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SPECIES RICHNESS WITHIN FAMILIES OF FLOWERING PLANTS

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Abstract.—Variation in species and genus richness among families of flowering plants was examined with respect to four classification variables: geographical distribution, growth form, pollination mode, and dispersal mode. Previous studies have estimated rates of species proliferation from age and contemporary diversity. Here we found that the earliest appearances in the fossil record are correlated with contemporary familial species richness, abundance in the fossil record, and the independent variables considered in this analysis. Thus, we believe that the fossil record does not provide reasonable estimates of the ages of families and that the rate of species proliferation cannot be calculated from such data without bias. Accordingly, our subsequent analyses were based on contemporary species richness of families. Although the classification variables were interrelated, each made largely independent contributions to familial species richness. Cosmopolitan families were 5.6 times more species-rich than strictly tropical families and 35 times more species-rich than strictly temperate families. Families including both herbaceous and woody growth forms were 5.7 and 14 times more species-rich than families with either growth form alone. Although animal pollination was significantly associated with elevated familial species richness, the effect was statistically weak. The most prominent effect was that families with both abiotic and biotic dispersal had more than 10 times as many species as families with either dispersal mode alone. Our analyses also revealed that families having both dispersal modes were more likely to have several growth forms, suggesting that evolutionary flexibility of morphology may be generalized over diverse aspects of life history. These results do not support the idea that pollination and dispersal by animals were primarily responsible for the tremendous proliferation of angiosperm species, either by producing population structures conducive to speciation or by applying selection for diversification. Instead, the importance of varied dispersal mode, growth form, and climate zone in predicting high familial species richness suggests that a capacity to diversify morphologically and physiologically may have been primarily responsible for high rates of species proliferation in the flowering plants.

Key words.—Angiosperms, diversification, geographical distribution, growth form, life-history flexibility, pollination, seed dispersal, speciation rate, species richness.

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Since at least 140 Mya, flowering plants (angiosperms) have undergone a spectacular diversification. During this period, they have replaced formerly dominant gymnosperms and other ancient vascular plants over much of the earth's surface (Crane and Lidgard 1990), and they presently number about 240,000 species. Increasing numbers of taxa of angiosperms in local floras through the Tertiary suggest that this radiation may be continuing (Knoll 1986). The rapid increase in angiosperm diversity has been linked to many of the unique attributes of flowering plants (Stebbins 1981), particularly their intimate association with animals for pollination and dispersal (Burger 1981; Regal 1982; Crepet 1984; Kiestler et al. 1984; Bawa 1992).

The number of species within a higher taxon may be influenced by ecological relationships among contemporary species, the history of spe-

cies production and extinction within the taxon, or both (Ricklefs and Schluter 1993). Ecological versatility of higher taxa may be indicated by the morphological and physiological diversity of their subordinate species. This versatility presumably reflects the variety of climate zones and habitats that they inhabit, as well as the variety of ways by which they may exploit the resources of the local environment. Thus, species richness in higher taxa may be related to the ability of subordinate lineages to diversify into different ecological roles (Lack 1947; MacArthur 1969, 1972). Species number also may increase with time, at rates governed by speciation and extinction, independently of local ecological interactions (Rosenzweig 1975; Stanley 1979; Niklas et al. 1985).

The great diversity of angiosperms suggests that, compared to other plant groups, their attributes either promote diversification, escalate speciation, reduce vulnerability to extinction, or facilitate some combination of these factors. Adaptations for pollination and dispersal by animal

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agents might influence rates of both speciation and extinction. Several authors have emphasized that efficient long-distance transfer of pollen by animals ensures cross pollination in sparse populations and reduces the probability of extinction in such populations (e.g., Regal 1977). Moreover, dispersal by animals increases the probability that seeds arrive at suitable habitats or avoid pathogens and predators (Connell et al. 1984) and should thus also reduce vulnerability to extinction.

If one accepts the predominance of allopatric speciation in angiosperm proliferation, then pollination or dispersal by animals, or both, could result in high diversity when it promotes isolation of subpopulations, fosters evolutionary change of isolated populations, and diminishes hybridization in sympatry, or results in some combination of these effects. Many specific scenarios for these mechanisms have been suggested. For example, coevolution of plants and their pollinators and seed dispersers, coupled with the structural complexity of angiosperm flowers and fruits, may facilitate the evolution of isolating mechanisms (Stebbins 1981; Crepet 1984; Bawa 1992). Stanley (1979) has argued that the rate of diversification, in general, increases in relation to complexity of structures and interspecific relationships. Regal (1982) added that animal pollination promotes outcrossing and that the resulting large, genetically diverse populations may undergo rapid phyletic evolution. Regal (1977), Burger (1981), and Crepet (1984) also have emphasized that long-distance seed dispersal by animals creates populations of sparsely distributed individuals within which selection fosters the evolution of animal pollination. If so, then animal dispersal may indirectly promote diversification by favoring animal pollination. Long-distance seed dispersal also can promote the establishment of peripheral isolated populations (van der Pijl and Dodson 1966; Snow 1980; Tiffney 1984, 1986). One must keep in mind, however, that long-distance pollination and seed dispersal also may inhibit the formation of isolated populations by elevating gene flow (see also Loveless and Hamrick 1984).

Balancing the view that animal pollination and dispersal have been largely responsible for the evolutionary success of the angiosperms, Stebbins (1981) stressed the role of additional innovations of morphology and development in the predominance of flowering plants over other seed plants. Among these were changes in gy-

noecium structure and fruit development that greatly increased speed of fertilization and seed production, and also the protection afforded the seed. According to Stebbins, these attributes, which enhanced seed production, dispersal, and seedling establishment, also promoted reproductive flexibility and ecological opportunism.

Factors that may have caused angiosperms to displace gymnosperms, if this did indeed happen by competitive exclusion, need not have promoted their remarkable diversification. Competitive superiority may result from attributes different from those that foster speciation and diversification. Thus, the problems of angiosperm dominance and angiosperm diversity tentatively should be kept separate. Factors that promoted angiosperm diversity early in their history also may have differed from those that promoted and maintain contemporary diversity. Furthermore, the relative contributions to angiosperm species diversity of morphological and, therefore, ecological versatility and of mechanisms of species production must be clearly distinguished (Regal 1977; Midgley and Bond 1989).

The explanations outlined above relating modes of pollination and dispersal to diversity may be phrased in terms of hypotheses which, for the most part, cannot be addressed by experimental study. Hypotheses that are confined to the practical domain of investigation, for example relating dispersal mode to the genetic structure of populations (Hamrick and Loveless 1986), may not be generalizable to the larger issue of speciation.

The case for animal pollination and dispersal playing a role in angiosperm speciation is built largely upon deduction and circumstantial evidence. If this hypothesis were true, however, one would expect different modes of pollination and dispersal to be associated with greater or lesser species richness in contemporary clades. At present, empirical relationships between species number and reproductive biology afford the best possibility of providing support for these ideas. Yet, the evidence has been largely ambiguous, conflicting, or unconvincing.

Tiffney (1986) determined that, within the subclass Hamamelidae, families with biotically dispersed fruits or seeds had greater numbers of species than those that are abiotically dispersed. In contrast, Herrera (1989) found no difference in species richness between angiosperm families with abiotic and biotic dispersal. Fleming (1991) came to the same conclusion as Herrera, but also

found, as did Herrera, that families exhibiting both biotic and abiotic fruit dispersal had greater numbers of species than those with either dispersal mode alone. Neither author commented upon the significance of this pattern.

