Angiosperm growth habit, dispersal and diversification reconsidered

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Summary

Previous studies have sought to elucidate the relationship between dispersal mode (biotic versus abiotic) and the taxonomic diversification of angiosperm families, but with ambiguous results. In this study, we propose the hypothesis that the combination of (1) the large seed size required of plants germinating in closed, light-poor environments and (2) the necessity to move disseminules away from the maternal plant in order to avoid intraspecific competition, predation and pathogens should favour biotically-dispersed relative to abiotically-dispersed woody arborescent angiosperms, resulting in higher diversification of the former. In this paper, we seek patterns of diversification that support this hypothesis. We examine the association between dispersal mode, growth habit and taxonomic richness of monocotyledon and dicotyledon families using (1) contingency table analyses to detect the effect of dispersal mode on the relative abundances and diversification of woody versus herbaceous taxa and (2) non-parametric analyses of variance to detect the statistical effect of dispersal mode on taxonomic diversification (mean number of species per genus, genera per family and species per family) in monocot and dicot families dominated by biotic or abiotic dispersal. We found a clear statistical effect of dispersal mode on diversification. Among families of woody dicots, dispersal by vertebrates is associated with significantly higher levels of species per genus, genera per family and species per family than is abiotic dispersal. The same pattern is observed among woody monocots, but is not significant at the 0.05 level. Among families of herbaceous monocots and dicots, the situation is reversed, with abiotically-dispersed families exhibiting higher levels of diversification than vertebrate-dispersed families. When woody and herbaceous families are pooled, there is no association between dispersal mode and diversification. These data coincide with evidence from the fossil record to suggest vertebrate dispersal has positively contributed to the diversification of woody angiosperms. We suggest that vertebrate dispersal may have promoted the diversity of extant taxa by reducing the probability of extinction over evolutionary time, rather than by elevating speciation rates. Our results suggest vertebrate dispersal has contributed to, but does not explain *in toto*, the diversity of living angiosperms.

Keywords: vertebrate dispersal; fruit dispersal; seed dispersal; angiosperm diversification; comparative biology

Introduction

The angiosperms are the most diverse living group of vascular plants, numbering over 220 000 described species (Cronquist, 1981), compared to approximately 10 000 species of Pteridophytes and 750 species of gymnosperms (Mabberley, 1987). This difference in diversity has led to several decades of speculation regarding the primary factor or factors promoting angiosperm diversity. Two schools of thought have evolved.

One invokes the influence of animal vectors, both pollinators and fruit or seed dispersers, as promoting taxonomic diversification. Raven (1977), Regal (1977), Burger (1981), Crepet (1984), Doyle and Donoghue (1986) and Crepet *et al.* (1991), among others, have argued that insect

pollination has been a driving force in angiosperm speciation, creating and enforcing genetic isolation of populations through the taxonomic and behavioural diversity of insects. Similarly, Regal (1977), Burger (1981) and Tiffney (1984) have suggested that the taxonomic and behavioural diversity of vertebrate fruit and seed dispersers has contributed to angiosperm diversity.

In contrast to the proposed importance of plant–animal interactions as causes of angiosperm diversification are hypotheses that target a suite of physiological and developmental characters in angiosperms. Double fertilization, rapidity of growth, plasticity of morphological and chemical responses and the capacity for vegetative reproduction are all cited as inherent characters favouring the diversification of angiosperms relative to other groups (Stebbins, 1974, 1981; Bond, 1989; Midgley and Bond, 1991; see also Doyle and Donoghue, 1993). Proponents of this view have generally questioned the importance of biotic interactions (see especially Midgley and Bond, 1991) and have suggested that the key to angiosperm success lies in their ability to occupy a wide range of environments (Ricklefs and Renner, in press). Supporters of each viewpoint have provided general observations and correlations, coupled with specific examples, to support their contentions. Only recently, however, have comprehensive databases been used to evaluate statistical associations between dispersal mode, pollination and diversity.

The influence of biotic pollination versus wind pollination on diversification was evaluated statistically by Eriksson and Bremer (1992), who estimated rates of diversification of angiosperm families from the time of their first occurrence in the fossil record and the number of extant species per family. They concluded that the rate of diversification was significantly higher in insect-pollinated angiosperm families than in wind-pollinated ones. The validity of this conclusion is suspect, however, given that rates of evolution and extinction may have varied through time and that the dates of first occurrence of families are open to revision (e.g., Crepet *et al.*, 1992; Ricklefs and Renner, in press).

Two studies have evaluated the influence of biotic fruit and seed dispersal (relative to abiotic dispersal) on total angiosperm diversity (Herrera, 1989; Fleming, 1991); one study has evaluated its influence in a subset of all angiosperms (Eriksson and Bremer, 1992) and two additional studies have evaluated its influence within a single angiosperm family (Eriksson and Bremer, 1991; Bremer and Eriksson, 1992). Perhaps the most inclusive study was that of Herrera (1989), who offered and tested three predictions derived from the hypothesis that biotic fruit and seed dispersal has promoted angiosperm diversity. He argued that, 'If seed dispersal by animals contributed significantly to angiosperm diversification, one should expect to find (1) that this seed dispersal method was either a significant innovation of angiosperms (a feature unique to this group), or that it occurs proportionally more often in angiosperms than in gymnosperms; (2) that extant groups exhibiting this feature tend to be taxonomically more diverse than sister groups lacking it; and (3) that biotically-dispersed groups were of greater proportional significance during the early, critical periods of angiosperm diversification' (Herrera, 1989, p. 309). These predictions were tested using a database that included the current species diversity, dispersal mode and age of angiosperm families. Herrera (1989) concluded that 'None of the tests supports a role for animal dispersal *per se* in angiosperm diversification' (p. 320), although the third test is open to the criticisms of fossil data described above. This conclusion was also reached by Eriksson and Bremer (1992), who estimated rates of diversification for families with predominantly abiotic or predominantly biotic dispersal modes. They found no significant difference between the rates of diversification in groups dominated by one or the other of the two dispersal modes, although use of fossil data places this conclusion in question (Ricklefs and Renner, in press). Fleming (1991) briefly evaluated the association of fruit type and plant habit and the association of fruit type and species diversity, within extant angiosperm families. He concluded

that (1) 'Fleshy fruits are more likely to be produced by woody plants than by herbs' and (2) 'Families producing fleshy fruits are no richer in species than are other families' (p. 127).

Eriksson and Bremer (1991) and Bremer and Eriksson (1992) examined the influence of dispersal mode and plant habit on diversity in living members of the largely tropical family Rubiaceae. They concluded that 'Any attempt to reduce existing patterns of diversification to a relationship with animal dispersal alone failed' (Eriksson and Bremer 1991, p. 758). However, their data suggested 'a positive relationship between dispersal ability and rate of diversification when both fruit characteristics and life form were considered in combination' (Eriksson and Bremer, 1991, p. 758). For example, abiotically, dispersed genera of herbs within the Rubiaceae tended to be speciose, while biotically-dispersed herbaceous genera were relatively depauperate. Conversely, biotically-dispersed genera of shrubs tended to be highly speciose relative to abiotically-dispersed genera of shrubs. Similar conclusions were also supported by Bremer and Eriksson (1992).

These comparative studies demonstrate an ambiguous association between biotic dispersal and angiosperm diversification. One possible explanation for this is that the effect of biotic dispersal on angiosperm diversification may depend on previously unspecified ecological attributes of the included taxa. For example, in all but one of these studies, all angiosperm growth forms were pooled, potentially obscuring differences among them with respect to the role of animal dispersers.

Why might the effect of biotic dispersal on diversification be growth form specific? Consider first the evolutionary constraints placed on woody taxa. As a community, woody plants generally create a local environment that is light poor with a distinctive microclimate characterized by low wind velocities. Often these low-light communities persist over hundreds of generations, with seedling recruitment successfully occurring within the forest environment.

Seedling success in forest communities is subject to two constraints.

(1) Seedlings must possess sufficient energy reserves to allow them to become established in a low-light environment (Salisbury, 1942; Harper *et al.*, 1970; Levin, 1974; Rockwood, 1985; Foster and Janson, 1985; Foster, 1986; Mazer, 1989).

(2) Seedlings must disperse a sufficient distance from the parent tree to avoid competition among previously and simultaneously established siblings, to avoid parent–offspring competition and to escape attack and predation from pathogens and predators that have accumulated on the parent plant or on nearby siblings (Connell, 1978; Denslow and Moermond, 1982; Howe and Smallwood, 1982; Connell *et al.*, 1984; Gautier-Hión *et al.*, 1985; Moermond and Denslow, 1985; Estrada and Fleming, 1986; Debussche and Isenmann, 1989; Jordano, 1992).

