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How Important is Biotic Pollination and Dispersal to the Success of the Angiosperms? [and Discussion]

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How important is biotic pollination and dispersal to the success of the angiosperms?

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SUMMARY

The rise to dominance of the angiosperms has frequently been hypothesized to be due to reproductive innovations, especially those involving coevolution with biotic gene dispersers. Wind pollination is considered inefficient in comparison with insect pollination. The scope for speciation is considered to be greater when biotic gene dispersers are involved. The biogeographical restriction of extant conifers to stressful environments is also considered to be due to the inefficiency of wind pollination in species-rich environments.

We consider both fossil and contemporary evidence and conclude that biotic gene dispersal has not been as important as have innovations affecting growth rates in explaining the rise of angiosperms. We conclude that differences in growth rates, especially in the regeneration phase, can explain the rise of the angiosperms and the extant biogeography of gymnosperms.

1. INTRODUCTION

From the time they first appeared there was no stopping the angiosperms. Starting at the beginning of the Cretaceous at low palaeo-latitudes or at the mid-Cretaceous at high palaeo-latitudes there was a steady exponential increase in the number of angiosperm species at any particular location (Crane & Lidgard 1989). Today the angiosperms completely dominate the vegetation of low latitudes. However, gymnosperms still survive in high latitudes, high altitudes and nutrient-poor soils. What accounts for the surge of angiosperms in the past and their distribution in the present?

Competitive advantage has been invoked to explain the replacement sequence in the fossil record of all plant groups up to but excluding the angiosperms (Knoll 1984, 1986). Chaloner & Sheerin (1981) suggest that a change from an open 'r-selected' environment to a closed 'K-selected' forest might have led to reproductive changes from the homosporous to heterosporous condition because large propagules would be favoured in these more competitive, deeply shaded environments. Thus Knoll (1984) invoked improved architecture and conductance for why the rhyniophytes were replaced by the trimerophytes in the Devonian and similarly for why they in turn were replaced by progymnosperms and pteridophytes. Knoll (1984) argued that because of the life style of plants they, unlike animals, would not be prone to mass extinctions. Their seeds and buds would allow them to survive a short-term catastrophe like a bolide impaction. He argued that other factors such as progressive climatic change and vegetative competition determined replacement sequences in the plant fossil record. However, Knoll (1984) and others (Regal 1977; Raven 1977) reasoned that for the angiosperms, superior reproductive innovations explained their rise to dominance. The same reasoning has been invoked to explain the contemporary distribution of conifers (Regal 1977).

The supposedly superior reproductive innovations of angiosperms can be put into three classes. First those that favour increased levels of gene dispersal per unit effort. Faithful pollinators may have moved pollen further as well as facilitating a decrease in pollen production and thus of the costs of reproduction. Similarly vertebrate dispersers may have resulted in longer distance seed dispersal and to safer sites. Second are those attributes that facilitate increased levels of mate choice. Various incompatibility systems and gametophytic competition within the style allowed more careful screening of partners. Third are those attributes that favour increased rates of speciation or decreased rates of extinction. Coevolution with pollinators or dispersers, pollinator-mediated isolating mechanisms and dispersal away from pathogens and predators on or near parents may have lead to increased speciation rates or decreased extinction rates.

These classes may or may not be mutually exclusive. For example coevolution between plants and animals could increase levels both of gene flow and speciation. Alternately increased levels of gene flow could reduce the chances of isolation and thus decrease speciation rates. Paradoxically both better (Regal 1977; Raven 1977) and poorer gene flow (Niklas *et al.* 1983; Doyle & Donoghue 1986) of the angiosperms has been invoked to explain their success. There is very little information as to how greater levels of heterozygosity (a by-product of efficient gene dispersal), mate choice or speciation could lead to evolutionary success. For

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example there is no strong relation between heterozygosity and tree performance (Charlesworth & Charlesworth 1987) or geographic range (Ledig 1986).

Here we critically review arguments invoking the importance of coevolution with animal pollinators and dispersers in angiosperm success. We concur with Stebbins (1981) that traits associated with rapid growth and reproduction were far more important in angiosperm success and their contemporary distribution.

There are many measures of evolutionary success including diversity of a clade, longevity of a clade, its geographic spread and ecological abundance (Stebbins 1981; Doyle & Donoghue 1986; Wilson 1987; Bond 1989). There need be no necessary association between these different criteria. Speciose taxa may contribute a small percentage of the biomass of an area (e.g. Orchidaceae; *Ficus*) whereas single taxa may be ecologically important over large areas (e.g. *Pinus sylvestris*, *P. resinosa*; in Africa, *Colophospermum mopane*). Until recently, available reviews of fossil data provided numbers of species and little about abundance (Niklas *et al.* 1983), although this can be a misleading criterion of success. For example, there are now more species of fern than ever before although they are in a relative state of decline. We assess the importance of traits both for diversity and ecological dominance and their possible interdependence.

2. THE IMPORTANCE OF BIOTIC GENE DISPERSAL

(*a*) *Pollination*

Regal (1977, 1982), Raven (1977), Crepet (1983, 1984) and others have argued that angiosperm success can be attributed to biotic pollination. Wind pollination, characteristic of most gymnosperms, is traditionally considered to be an inefficient wasteful process relying on the excessive production of pollen (Whitehead 1983). Pollen flow is considered to be especially limited in a closed canopy environment. Therefore, anemophilic tree species should be restricted to species-poor environments where pollen movement between conspecifics would not be intercepted by other species. This argument is invoked to explain the almost total absence of anemophiles (angiosperm or gymnosperm) from diverse lowland tropical forests and their restriction to stressed (= species-poor) environments (Regal 1977). Regal (1977) suggested that the introduction of angiosperm canopies into essentially wind-pollinated Mesozoic communities diluted the efficiency of wind pollination and began the downward spiral of non-angiosperms.