Midgley and Bond (1991) used counterexamples to fault hypotheses relating animal pollination and dispersal to high diversity; they also concluded, in an analysis of monocot families in the Cape flora (South Africa), that pollination mode and species diversity are not correlated.

The most thorough analysis is that of Eriksson and Bremer (1992), who used the present-day numbers of species and ages of families as indicated by the fossil record to estimate exponential rates of proliferation of species within families. This approach, which was advocated by Stanley (1979), produces readily interpretable results only when the number of species per clade undergoes exponential increase at a more or less constant, hence characteristic, rate since its origin. When increase in species number is asymptotic or when species number fluctuates over time, average exponential rates of increase provide little information concerning the mechanisms of species proliferation. Under the assumption of exponential growth, however, number of species (S) increases according to $S = S_0 e^{kt}$ where S_0 is the initial number of species (assumed to be 1), k is the average exponential rate of proliferation (speciation – extinction), and t is the age of the taxon. By rearranging the logarithmic (base e) transform of this equation, $k = \ln(S)/t$. Eriksson and Bremer estimated the age (t) of each family by its earliest occurrence in the fossil record.

Having estimated k for 147 families of angiosperms, Eriksson and Bremer (1992) used one-way ANOVA to determine whether values of k are influenced by growth form, mode of pollination, and mode of dispersal. Statistical interactions between effects were not estimated (except for the growth-form \times dispersal-mode interaction: not significant) because the data set did not meet the assumption of homogeneity of variances. The results indicated that both animal dispersal and herbaceous growth form were associated with elevated species proliferation rate (k). As in the analyses of Herrera (1989) and Fleming (1991), biotic versus abiotic dispersal was not a significant effect; unlike Herrera and Fleming, Eriksson and Bremer did not include in their analyses families with both dispersal modes.

The reliability of Eriksson and Bremer's anal-

ysis depends in large part on how well earliest occurrences in the fossil record estimate the ages of taxa. Because more than half of all plant families have not been identified as fossils, one suspects that the records for most taxa are inadequate and that times of evolutionary appearance may considerably predate reported first occurrences in the fossil record. Even if the fossil record is taken at face value, families for which fossils have been recognized are unlikely to be a random sample of angiosperm taxa with respect to species richness, growth form, and modes of pollination and dispersal.

Although the growth-form \times dispersal-mode interaction was not significant in Eriksson and Bremer's analysis, it seems likely that other combinations of the three variables included in their study might interact in their statistical influence on species richness. Also, other studies have shown growth form and dispersal mode to be correlated (Westoby et al. 1990). Therefore, heterogeneity of species diversity with respect to any one variable could result fortuitously from its correlation with another variable that influenced diversity directly.

In this study, we first critically evaluate the assumptions that earliest appearance in the fossil record indicates the age of an angiosperm taxon and that diversity within a clade increases exponentially at a characteristic rate over time. Our analysis demonstrates either that earliest fossils provide unreliable estimates of age, or that diversity does not increase as an uncomplicated exponential function of time, or both. Because fossil data are therefore uninformative, inquiry into the consequences of dispersal and pollination mode for diversification must necessarily be limited to analysis of contemporary species richness of taxa rather than estimated rates of exponential proliferation. Accordingly, we have compiled a data base that includes, for all families of flowering plants, number of species and genera, geographical distribution, growth form, and modes of pollination and dispersal. These data were then analyzed in a four-way ANOVA to determine the contributions of each of the four independent variables (distribution, growth form, pollination, dispersal) to variation among families in species richness.

DATA AND ANALYSES

Two data sets were used in this study. The first was that of Eriksson and Bremer (1992, Appen-

dix) with some additions based on Taylor's (1990) summary and analyses of North American paleofloras. Eriksson and Bremer's data included only pollen records (Muller 1981), whereas those of Taylor were based primarily on macrofossils. Neither of these sources of data is entirely satisfactory, although Niklas et al. (1985) found general agreement between rates of species diversification calculated from occurrences of fossil pollen, on one hand, and fossil seeds and fruits, on the other. Thirty of the ages in Eriksson and Bremer's appendix were increased based on Taylor's figures. The following families for which North American fossil records are available were added to the list: Actinidiaceae, Aristolochiaceae, Berberidaceae, Hydrangeaceae, Lemnaceae, Melastomataceae, Simaroubaceae, Styracaceae, and Zingiberaceae.

The second data set included all families of flowering plants based on the systematic compilations of Cronquist (1988), Brummitt (1992), and Thorne (1992); where the circumscription of families differed between these authors, we chose the more conservative (wider) treatment. This resulted in the lumping of 18 small families for a total of 365 families. Taxa recognized as families may differ considerably in morphological distinctiveness because of different practices of systematists and varying degrees of differentiation of taxonomically informative characters.

Variables were numbers of genera (Brummitt 1992) and species (Mabberley 1987), geographic distribution, growth form, and modes of pollination and dispersal. Information on geographic distribution was taken from Thorne (1992). We divided distributions into four categories: (1) tropical, including families distributed at both low and high elevations, but not high elevations exclusively, and also including taxa extending to warm-temperate latitudes (most frequently southern Japan, North Africa–Mediterranean, Florida, and southern Australia); (2) temperate, including families that do not extend their distributions into the tropics at any elevation but may extend their distributions poleward to boreal zones—generally, plants inhabiting zones with frost; (3) subcosmopolitan (hereafter called cosmopolitan), including virtually all families given this designation by Thorne, but also including taxa that have more restricted distributions (e.g., only the Americas) that nonetheless include both lowland tropical and temperate areas; (4) tropical-montane and temperate, including most of the families given this designation

by Thorne; basically temperate in distribution but extending at high elevation into the tropics.

We handled growth form differently from Eriksson and Bremer (1992). For each family, we tabulated presence or absence of herbs, shrubs, trees, and woody climbers or lianas based on the summaries in Brummitt (1992), supplemented by Hegarty (1989) for lianas. Thus, a group with only herbs is represented as 1000 in our data set, and a group with only shrubs and trees as 0110. We then classified families as either herbaceous (H: lacking any woody representatives), woody (W: including one or more of the categories shrubs, trees, and lianas, but excluding herbs), and various (V: including herbs and at least one of the woody categories). Because we were interested in the capability of lineages within a family to adopt new growth forms, we accepted the occurrence of a growth form within a family regardless of its frequency.

Pollination and dispersal modes were determined from descriptions of the flowers and fruits of each family in Cronquist (1981) and Ridley (1930). In both cases, the categories were abiotic (A), biotic (B), and various (V). When Cronquist did not give pollination mode explicitly, this was either obtained from handbooks summarizing pollination observations (Knuth 1898–1908; Kubitzki et al. 1993), or inferred from floral structure, following empirically well-supported distinctions between wind and animal pollination syndromes (Faegri and van der Pijl 1976). Dry, indehiscent fruits or capsules generally indicate wind dispersal, whereas fleshy fruits, generally drupes or berries, indicate animal dispersal. Families with large, dry fruits adapted to dispersal by scatter-hoarding animals were classified as biotically dispersed. This approach is likely to result in an overestimation of abiotic dispersal because fruits and seeds adapted for transport on animals (epizoochory) are described in the same terms as wind-dispersed propagules. The complete angiosperm data set includes 365 families of monocots and dicots having a total of 13,469 genera and 240,090 species. The data set contains no missing values, although obviously some assignments were made with more confidence than others and the systematic positions of some groups are uncertain.