Large seeds are inefficiently dispersed by gravity or wind. Consequently, given that there is a strong tendency for tree species to exhibit large seed sizes relative to herbaceous species, presumably due to constraint (1) (Mazer, 1989, 1990 and references therein), these trees will require biotic dispersal agents in order to avoid mortality risks imposed by constraint (2).

How might vertebrate dispersal promote the diversification of arborescent taxa relative to abiotic dispersal? Elevated diversification is not necessarily generated by increased speciation rates due to reproductive isolation imposed by species-specific plant–animal interactions, as is commonly assumed. Higher diversification of one family relative to another can equally well be the result of a reduced probability of extinction. Over time, biotic dispersal of large seeds of woody plants could reduce the probability of extinction due to intraspecific competition and/or pathogen/predator attack. This could allow woody taxa with long-distance dispersal mechanisms to accumulate and to become more diverse than woody taxa without long-distance dispersal mechanisms. Consequently, we propose that, in woody taxa and over evolutionary time, biotic

dispersal ought to be associated with higher taxonomic diversification than abiotic dispersal, due to a reduction in the risk of extinction rather than to an elevated speciation rate.

Two ancillary points should be made. First, in many cases, woody taxa do evolve small, wind-dispersed seeds capable of colonizing light gaps made available by tree falls. That this strategy is less common among woody taxa than biotic dispersal suggests that it may be a less reliable means of achieving seedling establishment due to rarity of light gaps in the closed forest. Second, one apparent difference between woody and herbaceous taxa is that the maximum possible mass of a dispersal unit is clearly going to be greater for most woody individuals than for most herbaceous individuals for two reasons: woody stems are capable of supporting larger organs than non-woody stems and most woody taxa have a larger photosynthetic area than most herbaceous taxa, allowing the production of more resources to support reproductive effort, including large propagules. Thus, woody taxa have a greater structural and energetic potential to produce disseminules that absolutely cannot be wind dispersed. In contrast, most herbaceous taxa lack the photosynthetic area to generate propagules (collectively or singly) of very high mass and the physical structure to bear them. These conclusions are apparently borne out by observation (Thompson and Rabinowitz, 1989) and suggest that the potential to evolve fruits that are sufficiently rewarding to attract animal dispersers may be higher among woody taxa than among herbaceous taxa.

In this paper we present evidence that biotic dispersal is associated with elevated taxonomic diversity of extant species, genera and families in woody angiosperms and that abiotic dispersal is associated with elevated taxonomic diversity in herbaceous angiosperms. Our study differs from Herrera's (1989) in two respects. First, we examine the statistical influence of both dispersal mode and growth habit (and their interaction) on generic and specific diversity within families in the monocotyledons and dicotyledons. Second, we use a different data base than Herrera's (1989), the justification for which is explained below (see Materials and methods).

We focus on biotic dispersal by vertebrates, in particular by mammals and birds, which radiated in the Tertiary and dominate modern terrestrial faunas. However, insects, especially ants, also play a role in the dispersal of some taxa (Berg, 1975; Handel *et al.*, 1981; van der Pijl, 1982) as indicated by the presence of elaiosomes, arils, caruncles and other such structures. Such disseminules could be dispersed by ground-dwelling vertebrates or birds, but might equally be interpreted as insect dispersed. Hence, we assembled a separate data set of those angiosperms with external attractant structures. This permits a test to determine whether associations between dispersal type and habit are vertebrate specific or a function of biotic dispersal in the larger sense.

Materials and methods

Why a new database?

We chose to use a modified version of the data analysed by Herrera (1989) for two reasons. First, Herrera used Heywood (1978) as his source for the systematic classification of angiosperm families and for the number of genera and species per family. Heywood's (1978) book is a compilation of the work of 44 systematists, who contributed the descriptions of individual families. While this allowed the input of specialists on particular families, it also meant that the work reflects up to 44 different concepts of generic and familial limits. This was particularly obvious in cases where several generally recognized families of different ecologies were lumped together (e.g. the Theaceae). We have based our classification on Cronquist's (1981) *Integrated Classification of Flowering Plants*. Thus, while Herrera's database included 277 families, ours includes 383 families. We realize that other treatments (e.g. Willis, 1973; Thorne, 1992) offer still different systematic schemes and diversity estimates. We chose Cronquist's (1981) work because

it is the most recently published work that provides a complete revision of angiosperm classification undertaken by a single individual with an internally consistent set of systematic concepts. Further, Cronquist's (1981) presentation includes data on diversity, habit and fruit and seed morphology. We use Cronquist's (1981) estimates of the number of genera and species within each family, recognizing that these are estimates and that other summaries often cite different numbers (e.g. Willis, 1973; Heywood, 1978; Mabberley, 1987 (largely based on Cronquist, 1981); Thorne, 1992). Differences among the diversity estimates provided by different authorities do not severely compromise the present study, as our aim is to compare the relative success – measured as the diversification of families and genera – of particular dispersal modes and growth habits. We do not seek precise absolute measures of this success.

Second, we wished to assign families to 'dispersal classes' that, in some cases, differed from those established by Herrera. The most important differences between our classification and his are as follows.

(1) Herrera quite logically assumed that a fleshy fruit or seed indicated vertebrate dispersal and a dry fruit or seed indicated abiotic dispersal. However, this approach can be misleading on two levels. First, there are some large dry fruits which are clearly vertebrate dispersed. For example, although the eight genera of Fagaceae (oaks, beeches and their relatives) are dominated by non-fleshy fruits, they are vertebrate-dispersed. Within the Tertiary history of the family, only *Fagopsis* (Oligocene, North America; Manchester and Crane, 1983) was clearly abiotically dispersed. Herrera, however, classified Fagaceae as abiotically dispersed. Second, Herrera classified most small fruit and seeds as abiotically dispersed, although in some of these cases, empirical evidence indicates vertebrate dispersal. For example, species of the Potamogetonaceae, other aquatic angiosperms and many herbaceous Compositae and Polygonaceae, are known to be eaten by birds (e.g. Martin et al., 1951; Cook, 1987). Moreover, the geographic distribution of many cosmopolitan aquatic genera with locally differentiated species can most easily be explained by bird dispersal (Hutchinson, 1975; Tiffney, 1981a).

(2) Herrera limited his consideration of biotic dispersal to endozoochory, as he felt that this was the only mode that could be unequivocally inferred from morphology and that this was by far the most common and important form of vertebrate dispersal. While Herrera provided a sensible rationale for this decision, we feel that this approach had the potential to create a small bias in the data. Thus, we have included as 'animal dispersed' those diaspores which may be transported on the exterior of animals (dry fruits with hooks, barbs or 'glue'). This results in very minor differences between Herrera's data and ours in cases in which the same families are recognized.

(3) As noted above, we wish also to examine the influence on taxonomic diversity of those external outgrowths (e.g. elaiosomes, caruncles) which are often assumed or observed to attract insect dispersal agents (van de Pijl, 1982). We therefore assigned to each family a second dispersal mode category, based on the possession or absence of external attractant structures.

Data sources and scoring

Data recorded from Cronquist (1981) include the number of genera and species in each family, the dominant habitat of each family and the dominant dispersal type of each family. Where Cronquist (1981) cited generic or specific diversity as a range (e.g. 200–250 spp.), we close the median value (e.g. 225). In tabulating the dominant habitat and dispersal mode, we referred to Melchior (1964). Hutchinson (1964, 1967). Willis (1973), Heywood (1978) and Mabberley (1987), in addition to Cronquist (1981), to determine the nature and importance of these attributes in each family. We attempted to maintain Cronquist's concept of the familial limits in referring to these other works.

