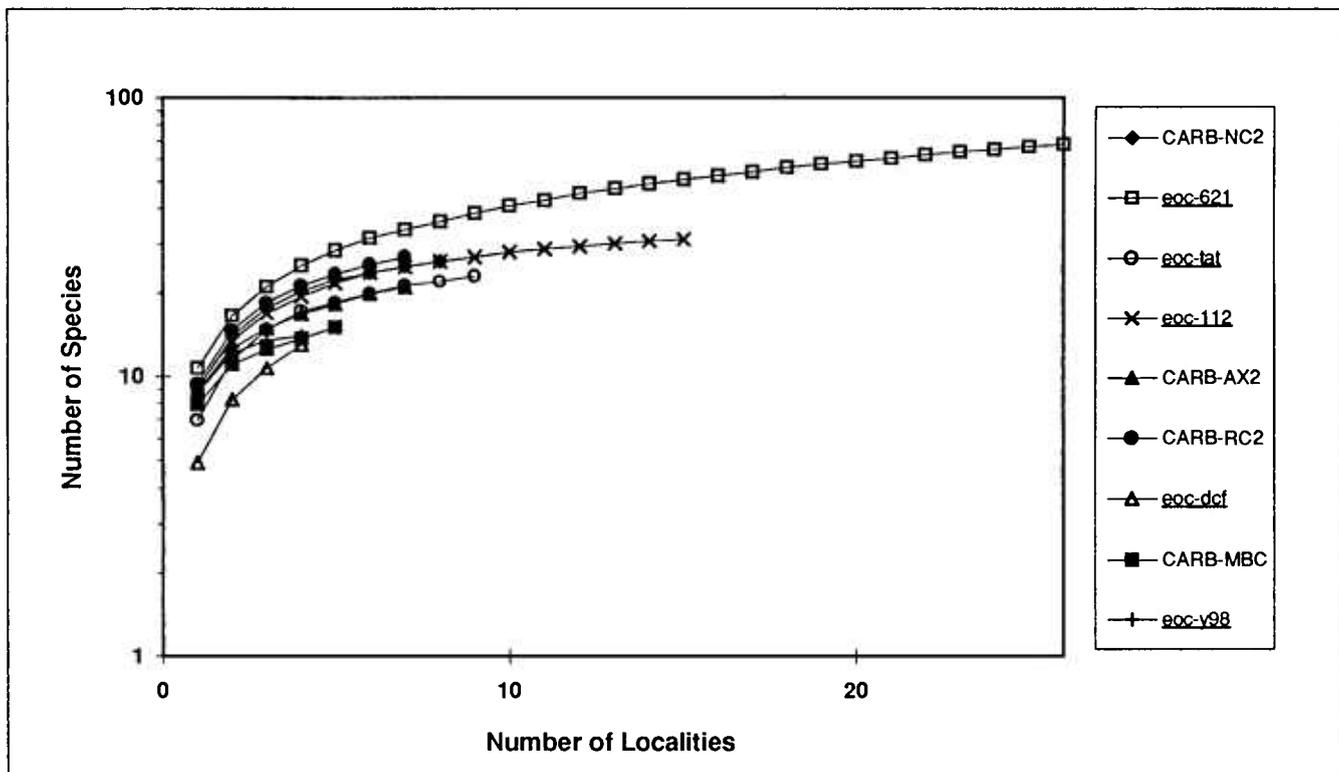
FIGURE 5—Bootstrapped estimates of mean number of species observed with different numbers of sites in a transect. Closed symbols are Paleozoic transects, open symbols and crosses are Cenozoic transects.

woody plants (Scheihing, 1980; Burnham et al., 1992). Gentry's data show a strong inverse correlation between number of species per sample and latitude, as well as a strong tendency for dry climate vegetation to have fewer species (Fig. 7).