Because a high species richness increases the probability that more than one category of distribution, growth form, pollination, and dispersal might be included within a family, cause and effect would be difficult to determine if species

richness and morphological diversity were statistically related. This problem of circularity is addressed in the discussion.

Statistical analyses were performed using the Statistical Analysis System (SAS) Version 6.04 (SAS Institute 1988) on an IBM-compatible PC. Details of the statistical analyses are explained in the Results section.

RESULTS

Age and Diversity of Families

Eriksson and Bremer (1992) used age and contemporary diversity to estimate the average rate of exponential increase (k) of species number within families. The resulting values of k varied between 0.01 and 0.39 My^{-1} and averaged 0.12 My^{-1} for the 109 families included in Eriksson and Bremer's analysis. Thus, the average exponential rate of increase in species number was 12% per million years, or a doubling time of 5.8 My. If earliest appearance in the fossil record accurately estimated, or correlated highly with, the age of a taxon (t), and if k varied independently of t , then older taxa would have more species (S) on average than younger ones. Specifically, the regression of $\ln(S)$ on t (My) would have a slope approximating 0.12 and it would pass through the origin [$t = 0$, $\ln(S) = 0$].

We tested the predicted relationship between $\ln(S)$ and t using Eriksson and Bremer's data set, including families we added (as explained above) and families excluded by Eriksson and Bremer because they were either monotypic ($n = 4$), young ($t < 15$ My, $n = 18$), or possibly not monophyletic ($n = 15$). There is little reason to exclude monotypic families when those with two or three species are retained. If one accepts first appearances as indicating age of taxa, there is also no reason to exclude younger taxa arbitrarily: if they can be recognized in Neogene deposits, why could they not be recognized in Paleogene or Cretaceous floras, if present? As for the 15 families that are regarded as not monophyletic, but as paraphyletic or polyphyletic by Eriksson and Bremer, these represent groups upon which systematists at this time do not agree; thus, their status is unresolved. The inclusion or exclusion of these families had no effect on the results of the analysis.

In our analysis, $\ln(S)$ was not statistically related to t ($F = 0.33$; $\text{df} = 1, 151$; $P = 0.57$; fig. 1). Including pollination mode, dispersal mode, distribution, or growth form as main effects in

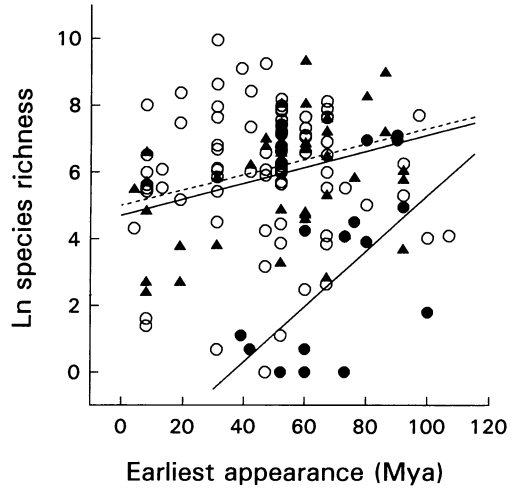


FIG. 1. Relationship between the natural logarithm of species richness and age (My) of earliest appearance in the fossil record for 153 families of flowering plants. The dashed line represents the slope of the regression within subclasses. The two solid lines represent regressions within the subclasses Hamamelidae (solid circles) and Rosidae (solid triangles).

analyses of covariance (ANCOVA) also failed to reveal significant relationships between $\ln(S)$ and t within categories of each of these effects. Only when subclass was entered as an effect was $\ln(S)$ significantly related to age ($F = 12.6$; $\text{df} = 1, 141$; $P = 0.0005$). The slope of the relationship (0.023 ± 0.007 SE) was less than that expected from the average of Eriksson and Bremer's estimates of k (0.12), and the intercept of the regression (5.0 ± 1.1) significantly exceeded zero ($t = 4.7$, $P < 0.0001$). The within-subclass relationship between $\ln(S)$ and t resulted from significant relationships within the Hamamelidae ($F = 7.4$; $\text{df} = 1, 14$; $P = 0.017$; $R^2 = 0.35$, $\ln S = -3.0 [\pm 2.4$ SE, $t = -1.3$, $P = 0.22]$ + $0.083 t [\pm 0.030$ SE, $t = 2.72$, $P = 0.017]$) and the Rosidae ($F = 6.3$; $\text{df} = 1, 48$; $P = 0.015$; $R^2 = 0.12$, $\ln S = 4.7 [\pm 0.6$ SE, $t = 8.3$, $P < 0.0001]$ + $0.024 t [\pm 0.009$ SE, $t = 2.5$, $P = 0.015]$) (fig. 1). Thus, this analysis suggests that first fossil occurrence estimates the earliest evolutionary appearance of families only in the Hamamelidae.

Our failure to find a significant general relationship between species richness and age of family indicates either that average exponential rate of increase in species number negatively covaries with age of family, or that ages of families cannot be estimated reliably from the fossil record. The first possibility, which was borne out by the data

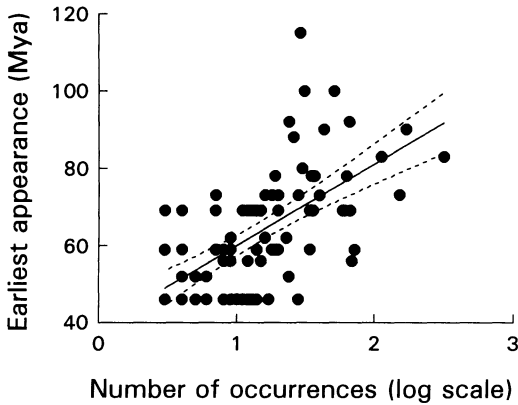


FIG. 2. Relationship between earliest appearance in the North American fossil record and number of occurrences in the North American fossil record of the Cretaceous and Paleogene for 89 families of flowering plants (after data in Taylor 1990). Dashed lines represent 95% confidence limits on the regression line.

($r = -0.70$, $P < 0.0001$), could arise as an artifact of the second. This possibility cannot, however, be evaluated directly. To examine the second possibility, we looked for biases in earliest appearance with respect to a variety of factors. Taylor (1990) compiled Cretaceous and Paleogene angiosperm macrofossils from North America. From this summary, we tabulated the number of fossil occurrences of members of each family and the earliest occurrence for 89 families of flowering plants. Our analyses related age (t , My) to $\log_{10}(\text{occurrences})$. The relationship was highly significant ($F = 56.9$; $df = 1, 87$; $P < 0.0001$; $R^2 = 0.40$; mean age = 64 My). The regression equation was $t = 39 (\pm 4 \text{ SE}, t = 11, P < 0.0001) + 21 \log_{10}(\text{occurrences}) (\pm 3, t = 8, P < 0.0001)$. Thus, each ten-fold increase in number of fossil occurrences was associated with a 21-My earlier first appearance in the fossil record (fig. 2). One might argue that older families would have a greater representation simply owing to their greater duration, but occurrences increased more than an order of magnitude more rapidly than the duration of a family. Families that occurred earlier in the history of angiosperm evolution might have been more abundant or perhaps lived in habitats with a higher probability of preservation. However, the simplest explanation seems to be that variation in first appearance results for the most part from variation in the representation of families in the fossil record.