Dispersal mode was scored following the approach of Herrera (1989). A family was identified

as 'biotic' if approximately 90% or more of its species are biotically dispersed. If a family was dominated by approximately 90% or more species with abiotic dispersal, it was scored as 'abiotic'. Families in which each mode was represented in more than approximately 10% of the species were scored as 'mixed'. Decisions concerning biotic versus abiotic dispersal were based on the morphology of the fruits as described by Melchior (1964), Hutchinson (1964, 1967), Willis (1973), Heywood (1978), Cronquist (1981) and Mabberley (1987) and on references to dispersal provided by Ridley (1930) and van der Pijl (1982). Generally, taxa possessing indehiscent fleshy fruits, fruits or seeds clearly dispersed on the exterior of animals by hooks or sticky substances (e.g. Pedaliaceae, Loranthaceae) or seeds with sarcotestas, were considered as biotically dispersed. Fruits or seeds of small size or with wings, ballistic mechanisms or pappus-like structures were considered abiotically dispersed. There was one exception to these generaliz-ations. Many taxa that produce seeds and fruits without flesh (which could therefore be classified as abiotic in the above scheme) are commonly known to be dispersed by rodents and birds (cf. Ridley, 1930; Martin *et al.*, 1951). Where this is clearly a significant mode of dispersal in the group, we have been conservative and classified the family as mixed (e.g. Polygonaceae, Potamogetonaceae). In most cases, we classed families as did Herrera (1989), but in several cases our conclusions were different. Some of these changes reflected the different familial limits as defined by Heywood (1978) versus Cronquist (1981). In others (e.g. Fagaceae), we simply disagreed with Herrera's (1989) assignment to dispersal type.

In some cases it was difficult to estimate the proportion of species within a family that possess a particular dispersal mode (e.g. an author would cite fleshy fruits as 'common' without indicating whether they were overwhelmingly dominant or would report that a family had dry fruits with rare fleshy ones present). In these cases, we attempted to be conservative, reporting a family as mixed unless other data indicated the dominance of biotic or abiotic dispersal.

Habit was scored using three classes. If a family contains approximately 90% or more woody species (trees, vines or shrubs) or approximately 90% or more herbaceous species, it was assigned to the classes woody or herbaceous, respectively. In families with both woody and herbaceous species, but in which neither type exceeds approximately 90% of all species, the family was scored as mixed. In some families the numerical dominance of one form was not entirely clear from the literature, but ecological data suggested that one habit was clearly unusual and derived in the group (e.g. woody species among Compositae, Lobeliaceae). In such cases we scored the family as mixed, woody or herbaceous as appropriate.

Data concerning the presence of reward structures on seeds (arils, caruncles, elaiosomes, funicular or raphal outgrowths, etc.) were scored in a similar manner. Families were scored as 'dominant' (attractant structures in approximately >90% of species), 'absent' (attractant structures in approximately <10% of the species) and 'mixed' (attractant structures in approximately >10% but approximately <90% of species). Other characters were recorded as in the data set summarizing the occurrences of vertebrate dispersal. The tabulated raw data are available from the authors on request.

One disadvantage of our data set is that we do not have an individual measure of the number of species per genus for each genus in each family. Our estimate of the mean number of species per genus for each family is based on the total number of genera and species in the family. Consequently, our method does not provide a standard deviation for the number of species per genus in each family; each family contributes only one value. A statistical test of the effect of dispersal mode on generic diversification rates could be performed on a data set that included the number of species per genus in each of the 12 000+ genera of angiosperms. This type of data set would possibly provide more accurate information concerning the dispersal mode of each genus and would appear to include many more degrees of freedom.

For several reasons we believed that the use of such a detailed data set was not warranted. First, a statistical analysis based on this data set would require the assumption that genera represented statistically independent data points with respect to species diversity. Given that related genera might share high or low species numbers for reasons other than dispersal mode, the assumption of independence would be tenuous. We felt it was more prudent to assume that families, rather than the 12 000 genera they include, represent independent data points with respect to the mean number of species per genus. Second, a 12 000-genus data set would provide no additional information concerning the effect of dispersal mode on the mean number of genera per family or species per family. Finally, the time and expense necessary to provide such a data set renders it impractical at present.

It is important to note that, because we have only one value for the mean number of species per genus for each family (and so the degrees of freedom are based on the number of families rather than the number of genera), out test for the effect of dispersal mode on the mean number of species per genus is relatively conservative. It is true that in some of the families to which we assigned a particular dispersal mode (or habit), there may exist occasional genera that deviate from that dispersal mode (or habit). Nonetheless, we wished to compare the diversification of families that represent the end-points of the dispersal 'spectrum' (biotic versus abiotic dispersal) and we are confident that our classification scheme provides a clear distinction among families on the basis of our chosen categories. In all cases in which families had mixed suites of dispersal modes or growth habits, they were classified as 'mixed' and were excluded from the desired comparisons.

Statistical tests

Contingency table analyses were conducted using the entire data set and then separately on dicot and monocot families. Using the entire data set, we evaluated the 3×2 contingency table (three dispersal modes $\times$ two angiosperm classes) to address two questions: (1) Do the relative abundances of families, genera, and species statistically differ between the dominant dispersal mode of the contributing families? (2) Does the association between dispersal mode and taxon frequencies differ between the dicots and monocots?

In order to control for the possibility that growth habit may be a confounding factor that makes it difficult to detect a direct statistical association between dispersal mode and taxonomic frequencies, we conducted contingency table analyses that take this factor into account. Within the dicots, we evaluated the 3×3 contingency table (three dispersal modes (biotic, mixed and abiotic) $\times$ three growth habits (woody, mixed and herbaceous) to determine whether the dominant dispersal mode of dicot families is associated with the relative abundances of dicot taxa (families, genera and species) and, if so, whether this association is affected by the dominant growth habit of the contributing families. In the monocots, as there were no families of 'mixed' growth habits, we analysed the 3×2 contingency table (three dispersal modes $\times$ two habit types). For all contingency table analyses, we examined the adjusted standardized residuals (Everitt, 1977) in order to identify the categories that contributed significantly to the chi-square value at the 0.05 significance level.

If we detected no significant association between taxonomic abundances, growth form and/or dispersal mode, then growth form and dispersal mode would appear to be independent of the diversification of families, genera or species.

Of course, the presence of a strong association between dispersal mode and taxonomic abundances does not unequivocally demonstrate a causal relationship between dispersal mode and taxonomic diversification. It is possible, for example, that when conducting a contingency table analysis on the number of extant species represented by biotically-versus abiotically-

dispersed families, the presence of a single, highly species-rich‹??? pg/43› biotically-dispersed family could be responsible for a significant chi-square value. In this case, although the chi-square test would suggest that biotic dispersal generally promotes taxonomic diversity at the species level, this association would be spurious. If contingency table analyses do detect a strong association between dispersal mode and taxonomic abundances, however, then the performance of more rigorous tests aimed to detect a statistical effect of dispersal mode on diversification is warranted.

Consequently, when we detected a statistical association between dispersal mode and taxonomic abundances within growth habit categories from the contingency table analyses, we conducted non-parametric analyses of variance (ANOVA: Kruskal–Wallis and Mann–Whitney U-tests) to determine whether the mean number of species per family, genera per family or species per genus (for each family) differed among dispersal modes and whether the statistical effect of dispersal mode on taxonomic diversification differed between growth habits. We analysed data representing each habit separately as well as data pooled across habits, estimating the statistical effect of dispersal mode on mean species per family, genera per family and species per genus. The monocots and dicots were analysed separately.

Unlike the contingency table analyses, the non-parametric ANOVAS are not subject to strong biases produced by one or a few highly diverse families (outliers) that may create a spurious association between dispersal mode and taxonomic diversification. These ANOVAS are based on the ranks of families with respect to the mean number of genera per family, species per genus and species per family, rather than on the absolute numbers of taxa representing each taxonomic level. Any strong biases due to outlier families are thus eliminated.

Similar contingency table analyses and Kruskal–Wallis and Mann–Whitney U-tests were conducted for the data on disseminules with external attractant structures.

The detection of a significant association between dispersal mode and taxonomic diversification within or across growth habits suggests the presence of either (1) a direct effect of dispersal mode on diversification within families (e.g. by decreasing the probability of extinction of genera or species, or by increasing the probability of speciation or the origin of new genera) or (2) an indirect effect of dispersal mode on diversification within families, mediated by another unidentified ecological attribute(s) correlated with dispersal mode.

Results

Effect of dispersal mode on the relative abundances of taxa

Table 1 summarizes the numbers of families, genera and species in families dominated by biotic, abiotic and mixed dispersal modes. Contingency table analyses indicate that the frequencies of taxa are not independent of the mode of dispersal of the families to which they belong. In addition, the relationship between dispersal mode and taxon frequencies differs for the dicots relative to the monocots.

Among dicot families, genera and species, those dominated by biotic dispersal are significantly overrepresented relative to those dominated by abiotic dispersal. Among monocot families, the pattern is reversed, with abiotically-dispersed families, genera and species occurring significantly more frequently than biotically-dispersed families. From these results, we conclude that: (1) taxonomic abundances are not independent of dispersal mode and (2) the monocots and dicots differ with respect to the distribution of their families, genera and species among dispersal categories.