The Paleozoic data points are far below any of the modern equatorial samples reported by Gentry, most of which have an order of magnitude more species. However, there are many examples of low-diversity floras in the wettest part of the lowland tropics, especially in areas such as swamps and lower delta plains that are physically stressed (Anderson, 1964; Gastaldo and Huc, 1992). The Cenozoic samples from 45 degrees N are close in species number to modern samples from the same latitude, but this ignores the climatic differences between the early Cenozoic and the present. Eocene climate at 45 degrees N was subtropical or warmer, similar to modern climate at 20–30 degrees N (Wing and Greenwood, 1993). When the Eocene samples are compared to Gentry's samples of modern subtropical vegetation, they have about half the number of species, but once again edaphic factors are not taken into account. Much of the difference in species richness between Gentry's one-tenth hectare plots and the fossil site-level data may be explained by the habitats being sampled. Gentry's data are for terra firma forests, the fossil sites likely represent environments that were habitable only by species that could tolerate high water table and sediment influx.

IMPLICATIONS FOR THE FACTORS GENERATING PLANT DIVERSITY

The similarity in site-scale richness of arborescent plants in wet floodplain habitats from the Carboniferous and Cenozoic implies that evolutionary innovations like heterospory, seeds, insect pollination, and animal dispersal of seeds have had relatively little impact on the number of species that can occupy the same small area in this type of habitat. Were lowland, wetland habitats "saturated" with species fairly early in the history of life on land? The environments we are sampling are wet, somewhat dysoxic, and regularly disturbed by sedimentation and flooding. Perhaps under these physical conditions the development of seeds and other reproductive "advances" is not significant in permitting more species to coexist. Species packing may be set by ability to intercept light, gather nutrients, tolerate flooding, and by the size of individuals. Disturbance regimes at the landscape scale also may affect the ability of species populations to coexist on similar resources. We do not know if site-scale richness increased in other habitats, but even if wet floodplains are not representative of the diversity history of other terrestrial habitats, they do dominate the fossil record of terrestrial plants. Although we might expect a close correspondence between the diversity history of wet floodplains and the diversity
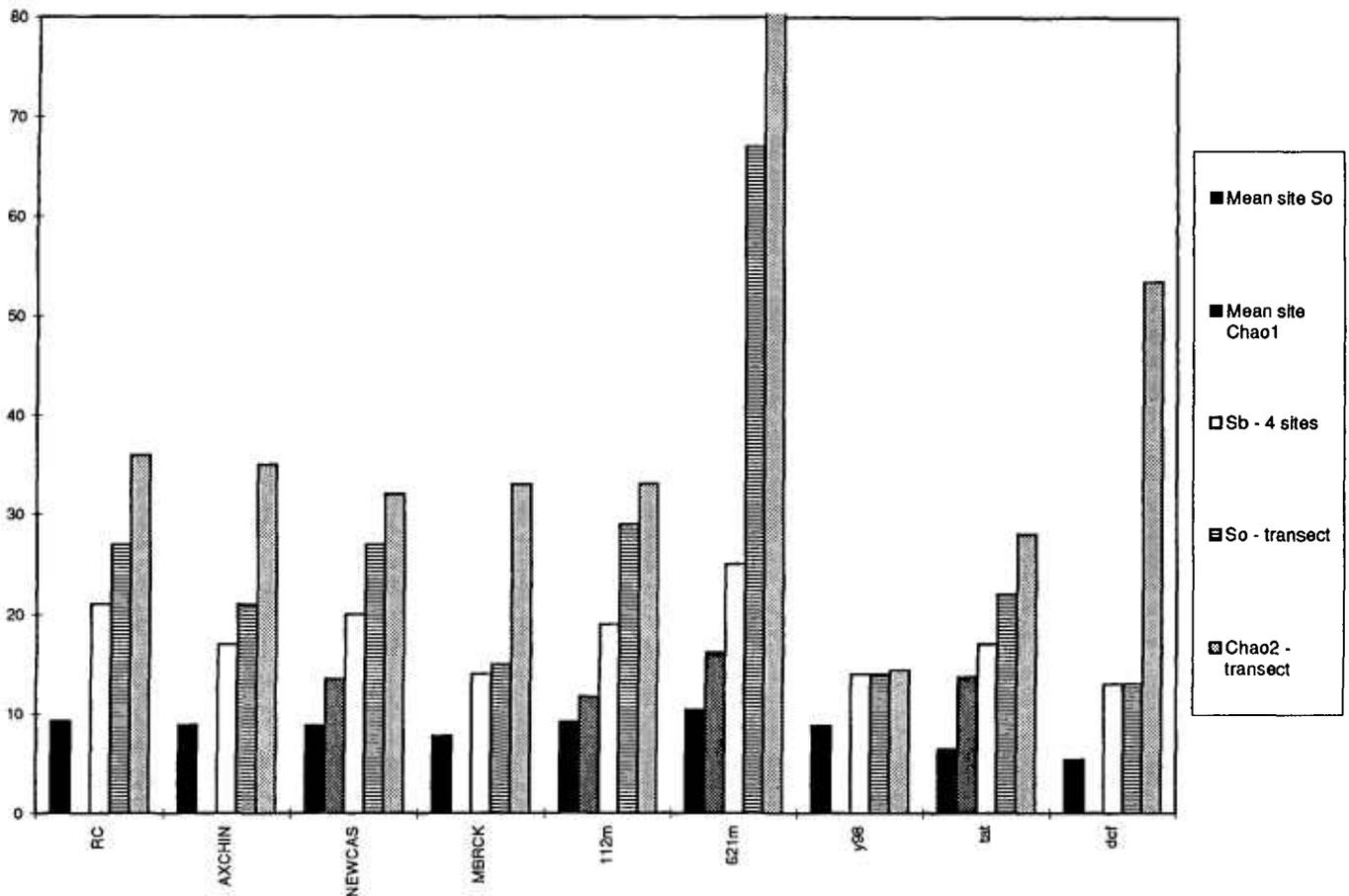
FIGURE 6—Histograms showing the number of species observed and estimated at different spatial scales. S_o—species observed, S_b—species estimated using the bootstrap method, Chao1—Chao1 estimate based on number of singletons and doubletons from quantitative site data, Chao2—Chao2 estimate based on number of species occurring at only one or two sites in a transect. Chao1 could not be calculated for uncensused sites. Paleozoic transects are RC, AXCHIN, NEWCAS, and MBRCK; Cenozoic transects are 112m, 621m, y98, tat, and dcf.