One may also examine the relationship between presence of a family in the fossil record

and its contemporary species richness. Of the 365 families represented in our data set, 153 have been reported from fossil deposits according to the list in the appendix of Eriksson and Bremer (1992) as modified slightly by us (see Data and Analyses). Families with fossil representatives had more than ten-fold more contemporary species [$\log_{10}(\text{species}) = 2.47 \pm 0.91 \text{ SD}$] than did those absent from the fossil record ($1.28 \pm 0.98 \text{ SD}$) on the average ($F = 140$; $df = 1, 363$; $P < 0.0001$; $R^2 = 0.28$; Wilcoxon $Z = 10.1$, $P < 0.0001$; Kruskal-Wallis $\chi^2 = 103$, $P < 0.0001$). They also had almost ten times more genera [$\log_{10}(\text{genera}), 1.27 \pm 0.76 \text{ SD}$ vs. $0.51 \pm 0.58 \text{ SD}$; $F = 118$; $df = 1, 363$; $P < 0.0001$; $R^2 = 0.25$].

We further explored the possibility that the occurrences of families in the fossil record are biased. Geographical distribution, growth form, and modes of pollination and dispersal were compared by contingency analysis between families recorded as fossils and those not recorded (table 1). These analyses indicate that families with restricted distributions had a lower probability of being recorded as fossils, whether tropical (32%) or temperate (25%) than families presently ranging over both latitudes, whether at low elevation (subcosmopolitan) (66%) or high elevation in the tropics (60%). Dispersal mode also was associated with probability of appearance in the fossil record: abiotic 30%, biotic 38%, various 69%. Neither growth form nor pollination mode were significantly associated with probability of appearance in the fossil record. A categorical regression model (SAS Procedure CATMOD) including all four factors simultaneously reinforced this result: distribution ($\chi^2 = 21.75$; $df = 3$; $P < 0.001$); growth form ($\chi^2 = 4.25$; $df = 2$; $P = 0.12$); pollination ($\chi^2 = 0.47$; $df = 2$; $P = 0.79$); dispersal ($\chi^2 = 14.06$; $df = 2$; $P < 0.001$).

The foregoing analyses suggest that occurrence of angiosperm families in the fossil record is extremely biased with respect to both the dependent variable in Eriksson and Bremer's (1992) analysis (number of species) and two independent variables (geographical distribution and dispersal mode). Furthermore, the earliest appearance recorded for each family that does appear in the fossil record also is biased with respect to contemporary species and genus richness and with respect to the numerical abundance of a family in the fossil record. We conclude that earliest appearances, in general, bear little relation to the ages of most families of flowering plants and that

TABLE 1. Relationship of presence or absence of families of flowering plants in the fossil record to geographical distribution, growth form, and modes of pollination and dispersal. Statistics are likelihood-ratio χ^2 values with 3 or 2 degrees of freedom.

	Fossil record		χ^2	<i>P</i>
	Absent	Present		
Geographic distribution*			39.5	<0.001
Tropical	129	62		
Temperate	40	13		
Cosmopolitan	31	60		
Tropical-montane	12	18		
Growth form			7.5	0.024
Herbaceous	82	40		
Woody	105	85		
Various	25	28		
Pollination mode			0.5	0.782
Abiotic	34	23		
Biotic	164	117		
Various	14	13		
Dispersal mode			37.5	<0.001
Abiotic	114	49		
Biotic	71	43		
Various	27	61		

* For explanation of categories, see Data and Analyses.

they should not be used to estimate rates of proliferation of species within families.

Because first recorded appearances seem to be poorly related to the evolutionary ages of families, only contemporary species richness conveys useful information concerning the propensity of a flowering plant family to diversify. Accordingly, all subsequent analyses are based upon the contemporary number of species in families.

Relationships among the Independent Variables

The numbers of families sharing the possible combinations of distribution types, growth forms,

pollination modes, and dispersal modes are shown in tables 2 and 3. Each of the six two-way contingency tables shows significant heterogeneity, but the most prominent associations involve growth form, distribution, and dispersal mode. Woodiness and animal dispersal appear to be more prominent in tropical and tropical-montane and temperate floras, whereas herbaceous growth and abiotic dispersal are particularly well represented among cosmopolitan families (table 2). Accordingly, abiotic dispersal is strongly associated with herbaceous growth (table 3). Pollination mode is weakly associated with distribution and growth form—the only notable

TABLE 2. Relationship between geographical distribution and numbers of angiosperm families in the classification categories of growth form, pollination mode, and dispersal mode. Statistics are likelihood-ratio χ^2 values with 6 degrees of freedom. H, herbaceous; W, woody; V, various; A, abiotic; B, biotic.

		Geographical distribution				χ^2	<i>P</i>
		Trop	Temp	Cosm	TrMt		
Growth form	H	48	21	48	5	57.1	<0.001
	W	121	27	19	23		
	V	22	5	24	2		
Pollination mode	A	20	14	17	6	15.6	0.016
	B	160	37	65	19		
	V	11	2	9	5		
Dispersal mode	A	67	36	52	8	42.3	<0.001
	B	76	12	12	14		
	V	48	5	27	8		

TABLE 3. Numbers of angiosperm families having combinations of the classification for growth form and modes of pollination and dispersal. Statistics are likelihood-ratio χ^2 values with 4 degrees of freedom. H, herbaceous; W, woody; V, various; A, abiotic; B, biotic.

Growth form	Pollination mode			Dispersal mode	Growth form			Pollination mode	Dispersal mode		
	A	B	V		H	W	V		A	B	V
H	27	88	7	A	84	59	20	A	34	19	4
W	27	146	17	B	17	86	11	B	117	86	78
V	3	47	3	V	21	45	22	V	12	9	6
	$\chi^2 = 10.2$ $P = 0.037$				$\chi^2 = 58.7$ $P < 0.001$				$\chi^2 = 14.5$ $P = 0.006$		

heterogeneity is the near absence of abiotic pollination among families having *both* biotic and abiotic dispersal.

Effects of Classification Variables on Species Richness

Species richness [$\log_{10}(\text{species number}), \log(S)$] is significantly associated with the four classification variables which, in descending order of their statistical influence, are dispersal mode, geographical distribution, growth form, and pollination mode. The statistical effects of these variables were initially examined in a four-way analysis of variance. Neither the four-way interaction term nor any of the three-way interaction terms were significant ($P > 0.25$). Among the two-way interactions, only that between growth form and dispersal mode was significant (higher-order interactions combined with error term, $F = 3.66$; $df = 4, 324$; $P = 0.0062$; accounting for about 2% of the total sums of squares, SS). This interaction will be addressed in more detail below, but for the moment we shall consider the model variables as essentially independent in their contribution to variation in species richness.

An ANOVA including only the main effects (table 4) explains 41% of the total variation in log-transformed species richness. All four main effects were significant. The type-III sums of

squares presented in table 4 (SAS Proc GLM; SAS Institute 1988) indicate the unique contributions of each of the classification variables to variation in species richness, that is, their contributions with the effects of the other three variables statistically removed. The sum of these type-III SS represents only 69% of the total model SS because of the correlations among the classification variables described above. In order of size of effect, the classification variables are dispersal mode (11.6% of the total SS), geographical distribution (8.9%), growth form (5.1%), and pollination mode (2.7%).

A profile of the two most prominent effects, those involving geographical distribution and dispersal mode, is shown in figure 3. A two-way ANOVA of these effects has no significant interaction ($F = 1.8$; $df = 6, 353$; $P = 0.10$). Regardless of dispersal mode, cosmopolitan families tend to be more diverse, and temperate families less diverse, than tropical or tropical-montane and temperate families. Regardless of distribution, and as previously found by both Herrera (1989) and Fleming (1991), families exhibiting variable dispersal modes tend to be more diverse than those with either biotic or abiotic dispersal alone. Standard deviations of $\log_{10}(\text{species})$ number among families within each of the 12 combinations of distribution and dis-

TABLE 4. Analysis of variance of the effects on angiosperm familial species richness of geographical distribution, growth form, and modes of pollination and dispersal.