Table 2 presents a contingency table of the frequencies and proportions of families, genera and species within families of dicots, classified by dispersal type (abiotic, mixed and biotic) and by

Table 1. Frequency of families, genera and species of dicotyledons and monocotyledons which are biotically dispersed (biotic), abiotically dispersed (abiotic) or which include both abiotic and biotic dispersal (mixed)

Frequency of families

	Dicots Number	Dicots Pro-portion	Monocots Number	Monocots Pro-portion	Sum Number	Sum Pro-portion
Biotic	104+	0.327	12-	0.185	116	0.303
Mixed	74	0.233	12	0.185	86	0.224
Abiotic	140-	0.440	41+	0.631	181	0.473
Sum	318		65		383	

(Chi square = 8.316; p = 0.0156; df. = 2)

Frequency of genera

	Dicots Number	Dicots Pro-portion	Monocots Number	Monocots Pro-portion	Sum Number	Sum Pro-portion
Biotic	1401+	0.149	344-	0.127	1745	0.144
Mixed	4190+	0.445	566-	0.209	4756	0.393
Abiotic	3817-	0.406	1793+	0.663	5610	0.463
Sum	9408		2703		12 111	

(Chi square = 605.391; $p \leq 0.0001$; df. = 2)

Frequency of species

	Dicots Number	Dicots Pro-portion	Monocots Number	Monocots Pro-portion	Sum Number	Sum Pro-portion
Biotic	25 515+	0.149	6205-	0.122	31 720	0.144
Mixed	80 586+	0.474	11 638	0.229	92 224	0.417
Abiotic	64 048-	0.376	33 019+	0.649	97 067	0.439
Sum	170 149		50 862		221 011	

(Chi square = 13 800.299; $p \leq 0.0001$; df. = 2)

Number, number of taxa; proportion, proportion of total number of families, genera or species in each category. Superscript + and - indicate where observed values were greater or less than the expected value at the 0.05 level of significance. The data sources and protocol are explained in Materials and methods sections. Chi square and p-values beneath each table indicate the results of the 3 × 2 contingency table analysis conducted in the table.

Table 2. Frequencies of families, genera and species of dicotyledons which are biotically dispersed (biotic), abiotically dispersed (abiotic) or which include both abiotic and biotic dispersal (mixed) in each of three categories of habit: arborescent (woody), herbaceous (herbaceous) and containing both woody and herbaceous members (mixed)

Frequency of families

	Woody Number	Woody Pro-portion	Mixed Number	Mixed Pro-portion	Herbaceous Number	Herbaceous Pro-portion
Biotic	88+	0.449 1.38x	6-	0.139	10-	0.127 1x
Mixed	44	0.224	17+	0.395	13	0.165
Abiotic	64-	0.326 1x	20	0.465	56+	0.709 5.6x
Sum	196		43		79	

(Chi square = 48.527; $p \leq 0.0001$; df. = 4)

Frequency of genera

	Woody Number	Woody Pro-portion	Mixed Number	Mixed Pro-portion	Herbaceous Number	Herbaceous Pro-portion
Biotic	1251+	0.407 3.7x	130-	0.043	20-	0.006 1x
Mixed	1485+	0.483	1916+	0.631	789-	0.239
Abiotic	338-	0.109 1x	989-	0.326	2490+	0.755 124.5x
Sum	3035		3299		3074	

(Chi square = 4317.543; $p \leq 0.0001$; df. = 4)

Frequency of species

	Woody Number	Woody Pro-portion	Mixed Number	Mixed Pro-portion	Herbaceous Number	Herbaceous Pro-portion
Biotic	20 572+	0.403 4.53x	4745-	0.084	198-	0.003 1x
Mixed	25 919+	0.508	37 620+	0.664	17 047-	0.273
Abiotic	4539-	0.089 1x	14 315-	0.252	45 194+	0.724 228.25x
Sum	56 680		62 439		51 030	

(Chi square = 75 730.695; $p \leq 0.0001$; df. = 4)

Number, number of taxa; proportion, proportion of total number of families, genera or species in each category. Superscripts + and - indicate where observed values were greater or less than the expected value at the 0.05 level of significance. The sources and protocol are explained in Materials and methods section. Chi-square and p-values beneath each table indicate the results of the 3 × 2 contingency table analysis. The factorial difference in diversity between biotic and abiotic taxa representing woody and herbaceous growth habits at each of the three taxonomic levels is indicated by x and Nx.

habit (woody, mixed and herbaceous). This analysis allows us to determine whether the relationship between dispersal mode and taxon frequency differs among woody, mixed-habit and herbaceous dicot families.

Among woody dicot families, biotically-dispersed families, genera and species are disproportionately more numerous than abiotically-dispersed families, genera and species. Among herbaceous families, the pattern is reversed, with abiotically-dispersed taxa significantly overrepresented relative to biotically-dispersed taxa. Consequently, there is a strong interaction between dispersal mode and habit that is associated with taxonomic abundances.

In addition to detecting a non-random association between dispersal mode and the relative abundances of taxa, these contingency table analyses provide information concerning the association between dispersal mode and the rate of taxonomic diversification. A comparison of the proportions of taxa in each cell of the contingency tables of families, genera and species is of critical importance. If each family possessed the same number of genera and species, the proportions of taxa at the lower taxonomic levels would be identical to the proportions 'set' at the family level. However, if there is differential diversification of families according to dispersal mode, the proportions of biotic versus abiotic taxa observed at the lower levels will differ from those exhibited at the family level. The same reasoning applies if each dispersal category contained a fixed proportion of genera. If speciation rates within genera did not differ among dispersal modes and growth habits, then the proportions in each category observed at the species level would be identical to those at the genus level.

Our data show clearly that the proportions of taxa representing each dispersal mode change significantly as one progresses from higher (family level) to lower taxonomic levels in the dicots. Table 2, (presenting the number of dicot families in each dispersal mode/growth habit combination), shows that woody, biotically-dispersed families and herbaceous, abiotically-dispersed families are over represented relative to the distribution of families expected by chance. There are 1.38 times more biotically-dispersed than abiotically-dispersed woody dicot families and 5.6 times more abiotic than biotic herbaceous families. This suggests that there is some factor associated with particular dispersal mode/growth habit combinations that may promote taxonomic diversity at the family level.

At the generic level, the effect of dispersal mode on taxonomic abundances is stronger than at the family level. There are 3.7 times as many biotically-dispersed as abiotically-dispersed woody genera and 124.5 times as many abiotically-dispersed as biotically-dispersed herbaceous genera. The number of families in each dispersal mode/growth habit category cannot alone account for this disparity in the numbers of genera represented. Rather, the diversification rate of biotically-dispersed woody families and abiotically-dispersed herbaceous families to produce new genera must be higher than that of their abiotically- and biotically-dispersed counterparts.

Finally, at the species level, there are 4.53 times as many woody biotically-dispersed taxa than abiotically-dispersed taxa and 228.25 times as many herbaceous abiotic taxa than biotic taxa. Again, the number of genera alone cannot account for these differences in species abundances. Rather, speciation rates within woody, biotically-dispersed genera and in herbaceous, abiotically-dispersed genera are higher than in genera representing the alternative combinations. Further, the degree to which species diversify according to dispersal mode (relative to the number of genera they represent) is far greater in herbaceous taxa than in woody taxa. In other words, the statistical effect of dispersal mode on the diversification of the contributing families differs for woody versus herbaceous taxa.

This pattern could conceivably be the result of a difference in the ages of the contributing families, for example, if herbaceous, abiotically-dispersed families were on average much older than herbaceous, biotically-dispersed families, they would have had a longer time to accumulate

generic and specific diversity. There is no evidence in the fossil record to support this view, however. In particular, many herbaceous, abiotically-dispersed families appear to have diversified relatively recently, in the Neogene (e.g. Muller, 1981; Tiffney, 1981b).

Table 3 presents contingency tables of the observed frequencies and proportions of families, genera and species within families of monocots, as influenced by dispersal mode and habit. Dispersal mode and growth habit are associated in monocots in the same manner as observed in dicots, although to a less pronounced degree. Woody, biotically-dispersed monocot families, genera and species and herbaceous, abiotically-dispersed monocot families, genera and species are more numerous than would be expected by chance. The number of families in each dispersal mode/growth form category cannot account for the generic abundances in the absence of differential diversification rates, nor can the number of genera account for the observed differences in species abundances. Rather, the speciation rates of woody, biotically-dispersed monocot genera appear to be much higher than those of woody, abiotically-dispersed genera, assuming that these genera are on average of similar age. The rate of diversification within herbaceous, biotically-dispersed families and genera does not differ markedly from that of herbaceous, abiotically-dispersed families and genera, for the proportions of taxa in these categories do not change greatly from the family to the genus to the species level. These results stand in contrast to the pattern observed in the dicots (Table 2), where the change in proportions of biotically- and abiotically-dispersed families, genera and species is far higher among herbaceous than woody families.