history recorded by the plant fossil record as a whole, this is not the case.

How do we explain the increase in global richness reported by Niklas et al. (1980, 1983, 1985) if site and transect diversity did not increase? As discussed by Niklas et al. (1980), the increase in global plant species number is strongly related to increasing outcrop area toward the Recent. They state:

"It is clear that the geological biases of sampling associated with temporal patterns of nonmarine sedimentation and erosion explain most of the information contained in the histogram of Phanerozoic vascular plant diversity; however the correlation between outcrop area and apparent species diversity is not exact. Once the 'sampling effect' has been filtered out mathematically, residuals . . . remain, and these require consideration." (p. 34–35, Fig. 3).

The time periods with few species per million years per outcrop area are the Triassic, Jurassic, and Permian—this is the Pangean interval, during which climate in regions

that contain the bulk of described species (i.e., North America and Europe) was warm and had highly seasonal precipitation (Parrish and Peterson, 1988; Ziegler, 1990). Permian through Jurassic terrestrial sediments in this region include widespread evaporite, aeolian dune, and oxidized soil deposits, none of which are conducive to plant preservation. The geological periods with many species per million years per outcrop area are the Devonian, Carboniferous, Cretaceous, and Tertiary. Except for the Devonian these are the three major global coal forming intervals in North America (Niklas et al., 1980). With the exception of the Devonian, global plant species number can be explained largely by a combination of period duration, outcrop area, and paleoclimate, with no need to invoke a secular increase in the number of plant species through the Phanerozoic. The global plant species data set (Niklas et al., 1980, 1985; Niklas and Tiffney, 1994) does not provide strong evidence for a major increase in plant diversity from the Carboniferous to the early Cenozoic, in spite of the roughly 50% greater number of species recorded for early Cenozoic (Niklas and Tiffney, 1994).