Source	df	SS	MS	F	P
Model	9	188.7	21.0	27.8	<0.0001
Error	355	267.9	0.75		
Total	364	456.6			
Dispersal mode	2	53.1*	26.5	35.2	<0.0001
Distribution	3	40.5	13.5	17.9	<0.0001
Growth form	2	23.5	11.8	15.6	<0.0001
Pollination mode	2	12.5	6.2	8.3	0.0003

* Type-III sums of squares (SAS Proc GLM).

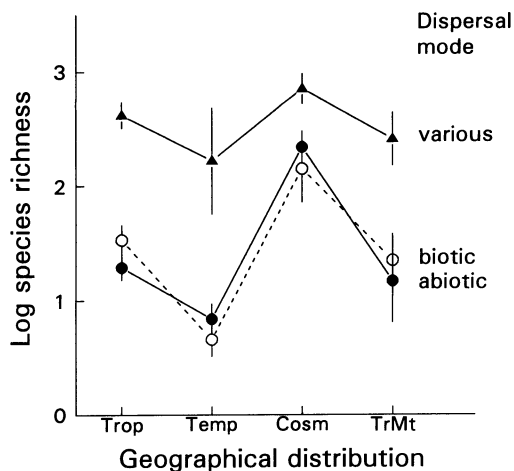


FIG. 3. Profile analysis of the combined effects of geographical distribution and mode of dispersal on familial species richness of flowering plants. The statistical interaction between distribution and dispersal mode was not significant, indicating that the lines do not diverge significantly from parallel. Error bars represent 1 SE of the mean.

persal mode varied between 0.52 and 1.10, indicating reasonable homogeneity of residual variances ($F_{\max} = 4.5$, $P > 0.05$).

The profile diagram of the effects of growth form and dispersal mode (fig. 4) shows the one significant interaction detected in the ANOVA (two-way interaction, $F = 5.3$; $df = 4$, 356; $P = 0.0004$). This interaction arises from the fact that woody families with variable dispersal modes are unusually diverse compared to woody families with either biotic or abiotic dispersal alone. When families with variable dispersal modes were removed from the four-way ANOVA, the growth-form \times dispersal-mode interaction disappeared ($F = 1.5$; $df = 2$, 266; $P > 0.2$), and dispersal became an insignificant effect in the model ($F = 3.0$; $df = 1$, 266; $P = 0.053$).

Because of the general absence of interactions in the data set, the effects of the classification variables on familial species richness can be appreciated most readily in a series of one-way ANOVAs treating each variable individually (table 5). These effects may be summarized as follows (values in parentheses are geometric means, that is, antilogs of means of log-transformed variables): (a) geographical distribution, cosmopolitan (293) > tropical (52) = tropical-montane and temperate (38) > temperate (8); (b) growth form, various (430) > herbaceous (75) > woody (30); (c) pollination mode, various (108) = biotic

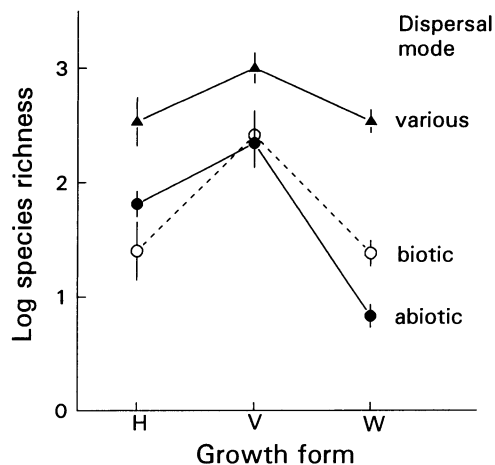


FIG. 4. Profile analysis of the combined effects of growth form and dispersal mode on familial species richness of flowering plants. The statistical interaction between form and dispersal was significantly greater than zero, indicating a nonparallel response of species richness to certain combinations of form and dispersal mode. Specifically, among families with woody growth form families with various dispersal modes had higher species richness than expected from the number of species in families having either biotic or abiotic dispersal alone; families with biotic dispersal had higher species richness than families with abiotic dispersal (Wilcoxon $Z = -3.1$, $P = 0.0021$, $n = 86$, 59). Among herbaceous families, species richness did not differ between those with biotic and abiotic dispersal ($Z = -1.5$, $P = 0.127$, $n = 17$, 84).

(77) > abiotic (14); (d) dispersal mode, various (448) > abiotic (33) = biotic (30). Results (c) and (d) are consistent with those of Ericksson and Bremer (1992), although the latter did not include families with various dispersal or pollination modes in their statistical analysis.

Because of the strong influence of the "various" growth-form category on familial species richness, we investigated the effect of growth form in more detail. We found that the species richness of a family is directly related to the number of growth forms represented in that family ($F = 75$; $df = 1$, 363; $P < 0.0001$; $R^2 = 0.171$; table 6). The contribution of each type of growth form to familial species richness can be estimated by multiple regression in which the presence and absence of each growth form are coded as 1 and 0. This model is highly significant ($F = 37$; $df = 4$, 360; $P < 0.0001$; $R^2 = 0.293$) but includes correlated variation in geographic distribution, pollination mode, and dispersal mode as well. The contribution of each type of growth form to species richness can be estimated by the slopes

TABLE 5. One-way ANOVAs of the effects on angiosperm familial species richness of each of the classification variables. $P < 0.0001$ in all categories.

	<i>N</i>	Mean*	SNK†	<i>F</i>	<i>R</i> ²
Geographic distribution				26.8	0.182
Cosmopolitan	91	2.467	a		
Tropical	191	1.718	b		
Trop-Mont & Temp	30	1.585	b		
Temperate	53	0.929	c		
Growth form				25.8	0.125
Various	53	2.633	a		
Herbaceous	122	1.877	b		
Woody	190	1.479	c		
Pollination mode				11.8	0.061
Various	27	2.032	a		
Biotic	281	1.884	a		
Abiotic	57	1.142	b		
Dispersal mode				43.3	0.193
Various	88	2.651	a		
Abiotic	163	1.519	b		
Biotic	114	1.479	b		

* Mean is the average of the \log_{10} -transformed number of species.

† Significance of differences between means tested by Student-Newman-Keuls procedure; different letters indicate significantly different values.

of species number on the dummy variables (table 7). In this case, presence of herbaceous taxa contributed most (presence associated with 15.5-fold increase in diversity over absence), followed by lianas (6.9-fold) and shrubs (4.6-fold). The presence or absence of trees within a family had relatively little influence (1.7-fold) on species richness.

The Relationship between Species Richness and Genus Richness

Genera are not necessarily natural units and, compared to species, their definition is even more prone to the biases of systematists (Walters 1986). Nonetheless, numbers of genera may generally indicate the relative age of the taxonomic diversity of a family better than numbers of species

per se. That is, a family with a high species-to-genus ratio would imply recent bursts of species production, while a low ratio would suggest a greater degree of differentiation among the species. Numbers of genera and species within families are strongly correlated ($R^2 = 0.780$, $P < 0.0001$). The regression of $\log_{10}(\text{genera})$ on $\log_{10}(\text{species})$ may be described by $\log(G) = -0.23 (\pm 0.03 \text{ SE}) + 0.60 (\pm 0.02 \text{ SE}) \log(S)$. Because the slope of this relationship is less than one, number of species increases proportionately faster than number of genera, and more species-rich families have higher species-to-genus ratios than do less species-rich ones.