In sum, similarly to the dicots, dispersal mode is associated with monocot diversification and the effect of dispersal mode on the diversification of contributing taxonomic families differs for woody versus herbaceous families.

Effect of dispersal mode on the diversification of taxa

Table 4 presents the mean values of species per family, genera per family and species per genus in dicots according to the dispersal mode of the contributing families. The table also presents the results of Kruskal–Wallis tests conducted to detect a significant effect of dispersal mode on these three measures of diversification within families representing each growth habit category, as well as across all habits. One primary question is addressed: Is the diversification of dicot families as measured by three assays (mean number of species per family, genera per family and species per genus) associated with the mode of dispersal of woody, mixed or herbaceous families or across all growth habits?

Ten of the 12 Kruskal–Wallis tests detected significant statistical effects of dispersal mode on diversification. However, in ten cases the highest mean value was for the 'mixed dispersal' category. In order specifically to detect significant differences between the diversification of biotically- and abiotically-dispersed families representing different growth habits and across all growth habits, Mann–Whitney U-tests were conducted. This test excluded the means of the mixed dispersal mode category.

Over all dicot families (including all habit types), the Mann–Whitney U-test suggests that there are no significant differences between biotically- and abiotically-dispersed angiosperm families in any of the three measures of diversification. Among woody dicots, however, the mean number of species per family, genera per family and species per genus are all significantly higher for biotically-dispersed families than among abiotically-dispersed families. Among herbaceous dicots, the mean number of species per family and genera per family is significantly higher among abiotically-dispersed families than among biotically-dispersed ones. The mean number of species per genus is not significantly influenced by dispersal mode in herbaceous families, but it exhibits the same trend as species per family and genus per family.

Table 3. Frequencies of families, genera and species of monocotyledons which are biotically dispersed (biotic), abiotically dispersed (abiotic) or which include both abiotic and biotic dispersal (mixed) in each of two categories of habit: arborescent (woody) and herbaceous (herbaceous). Note that there are no families of monocotyledons containing both woody and herbaceous members (mixed)

	Frequency of families				Frequency of genera				Frequency of species			
	Woody		Herbaceous		Woody		Herbaceous		Woody		Herbaceous	
	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion
Biotic	3+	0.500 3x	9−	0.152 1x	215+	0.870 23.89x	129−	0.052 1x	4060+	0.749 73.82x	2145−	0.047 1x
Mixed	2	0.333	10	0.169	23−	0.093	543+	0.221	1300+	0.240	10 388−	0.228
Abiotic	1−	0.166 1x	40+	0.678 6.5x	9−	0.036 1x	1784+	0.726 13.83x	55−	0.010 1x	32 964+	0.725 15.37x
Sum	6		59		247		2456		5415		45 447	
	(Chi square = 6.611; p = 0.0367; d.f = 2)				(Chi square = 1358.358; p ≤0.0001; df. = 2)				(Chi square = 23 392.267; p ≤0.0001; df. = 2)			

Number, number of taxa; proportion, proportion of total number of families, genera or species in each category. Superscripts + and − indicate where observed values were greater or less than the expected value at the 0.05 level of significance. The data sources and protocol are explained in Materials and methods section. Chi square and p-values beneath each table indicate the results of the 3×2 contingency table analysis conducted in the table. The factorial difference in diversity between biotic and abiotic taxa representing woody herbaceous growth habits at each of the three taxonomic levels is indicated by $\times$ and $N\times$.

Table 4. Mean numbers of species per family, genera per family and species per genus in dicotyledon families that are biotically dispersed (biotic), abiotically dispersed (abiotic) and which include both abiotic and biotic dispersal (mixed) in habit categories woody (dominated by woody plants), herbaceous (dominated by herbaceous plants) and mixed (containing both woody and herbaceous members). 'All habit categories' summarizes parameters for all taxa in each habit category.

	Woody			Mixed			Herbaceous			All habit categories		
	Species per family	Genera per family	Species per genus	Species per family	Genera per family	Species per genus	Species per family	Genera per family	Species per genus	Species per family	Genera per family	Species per genus
Biotic												
Mean	233.8[b]	14.2[b]	19.9[b]	790.8[a]	21.7[a]	62.2[b]	19.8[a]	2.0[a]	13.7[a]	245.3[a]	13.5[a]	21.7[a]
SD	415.01	27.22	41.67	720.14	31.49	61.26	19.25	2.00	16.86	439.40	26.30	42.17
n	88	88	88	6	6	6	10	10	10	104	104	104
Mixed												
Mean	589.1	33.8	20.7	2212.9	112.7	22.1	1311.3	60.7	25.7	1089.0	56.6	21.9
SD	787.96	39.54	26.42	2141.39	118.18	10.06	2701.42	106.04	38.94	1738.97	82.95	26.19
n	44	44	44	17	17	17	13	13	13	74	74	74
Abiotic												
Mean	70.9[a]	5.3[a]	12.9[a]	715.8[a]	49.5[a]	22.3[a]	807.0[b]	44.5[b]	29.4[a]	457.5[a]	27.3[a]	20.8[a]
SD	157.88	13.19	25.20	897.55	81.36	15.23	2749.85	157.73	52.52	1800.30	106.02	38.35
n	64	64	64	20	20	20	56	56	56	140	140	140
H	40.10	42.78	17.03	8.75	11.65	4.91	10.06	14.60	1.22	46.55	56.62	11.26
p	0.0001	0.0001	0.0002	0.0126	0.0029	n.s.	0.0065	0.0007	n.s.	0.0001	0.0001	0.0036
df.	2	2	2	2	2	2	2	2	2	2	2	2
Z	−2.88	−2.64	−2.21	−0.34	−0.79	−2.07	−2.15	−2.82	−0.84	−0.02	−0.51	−0.35
p	0.0040	0.0083	0.0270	n.s.	n.s.	0.0384	0.0318	0.0049	n.s.	n.s.	n.s.	n.s.
Total												
Mean	260.4	15.7	17.8	1318.1	70.6	27.8	790.4	41.8	26.8	535.1	29.6	21.4
s.d.	508.22	29.01	33.84	1646.10	98.52	28.05	2564.42	139.79	47.32	1510.67	83.64	37.16
n	196	196	196	43	43	43	79	79	79	318	318	318

Mean, mean number of species per family, species per genus or genera per family calculated from the raw data. SD, standard deviation. n, number of families contributing to generic or species diversity. For the data represented by each column (e.g. species per family among woody dicots) the results of a Kruskal–Wallis test conducted to detect a significant effect of dispersal mode on mean taxonomic diversity is recorded (H corrected for ties, p and df.; n.s., not significant). Also beneath each column are reported the results (Z corrected for ties, p) of a Mann–Whitney U-test conducted to detect significant differences between biotically- and abiotically-dispersed families with respect to species per family, genera per family and species per genus. Shared superscripts indicate that mean values within a column do not differ significantly at the 0.05 level.

Table 5. Mean numbers of species per family, genera per family and species per genus in monocotyledon families that are biotically dispersed (biotic), abiotically dispersed (abiotic) and that include both abiotic and biotic dispersal (mixed) in habit categories woody (dominated by woody plants) and herbaceous (dominated by herbaceous plants). Note that there are no families of monocotyledons containing both woody and herbaceous members. 'All habit categories' summarizes parameters for all taxa in each habit category.