Although the pattern of increasing diversity in the global data set is weak, it is clear that global diversity of terrestrial plants must have increased from one at the first appearance of plants on land to millions at present. How can richness at the level of site and transect *not* have risen? A similar problem has been recognized in the marine realm, where it has been argued that within-habitat richness did not increase much from the Ordovician to the late Paleozoic (Sepkoski, 1988). Sepkoski's observations are at a coarser temporal and spatial scale than ours, but they find a similar paradox—the Paleozoic increase in species richness at "alpha" and "beta" scales is not sufficient to explain the increase in "gamma" diversity through the same period. Where does the additional large-spatial-scale diversity come from? Increased vertical complexity, or tiering, should be manifested as an increase in richness at the smallest spatial scale (sites). Increased environmental specificity should be evident at a slightly larger spatial scale (groups of sites in the same general environment). In the title of his paper Sepkoski queried "Alpha, beta, or gamma: where does all the diversity go?" The question raised by our analysis of site and transect scale plant diversity is: "Where does all of the global diversity come from?" In the plant case, global diversity increases may have been generated largely by expansion into new kinds of "marginal" environments rather than by increased packing in old ones (DiMichele and Aronson, 1992; Valentine et al., 1991).

It is evident that lowland, wetland vegetation underwent a total change in species and higher taxon composition between the late Paleozoic and the early Cenozoic. When examined at a finer temporal scale, species turnover in the wetlands proves to have been a mixture of both gradual replacement and catastrophic change (Phillips and Peppers, 1984; Phillips et al., 1985; Knoll, 1984). Following major extinctions, wetlands were reoccupied by lineages that previously occupied environments peripheral to the wetlands, ultimately the more drought-tolerant (and extinction resistant) seed plant lineages. As dominance of the wetland habitats was relayed from lycopsids to ferns to pteridosperms to conifers to angiosperms, why was local richness not ratcheted up with increases in reproductive "sophistication" that would presumably have permitted the existence of more dispersed plant populations and therefore the coexistence of more species in a local area? We can only guess that the physical rigors of survival in these habitats have always placed a low limit on the number of species they support.

Plant Diversity at Larger Spatial Scales

If global increase in the number of plant species cannot be explained at the small spatial scales we have studied, is there any direct evidence of increasing diversity at larger spatial scales? Landscape-scale diversity is beyond the scope of this paper, but it may be assessed in a preliminary way by comparing floras that were transported prior to deposition. The late Pennsylvanian Mazon Creek flora, the most widely collected and best studied Paleozoic flora in
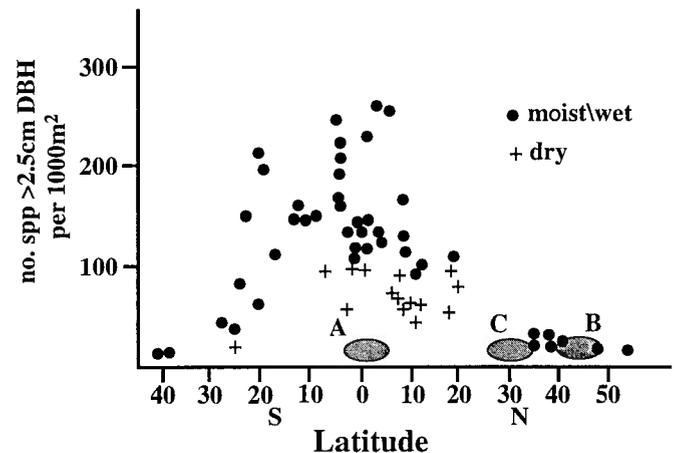
FIGURE 7—Plot of number of species >2.5 cm dbh on tenth-hectare plots in living forests. Data from Gentry (1988). Compare richness of Paleozoic (A) and Cenozoic (B) sites in this study with comparable samples from the same latitude and of the same spatial scale. Although the Cenozoic sites are from paleolatitude 45° N, they lived under a climate more similar to that currently found at 20–30° N. (C) marks the appropriate point of comparison considering the paleoclimate of the Cenozoic floras.

the world, has only 96 species (Pfefferkorn, 1989). Deposition of the Mazon Creek plants in a nearshore, shallow marine setting took place over a substantial interval of time, but probably less than 10,000 years. Plant remains were transported to the site of deposition by rivers that presumably sampled a large area of low coastal plain. A roughly similar taphonomic setting and depositional environment are inferred for the Eocene London Clay flora, although the remains are mostly fruits and seeds (Collinson, 1983). Over 500 distinct forms have been recorded from the several million year span of the London Clay Formation, and over 300 from the most speciose single locality at Sheppey (Collinson, 1983). It should be noted that most of the major localities in the London Clay span substantial stratigraphic sections, and that the erosion and concentration of the petrified specimens on beaches by the waves has allowed very large numbers of specimens to be collected (Collinson, 1983). These factors almost certainly are important in explaining the richness of the London Clay flora, since it has many more species than other Tertiary assemblages.