When numbers of genera were subjected to a four-way ANOVA without interaction, the results were nearly identical to those obtained for

TABLE 6. Relationship of species richness to number of growth forms represented within a family.

Forms	<i>N</i>	Mean ^a	SNK ^b	SD	Min	Max
1	200	1.46	a	1.14	0.00	4.24
2	106	1.83	a	0.96	0.00	4.32
3	45	2.63	b	0.59	1.34	3.49
4	14	3.20	c	0.54	2.32	4.03

^a Mean is the average of the \log_{10} -transformed number of species.

^b Significance of differences between means tested by Student-Newman-Keuls procedure; different letters indicate significantly different values.

TABLE 7. Regression slopes of familial species richness on absence (0) and presence (1) of each of four growth forms.

Growth form	Sums of squares ^a	<i>P</i>	Intercept or slope	SE
Intercept		<0.0001	0.629	0.136
Herb	65.96	<0.0001	1.137	0.132
Liana	34.88	<0.0001	0.839	0.134
Shrub	29.46	<0.0001	0.663	0.116
Tree	2.91	0.0722	0.238	0.132

^a Type-III sums of squares.

TABLE 8. Analysis of variance of the effects on angiosperm familial generic richness of geographical distribution, growth form, and modes of pollination and dispersal ($r^2 = 0.36$).

Source	df	SS	MS	F	P
Model	9	75.3	8.37	22.5	<0.0001
Error	355	132.2	0.37		
Total	364	207.5			
Dispersal mode	2	23.1	11.5	31.0	<0.0001
Distribution	3	17.1	8.6	15.3	<0.0001
Growth form	2	6.7	3.4	9.0	<0.0001
Pollination mode	2	4.3	2.2	5.8	0.0033

species, as one might have expected (table 8). Again, geographical distribution and dispersal were the most important effects. Subjected to the same ANOVA, log-transformed ratios of species to genera [$\log(S) - \log(G)$] behaved in the same fashion, although with less of the total variance accounted for (table 9). When the log of species richness was entered as a covariate into this analysis, growth form, pollination, and dispersal were no longer significant effects ($P > 0.20$), indicating that their contribution to variation in $\log(S/G)$ results from the general allometric relationship of S to G , combined with the different numbers of taxa in each group. However, distribution remained a significant effect in the ANCOVA ($F = 4.4$; $df = 3, 354$; $P = 0.005$). The least-squares means of $\log(S/G)$ were ordered as tropical-montane and temperate (1.16) = tropical (1.01) > temperate (0.92) = cosmopolitan (0.91). We conclude that genus richness parallels species richness and, of the classification variables examined, only geographical distribution is associated with differences in recent rates of species production, as reflected in high species-to-genus ratios.

Taxonomic Effects

Cronquist (1988) recognized six subclasses of dicots and five subclasses of monocots. The dis-

tribution of the classification variables among the subclasses is extremely heterogeneous (table 10): distribution (likelihood-ratio $\chi^2 = 60$; $df = 30$; $P < 0.001$); growth form ($\chi^2 = 175$; $df = 20$; $P < 0.0001$); dispersal mode ($\chi^2 = 74$; $df = 20$; $P < 0.0001$); pollination mode ($\chi^2 = 135$; $df = 20$; $P < 0.0001$). In particular, woody families are strongly represented among dicots and herbaceous families among monocots and the Asteridae; monocots tend more often to be abiotically dispersed; abiotic pollination appears most frequently in the Hamamelidae among dicots, and in the Alismatidae and Commelinidae among monocots.

One may inquire whether taxonomic affiliation at the hierarchical level of subclass might make a contribution to species richness within families over and above the contributions of the four classification variables already assessed. We addressed this question with the five dicot subclasses having more than 20 families (table 10). Subclass alone was a significant effect ($F = 6.8$; $df = 4, 286$; $P = 0.0001$) but accounted for only 9% of the variation in species richness among families. The geometric mean number of species was highest in the Asteridae [$\log(S) = 2.39 \pm 1.15$ SD, $S = 247$] and lowest in the Hamamelidae [$\log(S) = 1.10 \pm 1.10$ SD, $S = 12$]. In a larger ANOVA that included the classification

TABLE 9. Analysis of variance of the effects on log-transformed ratios of species to genera within angiosperm families of geographical distribution, growth form, and modes of pollination and dispersal ($R^2 = 0.24$).

Source	df	SS	MS	F	P
Model	9	29.5	3.28	12.8	<0.0001
Error	355	91.1	0.26		
Total	364	120.6			
Dispersal mode	2	6.3	3.1	12.2	<0.0001
Growth form	2	5.6	2.8	10.9	<0.0001
Distribution	3	7.4	2.5	9.6	<0.0001
Pollination mode	2	2.7	1.4	5.3	0.0055

TABLE 10. Distribution of each of the classification variables within subclasses of flowering plants. $P < 0.001$ in all categories.

	Subclass											χ^2
	MAG	HAM	CAR	DIL	ROS	AST	ALI	ARE	COM	ZIN	LIL	
Distribution												60.2
Tropical	19	10	8	46	59	15	4	4	7	9	10	
Temperate	4	8	0	11	16	7	4	0	2	0	1	
Cosmopolitan	7	4	6	14	26	17	4	1	6	0	7	
Tropical-Montane	8	3	0	5	12	1	1	0	0	0	0	
Growth form												175.0
Herbaceous	7	1	8	12	20	23	13	2	14	8	14	
Various	5	2	4	12	14	10	0	1	0	1	4	
Woody	25	22	2	52	79	7	0	2	1	0	0	
Pollination												134.5
Abiotic	7	18	2	4	3	5	7	1	9	0	1	
Biotic	28	2	10	69	98	35	4	4	5	9	17	
Various	2	5	2	3	12	0	2	0	1	0	0	
Dispersal												74.4
Abiotic	9	12	7	37	41	19	13	1	12	2	10	
Biotic	25	8	4	23	37	6	0	4	2	3	2	
Various	3	5	3	16	35	15	0	0	1	4	6	
Total	37	25	14	76	113	40	13	5	15	9	18	

variables, the growth-form \times dispersal-mode interaction was only marginally significant ($P = 0.03$) and was subsequently ignored. None of the interactions between subclass and the four classification variables was significant ($P > 0.4$). In the five-way ANOVA without interaction, the four classification variables were all significant, as they were in the four-way analysis, and 46% of the total variance in species richness among families was explained by the model. In this larger model, however, the subclass effect was not significant ($F = 1.6$; $df = 5, 277$; $P > 0.17$). A similar analysis in which all the families were classified as either dicot or monocot also failed to reveal a taxonomic effect ($F = 0.02$; $df = 1, 354$; $P = 0.89$); furthermore, this distinction by itself does not significantly contribute to variation in species richness ($F = 0.4$; $df = 1, 363$; $P > 0.5$). Thus, taxonomic affiliation at the level of subclass, or between monocot and dicot, does not contribute to familial species richness over and above the contributions of the classification variables.

DISCUSSION

The results of this analysis can be summarized by the following points.

First occurrences of families in the fossil record underestimate the ages of most families and are biased with respect to species richness and the

classification variables used in this study. Thus, the results of studies that have used estimated first appearances of angiosperm families to calculate proliferation rates of species (e.g., Eriksson and Bremer 1992) or to compare ages of subsets of taxa having different attributes (e.g., Herrera 1989; Fleming 1991) should be reevaluated.