	Woody			Herbaceous			All habit categories		
	Species per family	Genera per family	Species per genus	Species per family	Genera per family	Species per genus	Species per family	Genera per family	Species per genus
Biotic									
Mean	1353.3[a]	71.7[a]	95.3[a]	238.3[a]	14.3[a]	19.6[a]	517.1[a]	28.7[a]	38.5[a]
SD	1440.01	111.23	128.37	588.76	36.02	30.94	939.90	62.18	69.73
n	3	3	3	9	9	9	12	12	12
Mixed									
Mean	650.0	11.5	86.7	1033.8	54.3	33.4	969.8	47.2	42.3
SD	70.71	9.19	75.43	1230.16	83.66	38.30	1122.90	77.54	46.33
n	2	2	2	10	10	10	12	12	12
Abiotic									
Mean	55[a]	9[a]	6.1[a]	824.1[a]	44.6[a]	15.7[a]	805.3[a]	43.7[a]	15.5[a]
SD	–	–	–	3042.30	173.81	20.3	3006.43	171.71	20.04
n	1	1	1	40	40	40	41	41	41
H	2.38	0.10	2.38	5.99	6.53	3.00	7.31	5.31	5.50
p	n.s.	n.s.	n.s.	n.s.	0.0383	n.s.	0.0259	n.s.	n.s.
df.	2	2	2	2	2	2	2	2	2
Z	−1.34	−0.45	−1.34	−0.66	−1.57	−0.26	−0.48	−0.78	−1.11
p	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Total									
Mean	902.5	41.2	77.5	770.3	41.6	19.3	782.5	41.6	24.7
SD	1059.04	77.99	94.72	2562.05	147.40	26.04	2457.20	142.01	40.05
n	6	6	6	59	59	59	65	65	65

Mean, mean number of species per family, species per genus or genera per family calculated from the raw data. SD, standard deviation. n, number of families contributing to generic or species diversity. For the data represented by each column (e.g. species per family among woody monocots) the results of a Kruskal–Wallis test conducted to detect a significant effect of dispersal mode on mean taxonomic diversity is recorded (H corrected for ties, p and df.; n.s., not significant). Also beneath each column are reported the results (Z corrected for ties, p) of a Mann–Whitney U-test conducted to detect significant differences between biotically- and abiotically-dispersed families with respect to species per family, genera per family and species per genus. Shared superscripts indicate that mean values within a column do not differ significantly at the 0.05 level.

Several observations are noteworthy. First, the diversification of dicot families is influenced by both dispersal mode and habit. Second, we could not detect an effect of dispersal mode on diversification rate when sampling families across all growth habits. Therefore, an analysis of the effect of dispersal mode on the diversification of the dicots without controlling for growth habit obscures the true nature of the relationship between dispersal mode and diversification. Third, the highest diversification rates appear in families that are the most ecologically diverse. For example, families characterized by mixed dispersal modes are represented by higher means than biotically- or abiotically-dispersed families and families of mixed growth habit are represented by higher means than woody or herbaceous families. In addition, families characterized by both mixed dispersal modes and mixed growth habit have the highest mean values for species per family and genera per family of any cell in Table 4.

Table 5 presents the mean values of species per family, genera per family and species per genus

according to the dispersal mode of the contributing families of monocots. Two questions are addressed by this analysis and by the comparison of Tables 4 and 5. First, is the diversification of monocot families associated with the mode of dispersal experienced by a family within or across growth habits? Second, does the diversification of angiosperm families with respect to dispersal mode and habit differ between monocots and dicots?

Within each growth habit type and across growth habits in the monocots, the Kruskal–Wallis test detects significant effects of dispersal mode on diversification in two out of nine comparisons. The Mann–Whitney *U*-tests, however, detect no significant effects of dispersal mode on any of the three measures of diversification. Among woody monocots, those with biotic dispersal have higher (but not statistically significantly so) mean numbers of species per family, genera per family and species per genus than do abiotically-dispersed woody forms. Conversely, among herbaceous monocots, those with abiotic dispersal have higher (but not statistically significantly so) mean numbers of species per family and genera per family than do biotically-dispersed herbaceous families. Over all habit types among monocots, although the association is not statistically significant, the mean number of species per family and genera per family for abiotically-dispersed families is higher than for biotically-dispersed families, while the mean number of species per genus is higher in biotically-dispersed families than in abiotically-dispersed families. This parallels the case in dicots.

In sum, there is no statistically significant difference in diversification between predominantly abiotically-dispersed and biotically-dispersed families within herbaceous or woody monocots or for monocots as a whole. However, the pattern of diversification among woody and herbaceous monocot families parallels that in dicots. Similar to our observations on dicots, monocot families characterized by 'mixed' dispersal modes feature higher means for taxonomic diversification than families dominated by a single dispersal mode in six out of nine cases.

Effect of external attractant structures on relative abundances and diversification of taxa

There is no statistical effect of external attractant structures on the relative abundances of families of woody or herbaceous dicots or monocots.

Table 6 presents a contingency table of the frequencies and proportions of families, genera and species within families of dicots, classified with respect to the possession of external attractants (dominant, mixed or absent) and by habit (woody, mixed or herbaceous). This analysis allows us to determine whether the relationship between the potential for biotic dispersal and taxon frequency differs among woody, mixed-habit and herbaceous dicot families when dispersal includes the potential for insect in addition to vertebrate dispersal.

Among woody dicot families, genera and species in families lacking attractants are significantly underrepresented, as are species in families dominated by attractants. Among herbaceous dicot families, genera and species in families both dominated by and lacking external attractant structures are overrepresented relative to mixed families.

Table 7 presents a contingency table of the frequencies and proportions of families, genera and species within families of monocots, classified with respect to the possession of external attractants and by habit. Among woody monocot families, genera and species are underrepresented in families dominated by external attractant structures and are overrepresented in families lacking them. Among herbaceous monocot families, genera and species are overrepresented in families dominated by external attractant structures and are underrepresented in families lacking them.

The Kruskal–Wallis tests (not shown) were inconclusive. The categories 'mixed habit dicot' and 'woody monocot' exhibited only two dispersal types, so they were not subjected to this test. Among dicots, four out of nine *p*-values were significant and among monocots, one *p*-value out of

Table 6. Frequency of families, genera and species of dicotyledons in which an external attractant structure is dominant, lacking (absent) or in which both conditions occur (mixed), in each of three categories of habit: arborescent (woody), herbaceous (herbaceous) and containing both woody and herbaceous members (mixed)

	Frequency of families						Frequency of genera						Frequency of species					
	Woody		Mixed		Herbaceous		Woody		Mixed		Herbaceous		Woody		Mixed		Herbaceous	
	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion
Dominant	5	0.025 1x	0	0.000	3	0.038 1x	20	0.007 1x	0⁻	0.000	34⁺	0.010 1x	125⁻	0.002 1x	0⁻	0.000	2903⁺	0.046 1x
Mixed	16	0.082	7	0.163	4	0.051	692⁺	0.225	504⁺	0.166	47⁻	0.014	9585⁺	0.188	11 995⁺	0.211	1570⁻	0.025
Absent	175	0.893 35x	36	0.837	72	0.911 24x	2362⁻	0.768 118.1x	2531⁻	0.834	3218⁺	0.975 94.65x	41 320⁻	0.809 330.6x	44 685⁻	0.786	57 966⁺	0.928 19.97x
Sum	196		43		79		3074		3035		3299		51 030		56 680		62 439	

(Chi square = 5.97; $p = 0.2017$; df. = 4) (Chi square = 687.59; $p = 0.0001$; df. = 4) (Chi square = 14 405.65; $p = 0.0001$; df. = 4)

Superscripts $^+$ and $^-$ indicate where observed values were greater or less than the expected value at the 0.05 level of significance. Data sources and protocol are explained in the Materials and methods section.

Table 7. Frequency of families, genera and species of monocotyledons in which an external attractant structure is dominant, lacking (absent) or in which both conditions occur (mixed), in two categories of habit: arborescent (woody) and herbaceous (herbaceous). No monocot families are classified as possessing mixed habit

	Frequency of families				Frequency of genera				Frequency of species			
	Woody		Herbaceous		Woody		Herbaceous		Woody		Herbaceous	
	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion
Dominant	0	0.000	5	0.085 1x	0⁻	0.000 1x	87⁺	0.035 1x	0⁻	0.000	1587⁺	0.035 1x
Mixed	1	0.166 1x	3	0.051	3⁻	0.012	376⁺	0.153	730⁺	0.135 1x	5600⁻	0.123
Absent	5	0.833 5x	51	0.864 10.2x	244⁺	0.988 81.3x	1993⁻	0.812 22.9x	4685⁺	0.865 6.42x	38 260⁻	0.842 24.1x
Sum	6		59		247		2456		5415		45 447	

(Chi square = 1.70; $p = 0.4270$; df. = 2) (Chi square = 48.98; $p = 0.0001$; df. = 2) (Chi square = 197.43; $p = 0.0001$; df. = 2)

Superscripts $^+$ and $^-$ indicate where observed values were greater or less than the expected value at the 0.05 level of significance. The data sources and protocol are explained in the Materials and methods section.

six was significant. Because the Kruskal–Wallis tests included the 'mixed' dispersal category, they could not detect the effect of the presence versus absence of external attractant structures on the diversification of woody versus herbaceous plants. The Mann–Whitney U-tests revealed no significant p-vlues, indicating that families dominated by external attractant structures did not differ from those lacking them with respect to any measure of diversification.