Many Tertiary compression assemblages have over 100 species, but most or all of these are derived from lake basins that probably had substantial surrounding topography (e.g., Florissant: MacGinitie, 1953; Green River: MacGinitie, 1969; Republic: Wolfe and Wehr, 1987). Paleozoic parallels, such as deposits from Early Permian intermontane basins in Northern Europe (Kerp et al., 1990), or late Pennsylvanian floras reflecting local, steep topographic gradients (Hamilton flora: Rothwell and Mapes, 1988; Kinney flora: Mamay and Mapes, 1992) are depauperate in comparison to the Cenozoic examples. It is from such allochthonous assemblages that a general picture emerges. The growth and distribution of plant species di-

versity is rooted in the physical environment. The timing of this diversification will be revealed by sampling of rare, "extra-basinal" assemblages, rather than by detailed studies or global compilations of a plant fossil record that is inevitably centered in the wet lowlands.

CONCLUSIONS

We offer the following generalizations based on the data collected and analyzed for this paper.

1) Measurement of plant diversity at the same temporal and spatial scales used by plant ecologists is possible even in the Paleozoic because many plant compression fossil assemblages are ecological "snapshots" that are highly localized in time and space. The extreme localness of this type of compression fossil assemblage requires that sampling be extensive and intense at each stratigraphic level in order to be representative of the flora of that time. It also means that the composition and diversity of assemblages is strongly influenced by environment of deposition and sampling intensity, which must be accounted for when trying to study temporal patterns of diversity change. The advantage to the highly localized fossil record of plants is that it preserves the composition and richness of local vegetation with a minimum of taphonomic overprinting.

2) After putting together a data set that is more carefully matched for depositional setting, taphonomic bias, and sampling effort than any other we know of, we are unable to demonstrate any difference in site or transect richness of wet floodplain forests in the late Paleozoic and early Cenozoic.

3) This similarity in local diversity across 250 million years may reflect early saturation of floodplain habitats in terms of the number of species they support. Evolutionary innovations and niche differentiation do not appear to have increased the diversity of wet floodplain vegetation through geological time.

4) The temporal pattern of global increase in plant diversity is poorly constrained, and its connection to key innovations in plant biology dubious. Major increases in global diversity may largely reflect colonization of new, successively drier and colder, environments through the Phanerozoic, coupled with increased representation of those environments in the sedimentary record of the Cretaceous and Tertiary.

5) Future studies of plant diversity through geological time should take advantage of the unusual taphonomic features of the plant fossil record that allow richness to be studied at a variety of temporal and spatial scales, especially those that make paleontological observations comparable to ecological ones.

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APPENDIX 1

Paleozoic species and sampling sites by transect. Numbers following site designations refer to species list.