The four classification variables used in the analyses—distribution, growth form, pollination mode, dispersal mode—accounted for 41% of the total variation in species richness among families, leaving 59% unaccounted for. The significance of this remaining variance is unknown.

As in other studies, we found that animal pollination was associated with higher species richness within families. In contrast with others, however, we emphasize that this factor accounts for a small portion of both the total and the explained variation in familial species richness. Both geographical distribution and growth form are more prominent effects.

As in other studies, we found that biotic dispersal per se does not contribute to species richness when families with various dispersal modes are not considered in the analysis. We are intrigued, however, by the strong statistical effect of multiple dispersal modes within families on species richness and discuss this further below.

Genus and species richness are strongly correlated in comparisons among families, and vari-

ation in species richness therefore appears to be closely tied to morphological diversification. In addition, systematic position (subclass) accounted for no additional variation in species richness after the effects of the classification variables were removed. Thus, currently accepted major groupings do not appear to contain information about familial species richness that is not revealed by geographical distribution and life-history attributes.

Much of the literature on pollination, dispersal, and species richness addresses the idea that biotic pollination and dispersal somehow enhance rates of speciation, either by establishing population structures conducive to subdivision or through rapid evolution brought about by the special character of the coevolutionary relationships between plants and their pollinators and dispersers. The enhancing effect of animal pollination on familial species richness is weak statistically, even though the 281 families with animal pollination have a geometric mean of 77 species compared to a geometric mean of 14 species for 57 abiotically pollinated families. That there are so many more animal-than wind- and water-pollinated families, however, may indicate that at a higher (earlier?) level animal pollination may have created entire new adaptive zones.

The fact that cosmopolitan families have more species than geographically more restricted families is not surprising considering the total surface area and variety of climate zones occupied by these families. It is worth considering, however, whether *within* climate zones cosmopolitan families are more diverse than families restricted to those climate zones. This appears to be the case. Cosmopolitan families have 5.6 times more species on the average than tropical families and 35 times more species than temperate families. It is unlikely that these differences could be due to area alone, particularly insofar as the greater area occupied by cosmopolitan taxa compared to tropical taxa includes the region occupied by temperate taxa, which have relatively few species per family.

With respect to growth form, herbaceous families tend to have more species than woody families, by a factor of 2.5. Perhaps the smaller herbaceous plants can exploit a wider variety of habitats and partition habitats more finely than can woody plants, permitting both increased ecological diversification and greater levels of coexistence within habitats (Ricklefs and Latham 1993). However, families with both woody and

herbaceous species are 5.7 times more species-rich than families with solely herbaceous species. This cannot be due to the addition of clades of woody taxa because woody families are, on average, less diverse than herbaceous families. Thus, proliferation of species within families would appear to be related to the capacity of taxa to adopt different growth forms.

The fact that families with both animal and abiotic dispersal have, respectively, 15 times and 14 times more species than families having only one or the other, represents the strongest effect on familial diversity detected in this study. It is puzzling that both Herrera (1989) and Fleming (1991) also found this pattern but did not comment on it. The pattern is also evident in Eriksson and Bremer's (1992) data set, but they excluded families with various dispersal modes from their analysis.

As in the case of growth form, the relationship between variety of dispersal modes within a family and its species richness suggests that the capacity to differentiate morphologically and adopt diverse life histories contributes importantly to species proliferation. This capacity may be generalized to many different aspects of the plant's life history. For example, it was noted earlier that families having various dispersal modes were more likely to have both herbaceous and woody members (25%) than either abiotically dispersed (12%) or biotically dispersed (10%) taxa. The number of growth forms per family (1–4) also is significantly associated with dispersal mode ($\chi^2 = 45$; $df = 6$; $P < 0.001$). The average number of forms is highest in families with various dispersal modes, intermediate in biotically dispersed families, and lowest in abiotically dispersed families (table 11). Animal pollination has a much weaker association with number of growth forms ($P = 0.02$), and for geographical distribution this association is insignificant ($P = 0.09$).

The relatively trivial contribution of biotic pollination, and the insignificant contribution of biotic dispersal per se, to the species richness of families raises important issues concerning the mechanisms of species proliferation. We presume that most of the variation in species richness between families of plants is due primarily to variation in the net rate of species proliferation. We have come to this opinion by the following reasoning. The oldest and youngest contemporary plant families differ in age by a factor of perhaps 4 (i.e., 35–140 My) and therefore a

TABLE 11. Relationship between dispersal mode and number of growth forms represented within angiosperm families.

Dispersal mode	N	Number of growth forms				Mean*	SNK†
		1	2	3	4		
Abiotic	163	0.72	0.21	0.05	0.01	1.35	a
Biotic	114	0.49	0.34	0.15	0.02	1.69	b
Various	88	0.33	0.43	0.16	0.08	1.99	c
Total		203	112	39	11		

* Mean is the weighted average of the number of growth forms.

† Significance of differences between means tested by Student-Newman-Keuls procedure; different letters indicate significantly different values.

standard deviation equivalent to perhaps 0.15 \log_{10} units [$\log_{10}(4/4)$], assuming ages of origin are lognormally distributed (Snedecor and Cochran 1980). The standard deviation of species richness among families of angiosperms is 1.12 \log_{10} units, or a factor of about 13. Accordingly, the standard deviation of net proliferation rates among families would be equivalent to 0.97 \log_{10} units, or a factor of about 10. Even if the ages of families spanned a larger range, the effect of age of origin on species richness nonetheless would be overshadowed by that of net proliferation rate. Hence, age seems less important than the average net rate of proliferation of taxa in determining contemporary species richness.

Hypotheses concerning the role of animal pollination and dispersal in the proliferation of angiosperm species have focused on the consequences of pollination and dispersal mode for population structure. Long-distance dispersal is one way in which isolated populations might become established. According to Regal (1982) and others, sparse distributions of individuals within populations resulting from biotic dispersal might then select strongly for animal pollinators that can cover long distances. Our data, however, reveal no significant relationship between animal dispersal and animal or various pollination (83% of 114 biotically dispersed families include biotic pollination; 79% of 163 abiotically dispersed families include biotic pollination).

Gentry (1983a) has compared animal-dispersed and wind-dispersed species in the Bignoniaceae, a large, woody, tropical family. Wind-dispersed species tend to have broad geographical ranges, and related species are distributed mostly allopatrically. Animal-dispersed species—which tend to be shrubs and subcanopy trees in the Bignoniaceae, as well as in other tropical, woody families (Gentry 1983b)—are much more narrowly distributed and are more

likely to exhibit sympatry among close relatives. The empirical patterns imply that wind dispersal in this family distributes propagules more widely than does animal dispersal. Renner (1990) has observed the same phenomenon in the Melastomataceae in which wind-dispersed taxa more frequently exhibit disjunctions suggestive of long-distance dispersal. This is consistent with the general conclusion of Loveless and Hamrick (1984), based primarily on allozyme studies, that wind dispersal reduces genetic diversity among populations of plants compared to animal dispersal. Genetic diversity within populations was not associated with dispersal mode. Among nine woody plant populations on Barro Colorado Island, Panama, dispersed either by animals or by explosive seed capsules, there was no statistical difference between dispersal modes in genetic diversity either within or between populations (Hamrick and Loveless 1986, 1989). It is well known that wind-dispersed (and wind-pollinated), temperate coniferous trees are extremely variable genetically within rather than among populations, compared to other groups of plants (Muona 1989; Muona and Harju 1989).