Discussion

Independence of observations in comparative studies

Comparative studies are vulnerable to the criticism that, since related taxa often share heritable morphological traits, they do not represent independent data points in the statistical analyses used to detect evolutionarily significant associations (Harvey and Pagel, 1991). So-called 'phylogenetic constraints' are thought to limit the ability of closely related taxa to diverge evolutionarily (at least with respect to these shared traits) and to result in an inflated value for the degrees of freedom associated with the statistical tests often applied to multispecies data sets. For example, if a higher taxon contains many lower taxa that share a suite of heritable traits (e.g. woodiness and biotic dispersal), then the lower taxa cannot generally be considered to represent independent data points in comparative studies that interpret the high occurrence of particular trait combinations as evidence for their adaptive significance (cf. Mazer, 1989). This is because the lower taxa do not necessarily represent independent evolutionary outcomes of natural selection favouring these trait combinations. However, it is pertinent to note that two studies (Tiffney, 1986; Bremer and Eriksson, 1992) have demonstrated the differentiation of dispersal modes within families, suggesting that dispersal mode is not necessarily a stable character fixed within a family. The problem of the non-independence of related taxa with respect to morpho-logical or ecological traits can be exacerbated if families that possess different combinations of traits diversify at different rates.

In this study, however, we were specifically interested in detecting and determining whether this differential diversification was associated with particular dispersal modes and/or growth habits. In other words, the differential diversification that can make the interpretation of some comparative studies suspect does not present a statistical difficulty for our study because it is precisely the phenomenon that we sought to detect. In sum, the comparison of many families within which growth habit and/or dispersal mode is nearly constant, but among which there is much morphological and ecological variation in other traits, is a sound way to detect direct or indirect effects of dispersal mode on the diversification rates of the families and genera represented. It is possible that families are not independent data points with respect to observed measures of diversification. However, Ricklefs and Renner (in press) estimated the statistical effect of subclass membership on familial species richness and found that subclass membership did not explain variation in species richness in families. The possible effects of ordinal membership remain unknown.

Families of mixed habit or dispersal are most diverse

In this study, we found that the most taxonomically diverse families are those that possess mixed ecological solutions involving abiotic and biotic dispersal, herbaceous and woody growth habits or both (Tables 4 and 5). This result implies that a greater range of ecological options included within a family provides a greater potential for diversification, in agreement with the findings of Fleming (1991) and Ricklefs and Renner (in press). However, because our data set recorded the abundances of genera and species within families as a whole, we could not detect any specific effect of dispersal mode on the relative abundances or diversification of taxa, or any interaction

between dispersal mode and growth habit within 'mixed' families. In future studies, species- or genus-level cladograms of 'mixed' families could be used to compare the rates of diversification in sister clades that differ primarily in the presence of a particular dispersal mode or growth habit, as Bremer and Eriksson (1992) have done for the Rubiaceae.

The association between external reward structures and measures of abundance was equivocal

This test was intended to provide a second estimate of the association of biotic dispersal and measures of diversity and to include the possibility that non-vertebrate animal dispersal might also be significant. External reward structures do play a role in insect, particularly ant, dispersal, but may also attract small vertebrates. Among woody dicots and monocots, while there were significant measures of over- and under representation among genera and species in families both dominated by and lacking external attractant structures, these values occurred in no clear pattern. Further, none of the Mann–Whitney *U*-tests detected a significant association between external attractant structures and diversification. We concluded that there were no significant statistical effects of the presence or absence of external reward structures on our three measures of diversification in either woody or herbaceous angiosperms.

Vertebrate dispersal is associated with elevated diversity in woody angiosperms

Herrera's (1989) conclusion that vertebrate fruit and seed dispersal is not important in angiosperm diversification is superficially borne out by our analysis of the pooled data included in the present paper (Tables 4 and 5). We found that across all angiosperm taxa, dispersal mode was not correlated with the diversification of families, genera or species. As is frequently the case in statistical analyses, however, the analysis of pooled data masks higher-order patterns and interactions.

When we controlled statistically for the potential effects of growth habit on the relative abundances and diversification of taxa, we found clear associations between dispersal mode and both taxon abundances and diversification. For example, herbaceous monocots and dicots are dominated by abiotic dispersal, while woody monocots and dicots are dominated by biotic dispersal (Tables 2 and 3). Our measures of diversification (species per genus, genera per family and species per family) concurred with this pattern; in woody taxa, diversification was highest for biotically-dispersed families, while in herbaceous taxa diversification was highest in abiotically-dispersed families (Tables 4 and 5). This suggests that among arborescent angiosperms, biotic dispersal directly or indirectly promotes diversification, while among herbaceous angiosperms, abiotic dispersal does so.

From our data, we feel that the most conservative conclusion is that biotic dispersal has had a significant influence on the diversity of woody angiosperms, but that it has only contributed to, not driven, the diversification of angiosperms as a whole. Assuming that biotic dispersal has influenced the diversification of arborescent angiosperms, it is possible to estimate its contribution to total angiosperm diversity. Excluding modern families of the 'mixed dispersal' category, if abiotic and biotic dispersal were equally distributed among species of arborescent dicot families and if we accept the number of living, abiotically-dispersed, woody angiosperms (4594) as the expected number of species in each dispersal category, then there should be approximately 4600 species of each dispersal type. Given that there are approximately 29 200 species of extant woody angiosperms in these two dispersal categories, this would lead to a decrease of approximately 20 000 species of woody angiosperms (or approximately 9% of the total angiosperm diversity). Nine percent is not terribly high and begs the question as to how many additional species are required to be generated by biotic dispersal for biotic dispersal to be judged to have had a 'significant influence' on angiosperm diversity.

Habit-specific effects of dispersal mode may explain unexpected differences between gymnosperms and angiosperms

Herrera (1989) supported his argument that biotic dispersal is not a major factor influencing angiosperm diversity with a comparison of the relative importance of biotic dispersal in angiosperms and gymnosperms. If biotic dispersal is an important determinant of angiosperm diversity, then Herrera (1989) reasoned it should be far more common in angiosperms than gymnosperms. He found that 64.3% (9/14) of gymnosperm families are dominated by biotic dispersal while only 27.1% of angiosperm families are dominated by biotic dispersal. Gymnosperms, however, possess *only* woody species. Indeed, perhaps one of the most striking distinctions between angiosperms and gymnosperms is the evolution of herbaceousness in angiosperms and the elevated opportunity for vegetative reproduction and rapid life cycles which it permits (Tiffney and Niklas, 1985). Thus, the comparison of gymnosperms should be with woody angiosperms, not all angiosperms. Our data-base differs from Herrera's (1989), but it is still noteworthy that out of 196 dicotyledon families that we class as woody (Table 2), 88 (44.9%) are biotically dispersed; similarly, 40.3% (20 572/51 030) of woody dicotyledon species are biotically dispersed. Among woody monocotyledons, 50% of the families (3/6) and 75% of the species (4060/5415) are biotically dispersed. These statistics appear to demonstrate that the proportions of biotic dispersal in woody monocots, woody dicots and gymnosperms are roughly similar, as might be expected if biotic dispersal promotes the diversification of all woody taxa to the same degree.

On the other hand, several lines of evidence indicate that woody, biotically-dispersed, angiosperms are doing 'something more' than biotically-dispersed gymnosperms. Biotically-dispersed woody angiosperms (24 632 species in our count, Tables 2 and 3) are far more diverse than gymnosperms (approximately 804 species; using figures of Herrera, 1989), in spite of their younger evolutionary age. Further, individual families of woody, biotically-dispersed, angiosperms have a mean of 270.68 species per family (91 families – 24 632 species) while biotically-dispersed gymnosperm families have a mean of 42.9 species per family (nine families – 386 species; gymnosperm data provided by C. Herrera). Biotically-dispersed gymnosperms thus have 1.6% the species diversity of woody, biotically-dispersed, angiosperms. More pointedly, abiotically-dispersed woody angiosperms far outnumber all gymnosperms (65 versus 14 families and 4594 species versus 804 species; the latter data provided by C. Herrera). These data clearly illustrate that biotic dispersal alone cannot explain the diversity of living angiosperms, but that angiosperm diversity must also stem from other features of their biology and ecology, including insect pollination, life history and vegetative and physiological features (Stebbins, 1974, 1981; Midgley and Bond, 1991; Ricklefs and Renner, in press). However, this observation does not detract from the conclusion that some feature associated with biotic dispersal, perhaps reduced extinction rates resulting from enhanced predator and pathogen avoidance, makes woody angiosperms more diverse than they would be if they possessed abiotic dispersal alone.