(1) *Alethopteris ambigua,* (2) *Alethopteris serlii,* (3) *Alethopteris zeilleri,* (4) *Annularia asteris,* (5) *Annularia carinata,* (6) *Annularia radiata,* (7) *Annularia sphenophylloides,* (8) *Annularia spicata,* (9) *Asterophyllites equisetiformis,* (10) *Asterophyllites* sp., (11) *Autunia conferta,* (12) *Brachyphyllum densum,* (13) calamites, (14) *Comia* sp., (15) cordaites, (16) *Culmitzia speciosa,* (17) *Daubreeia* sp., (18) *Dicopteris opulenta,* (19) Eremopteroid sphenopterid, (20) *Eusphenopteris striata,* (21) *Karinopteris* sp., (22) *Lepidodendron aculeatum,* (23) *Lilpopia raciborskii,* (24) *Linopteris* sp., (25) *Lobatopteris vestita,* (26) *Lobatopteris* sp., (27) *Mariopteris nervosa,* (28) *Mariopteris* sp., (29) *Nemejcopteris feminaeformis,* (30) *Neuropteris auriculata,* (31) *Neuropteris heterophylla,* (32) *Neuropteris obliqua,* (33) *Neuropteris ovata,* (34) *Neuropteris rarinervis,* (35) *Neuropteris scheuchzeri,* (36) *Odontopteris* sp., (37) *Oligocarpia* sp., (38) *Pecopteris cyathea,* (39) *Pecopteris miltonii,* (40) *Pecopteris "hemitelioides",* (41) *Pecopteris obliquinervis,* (42) *Pecopteris plumosa-dentata,* (43) *Pecopteris polymorpha,* (44) *Pecopteris unita,* (45) *Pecopteris* sp., (46) *Phasmatocycas kansanus,* (47) *Polysporia* sp., (48) *Pseudomariopteris ribyronii,* (49) *Sigillaria brardii,* (50) *Sigillaria* sp., (51) *Spermopteris* sp., (52) *Sphenophyllum cuneifolium,* (53) *Sphenophyllum emarginatum,* (54) *Sphenophyllum majus,* (55) *Sphenophyllum oblongifolium,* (56) *Sphenophyllum* sp., (57) *Sphenopteridium* sp., (58) *Sphenopteris bronnii,* (59) *Sphenopteris schatzlarensis,* (60) *Sphenopteris* sp. 1, (61) *Sphenopteris* sp. 2, (62) *Sphenopteris* sp. 3, (63) *Sphenopteris* sp. 4, (64) *Sphenopteris* sp. 5, (65) *Sphenopteris* sp., (66) *Synchysidendron* sp., (67) *Taeniopteris* spp., (68) UN small foliage, (69) *Walchia hypnoides,* (70) *Walchia pinniformis,* (71) *Walchia* sp., (72) *Wattia texana,* (73) *Zeilleropteris* sp.

Roaring Creek, Middle Pennsylvanian, Indiana

RC1 (USNM 38376): 2, 15, 22, 35, 39, 47, 50, 60
RC2 (USNM 38377): 2, 22, 27, 32, 35, 39, 50, 61
RC3 (USNM 38378): 2, 6, 9, 15, 20, 27, 31, 32, 34, 39, 59, 63
RC4 (USNM 38379): 2, 6, 7, 9, 15, 19, 27, 31, 32, 34, 35, 39, 52, 59, 64
RC8 (USNM 38383): 21, 22, 39
RC9 (USNM 38384): 2, 27, 31, 32, 35, 40, 52, 61, 62
RC10 (USNM 38385): 13, 15, 21, 22, 27, 31, 34, 35, 39, 68

AMAX Coal Company, Chinook Mine, Middle Pennsylvanian, Indiana

AC1 (USNM 38318, 38319): 1, 2, 4, 6, 9, 21, 33, 34, 35, 39, 42, 53, 66
AC2 (USNM 38315): 13, 25, 28, 45, 53, 54, 33, 34, 35, 66
AX1/1: 24, 25, 33, 34, 38, 39, 45
AX1/2: 13, 25, 34, 38, 39, 45, 53
AX1/3: 13, 33, 34, 38, 39, 45, 53
AX1/4: 2, 13, 25, 33, 34, 38, 39, 45, 53
AX2: 2, 13, 24, 25, 33, 34, 45, 53, 65

Newcastle Coal, Upper Pennsylvanian, Texas

1990-10: 5, 9, 10, 23, 35, 45, 49, 56
1990-11: 5, 23, 26, 30, 43, 44, 45, 48, 49, 55, 56, 57, 58
1990-36Az6/8: 5, 9, 26, 29, 33, 35, 48, 49
1990-36Az7: 5, 9, 26, 33, 35, 41, 45, 49
1990-36B: 8, 18, 23, 33, 48
1991-13A: 3, 5, 35
1991-13B: 5, 17, 23, 33, 35, 45, 48, 49, 56
USGS 10162: 5, 15, 23, 30, 37, 38, 43, 44, 45, 48, 55, 57, 58, 71

Mouth of Brushy Creek, Lower Permian, Texas

1992-9: 11, 15, 16, 36, 49, 51, 56, 67, 69, 70, 72, 73
1993-15A: 11, 12, 14, 16, 67, 69
1993-15B: 11, 14, 15, 67, 69
1993-15C: 11, 12, 14, 15, 16, 46, 67, 69, 73
1993-15D: 11, 12, 14, 15, 16, 70, 73