Rather than looking to biotic dispersal and pollination as causal factors in speciation propensity, we suggest that familial species richness and, by implication, rate of proliferation of taxa within families, is determined primarily by evolutionary flexibility, that is, by the capacity of species to adopt new life-history attributes. This is supported by the fact that species richness within families is strongly correlated with broad geographical and, presumably, ecological distribution, and with the presence of diverse growth forms and dispersal modes, over a family as a whole. For example, according to Gentry (1990, p. 128), "Speciation in continental Neotropical Bignoniaceae seems mostly to have involved modifications in vegetative characters and seed

TABLE 12. Analysis of covariance examining the effects on familial species richness in the Amazonian flora of Ecuador of classification variables, with global familial species richness as a covariate.

Variable	df	Type-III SS	F	P
Global species richness	1	17.5	82.4	<0.0001
Distribution	3	7.9	12.4	<0.0001
Growth form	2	0.1	0.2	0.8
Pollination mode	2	0.7	1.7	0.2
Dispersal mode	2	0.4	0.9	0.4

dispersal mode associated with occupying new, often somewhat marginal, habitats" (see also Gentry 1992). Prance and Mori (1983) reached similar conclusions with respect to diversification of the Lecythidaceae, as did Renner (1990) for Melastomataceae. Accordingly, it appears that the species richness of a family is related to its ability to exploit a wide range of ecological opportunities. Thus, for species proliferation, capacity for morphological and physiological diversification (Liem 1973; Liem and Osse 1975) may be more critical than population structures that are presumed to foster genetic differentiation. Ability to enter new habitats, adopt new growth forms, or use new pollination or dispersal modes may promote genetic isolation between populations. We suggest, however, that these capacities influence net diversification rates primarily by allowing the persistence of nascent species, because they can avoid either competitive exclusion by sister species, population consequences of pests or pathogens, or genetic hybridization and swamping (e.g., see Neill 1988).

If species proliferation were related to animal pollination enhancing the formation of new species, we would expect that biotically pollinated families would contain higher ratios of species to genera than do wind- or water-pollinated families. However, in spite of the positive allometry between number of species and number of genera within families, and even though biotic pollination is significantly associated with greater familial species richness, ratios of species to genera are actually, but not significantly, somewhat higher in wind-pollinated families [$\log(S/G) = 1.18$] than in animal-pollinated (0.98) or variously pollinated (0.71) families. Thus, species-to-genus ratios fail to support the idea that animal pollination affects population structure in such a way as to promote rapid speciation.

High familial species richness could be achieved either by high species diversity within local assemblages (alpha diversity), a high degree of hab-

itat specialization with high turnover of species between habitats (beta diversity) (Gentry 1986, 1988), geographical replacement of species within similar habitats (gamma diversity; Cody 1975, 1993), or some combination of these. Accordingly, if one compared the number of species in each family in a locally defined flora to the number of species in the same families worldwide, families with low beta and gamma diversity would have higher local diversities than families with high turnover between habitats and regions. This can be examined with respect to the classification variables in this study by an ANCOVA in which local familial species richness is regressed against global familial species richness and the effects of the classification variables on the elevation of the regression are tested. Geographical turnover of species would be inversely related to elevation of the regression.

We extracted numbers of species in each family represented in a tropical flora, that of the Amazon basin of eastern Ecuador, from Renner et al. (1990). The region, which consists primarily of lowland Amazonian rainforest and has an area of 71,000 km² below 600 m elevation, contains 142 families of flowering plants, having an average logarithmic diversity of $\log(S) = 0.880$ (7.6 species). In an ANCOVA with distribution, growth form, pollination mode, and dispersal mode included as main effects, and global species richness as covariate, only geographical distribution was significant (table 12). Overall the model accounted for 49% of the variation in familial species richness ($F = 12.6$; $df = 10, 131$; $P < 0.0001$). Thus, the Ecuadorian Amazonian flora samples angiosperm families without bias with respect to growth form and modes of pollination and dispersal, and none of these three classification variables results in greater or lesser turnover of species on a scale of the area and habitat diversity of eastern Ecuador.

Because geographical distribution was a significant effect in this ANCOVA, the analysis was

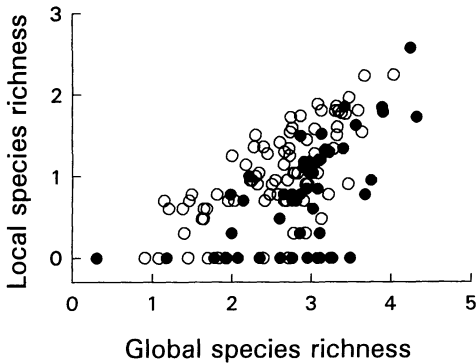


FIG. 5. Relationship between the species richness of 133 families of flowering plants that occur in the Amazonian region of eastern Ecuador and the global species richness of those families. Open circles represent primarily tropical distributions; filled circles represent cosmopolitan distributions. Data from Renner et al. (1990).

rerun with only geographical distribution as a variable, excluding seven tropical-montane families and two temperate families with only a few representatives in the eastern Ecuadorian flora (fig. 5). The flora contains 83 strictly tropical families and 50 cosmopolitan families, so that cosmopolitan families are somewhat overrepresented in the Ecuadorian flora (0.60 per tropical family) compared to their global proportion (0.48). In addition, as one might expect, the Ecuadorian flora samples families with higher species richness than the global mean [$\log(S) = 2.55$ versus 1.72 for tropical families; 2.90 versus 2.47 for cosmopolitan families]. The ANCOVA accounted for 45% of the total variation in familial species richness ($F = 52$; $df = 2, 130$; $P < 0.0001$). The slope of the regression of local species familial richness on global familial species richness was 0.56 ± 0.06 SE ($F = 95$; $df = 1, 130$; $P < 0.0001$), that is, local species richness varied approximately in proportion to the square root of global species richness; distribution was a significant effect ($F = 28.8$; $df = 1, 130$; $P < 0.0001$) with the elevation for tropical families being $0.46 \log_{10}$ units (a factor of 2.9) above that for cosmopolitan families. Thus, relative to tropical families, cosmopolitan families do exhibit greater turnover of species between areas (i.e., beta diversity) within the tropics. Whether this represents geographical or habitat replacement within tropical regions cannot be determined from this analysis.

Interpreting the relationship between species

richness and the presence of multiple growth forms or dispersal modes within families raises the issue of circularity. That is, versatility may promote diversification or, alternatively, species richness may sample greater morphological variety. If the occurrence of species within a family having one or another growth form or dispersal mode were a sampling process, then one would not expect the proportions of families having one but not the other to be as high as they are. For example, if abiotic and biotic dispersal were roughly equally probable, then samples of 10 or more would include only one dispersal mode with a probability of less than 0.002. Clearly, because of phylogenetic conservatism, species are not necessarily independent sampling units, although one family with only two species (*Rosiaceae: Mitrastemonaceae*) had both wind and animal dispersal. In our sample, 68% of families with 10 or more species and 27% of families with 10 or more genera had only a single dispersal mode. Furthermore, the morphological variety exhibited by a family should not be considered as the result of independently drawing species from some statistical distribution, or species pool. Instead, proliferation of species and diversification of such life-history traits as growth form and dispersal proceed hand in hand during the evolution and proliferation of a clade. The issue, then, is whether proliferation of species forces morphological and ecological diversification through such competitive mechanisms as character displacement (Grant 1972, 1986; Schluter and McPhail 1993), or whether life-history diversification permits species proliferation by releasing clades from the constraints of competition among their subordinate species.

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