Herrera (1989) evaluated one other test of the influence of dispersal mode on diversity. In an attempt to integrate fossil and modern information, he tabulated the first appearance of modern angiosperm families in the fossil record and their mode of dispersal. He reasoned that it was possible that the importance of different dispersal modes among families might have shifted through time and that the present-day distribution of dispersal modes among families might reflect recent geologic events masking earlier events. In particular, he predicted that if biotic dispersal played a role in an earlier phase of angiosperm diversification, this would be revealed by a cluster of first appearances of biotically-dispersed families in the fossil record.

We chose not to replicate his test at this time for two reasons. First, as Herrera (1989)

recognized 'The weakness of this test lies in its dependence on the assumption . . . that the dispersal method has generally remained constant over geologic time within individual families . . .' (p. 316). Tiffney (1986) has demonstrated the likelihood that dispersal mode changed from abiotic to biotic in the Juglandaceae and Fagaceae in the Late Cretaceous and Tertiary. Some disseminules described by Knobloch and Mai (1986) from the later Cretaceous of central Europe further suggest that fruit and seed morphologies within modern families and occasionally genera were changing in the later Cretaceous and early Tertiary. Additionally, Bremer and Eriksson (1992) mapped the distribution of fruit types within the Rubiaceae on a cladogram derived from chloroplast DNA studies. Fleshy fruits appear to have arisen 12 times within the family. While the authors concluded that the transition to a fleshy fruit was probably irreversible (unlike transitions between abiotically-dispersed morphologies), this certainly suggests that the origin of biotic dispersal within this family and possibly in all angiosperm families need not coincide with the origin of the family. Second, the antiquity of modern families is not firmly established. Recent data (Crepet et al., 1992, W.L. Crepet and K.C. Nixon, personal communication; B.H. Tiffney, unpublished) suggest a greater age for many angiosperm families than previously suspected. Further, the possibility that the current distinguishing characters of a family appeared at different times in the family's evolution renders identifying the precise time of appearance of a fully 'modern' family moot.

The historical impact of vertebrate dispersal on angiosperm diversification

Tiffney (1984) noted evidence for a strong association of dispersal type and habit in the fossil record of Tertiary angiosperms. The early Tertiary (~ 60–45 Ma) was marked by four simultaneous events: (1) the appearance and diversification of many modern families and genera of angiosperm forest trees, (2) the appearance of angiosperm fruits and seeds displaying features interpretable as associated with vertebrate dispersal, (3) the radiation of vertebrate groups (birds, bats and terrestrial mammals) associated with biotic dispersal in the present day and (4) the roughly simultaneous spread of these new angiosperms and dispersal agents around the Northern Hemisphere (Tiffney, 1984, 1985). In the late Tertiary (~ 25–2.5 Ma), a secondary radiation of angiosperm families and genera occurred, this time involving dominantly herbaceous groups (Muller, 1981; Tiffney, 1984), the majority of which possessed disseminules indicative of abiotic dispersal. These observations suggest that different combinations of angiosperm habit and dispersal mode were associated with high rates of diversification at different times in the Tertiary.

Tiffney (1984) assumed that, over ecological and evolutionary time, behavioural and geographic differences between speciating dispersal agents could enforce reproductive isolation among plant populations, enhancing diversification rates in biotically-dispersed plants. However, examination of the biology of contemporary dispersal agents and plants (Wheelwright and Orians, 1982; Herrera, 1985, 1986) tends to argue against tight co-relationships that would influence gene flow. Wheelwright and Orians (1982) note that seed dispersal differs from pollination in that (1) unlike pollination, where pollen is carried to the next flower, there is no 'target' to which the seed is carried and (2) that the reward to the seed disperser is attained at the outset and not reinforced at the end of the dispersal movement by further reward. As a result, they predict that disperser–plant relationships should be far less specific than pollinator–plant relationships. This is reinforced by the observation (Herrera, 1985) that fruits and seeds of modern morphology and assignable to modern genera have existed since the early Tertiary. During this same time, there have been major extinctions and radiations of vertebrate clades, far beyond simple species replacement. Thus, angiosperm disseminule morphology has not always evolved in response to successive changes in dispersal agents. 'Co-evolution' with dispersers may be viewed as 'loose' (Herrera, 1985; Flemming, 1991), with vertebrate dispersal agents only

rarely being species specific. This situation is not conducive to the interruption of gene flow and the generation of new species.

This suggests that Tiffney's initial assumption that species-specific co-evolutionary relationships between plants and dispersers promoted plant speciation was naïve. However, the historical pattern of the parallel diversification of vertebrate dispersal agents and woody angiosperm's remains and agrees with the statistical association between biotic dispersal and woody angiosperm diversification. We suspect that this association is due to vertebrate dispersal promoting lower rates of extinction. This contention could be tested in the fossil record by comparing the rates of species longevity for woody angiosperms that are biotically and abiotically dispersed. At present, such comparisons have only been done for herbaceous versus woody angiosperms in the fossil record (Niklas *et al.*, 1985).

Diversification of herbaceous versus woody taxa

Why are species in herbaceous angiosperm families twice as numerous as species in woody angiosperm families (107 886 versus 56 445 species, Tables 2 and 3)? Note that the importance of these figures is tempered by uncertainty as to the numbers of herbaceous and woody species among the 56 680 species within families of 'mixed habit'.

The greater diversity of living herbs could arise either through their possessing higher rates of origination due to narrow niche width and greater genetic variability or through a higher resistance to extinction allowing the accumulation of diversity over a long period of time or both. Without exploring the question in detail, we suspect that the short life cycles of herbaceous lifeforms relative to woody taxa permit more rapid responses to selection (and evolutionary change) in herbs than in trees. Additionally, Ricklefs and Latham (1992), as a result of an analysis of the geographic range in related disjunct taxa, have suggested that herbaceous taxa may have narrower ecological tolerances than woody taxa. This should result in a higher number of specialist herbs occupying a greater number of narrow niches, contrasted to a lower diversity of generalist woody species occupying fewer, broader niches. Niklas et al. (1985) have observed higher rates of originations in herbaceous families than in woody families in the fossil record. Herbs may not have always been so markedly more diverse than trees, as the fossil record indicates that most living herbaceous forms diversified in the later Tertiary (Muller, 1981; B.H. Tiffney, unpublished data) coincident with increasing seasonality of temperate global climates (Savin, 1977; Frakes, 1986). Jointly, these observations would favour a greater number of herbaceous species than tree species in the present day.

The distinction between herbaceous and woody plant diversity takes on a slightly different twist when separated by class. Among monocots, 89% of the total species diversity (45 447/50 862, Table 3) is supplied by herbs. In the 170 149 species of dicots, the comparison is less clear due to the presence of many families with both woody and herbaceous members ('mixed' families); however, it is striking that the breakdown is 30% woody species (51 030), 33.3% herbaceous species (56 680) and 36.7% species occurring in mixed woody–herbaceous families (62 439, Table 2). These percentages highlight the observation that the monocots are inherently a herbaceous group with strong reliance on vegetative reproduction, while the dicots reflect a greater diversity of ecological solutions (Tiffney and Niklas, 1985).

Conclusion

It may appear that we have demonstrated only a weak correlation between vertebrate dispersal and angiosperm diversity as a whole, thus pushing the direction of the search for causal factors towards insect pollination and aspects of vegetative ecology. We wish to temper this apparent

conclusion with two autonomous observations. First, biotic dispersal is clearly associated with the early Tertiary origin and subsequent maintenance of closed canopy angiosperm forests (Janson, 1983; Tiffney, 1984; Foster *et al.*, 1986; Armesto and Rozzi, 1989; Willson *et al.*, 1990) which now include major areas of temperate and tropical plant communities. While herbaceous and woody angiosperms exhibit a wide range of ecological 'strategies', biotic dispersal does contribute (indirectly or directly) to woody angiosperm diversity. The total diversity of angiosperms thus reflects a cumulative range of solutions. This is reinforced by the second point that, as previously observed, the physiological, morphological and reproductive complexity of the angiosperms is such that we suspect that their success is best ascribed to a host of complex, interactive, features.

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