(*b*) *Dispersal*

Regal (1977) argued that when bird and mammal seed vectors evolved they could carry large numbers of seeds into new environments and that these sites were also beyond the distribution of specialized seed predators. This, combined with insect pollination, allowed plants to produce out-crossed offspring in populations of widely dispersed individuals: precisely the conditions where wind pollination would be unreliable. Regal (1977) considered that many of the families of important insect pollinators long predated the origins of angiosperms whereas the timing of the origins of avian dispersers was more closely synchronized. However, fleshy 'fruits' are not particular to angiosperms and are common in many gymnosperms. Thus he reasoned that it was the combined effect of both types of biotic gene dispersal that was crucial in explaining the success of angiosperms.

(*c*) *Criticisms*

Midgley & Bond (1989, 1991) and Bond (1989) have questioned the biotic gene-dispersal hypothesis on many grounds. Pollination arguments can be challenged on the basis of changing understanding of wind pollination, genetic evidence and the timing of appearance of biotic partners in the fossil record.

Recent studies challenge the generalization that wind pollination is inefficient. In the Knysna Forest, Midgley (1989) found mature seeds on female individuals of the extant conifer *Podocarpus falcatus* that were 70 m away from the nearest reproductive male. This indicates that pollen can move considerable distance in closed canopy forests. Niklas (1985) has indicated that wind pollination is not as random a process as once conceived. Direct compilations of limited data on neighbourhood area suggest that wind-pollinated species have the largest gene flow (Crawford 1984). Ellstrand *et al.* (1990) reviewed the available data for genetic structure of gymnosperms and concluded that they generally have high diversity but low spatial differentiation. On the other hand the cycad they investigated had high spatial variation and low genetic diversity. New studies of gene movement show that the commonly held paradigm that gene flow is very limited (Ehrlich & Raven 1969) is not strictly accurate for either wind- or insect-pollinated plants (Devlin & Ellstrand 1990; Ellstrand & Marshall 1985) and the whole field needs review. This has important implications for those hypotheses for angiosperm success which assumed that biotic gene dispersal increased neighbourhood size over that of wind-pollinated and dispersed taxa. However at this stage there is no evidence that non-angiosperms have low genetic diversity or that they are characterized by low gene flow.

Contemporary biogeographic evidence for the restriction of gymnosperms to species-poor forests is weak. Some conifers are rare in forests (*Torreya*, *Podocarpus falcatus*) and southern hemisphere forests with podocarps can be as rich in species as forests without gymnosperms (Midgley & Bond 1989). Also it is hard to imagine how shrub-like early angiosperms (Crane 1987) diluted pollen movement of canopy gymnosperms in Cretaceous forests.

There is increasing evidence for pre-angiosperm insect pollination which also weakens the reproductive coevolution argument. Biotic gene dispersal is not an angiosperm apomorphy. Angiosperms are part of an anthophyte clade (Doyle & Donoghue 1986; Crane 1985) with flower-like structures some of which show direct evidence of pollination by insects (for example, the Bennettitales) long before the appearance of angiosperms (Crepet *et al.*, this symposium). Field studies indicate that contemporary cycads are also insect pollinated, and animal dispersed (Norstog *et al.* 1986). The fossil record of some of these insects dates back to the Jurassic (J. Donaldson, personal communication, 1991). Thus the evolution of insect-pollinated plants may have long preceded the appearance of angiosperms.

Crepet (1984) has argued that constancy of insect pollinators was a key to angiosperm success. The most constant pollinators are among the Apoidea, and Lepidoptera but these only evolved in the late Cretaceous and early Tertiary (Crepet 1984). Crepet explained the discrepancy by pointing to the supposed slow initial angiosperm diversification. However, recent compilations of palynological data suggests that the origins of angiosperms and their radiation were exponential (Crane & Lidgard 1989) so that insect radiation may have followed rather than preceded initial angiosperm radiation. We believe this casts serious doubt on any need to invoke the concomitant evolution of pollinators or dispersers for the success of angiosperms.

Coevolution arguments find no benefits in wind pollination. Yet wind pollination evolved very early in angiosperm history (Humphries 1988) and still predominates in large, successful families including graminoid monocots (Gramineae, Cyperaceae, Juncaceae, Restionaceae) and woody dicots (Fagaceae). It has evolved repeatedly from insect-pollinated ancestors at the level of families, genera (*Leucadendron*, *Acer*) and even species (*Plantago*, *Salix*). Anemophily is a neglected field relative to biotic pollination (most citations are pre-1960). There are few explanations (besides scarcity of insects, for example, Crepet (1981)) offered for its repeated evolution from insect-pollinated ancestors. The bottom line is that we have no answer for questions like 'what is the difference for the plant whether it is wind, bird or insect pollinated?' What is worse is that there is no real paradigm to take on such important evolutionary questions.

Vertebrate dispersal of fruits probably also had little to do with angiosperm success (Tiffney 1984, 1986; Herrera 1989). Vertebrate-dispersed fruits occur in many gymnosperms (*Taxus*, *Torreya*, *Podocarpus*, *Pinus pinea*, etc.), including extinct Jurassic forms and the insect-pollinated cycads (Tiffney 1986; Herrera 1989). Early angiosperms were abiotically dispersed and fleshy fruits (and appropriate frugivorous birds) only became common in the Tertiary, long after the initial angiosperm radiation (Tiffney 1984, 1986). In summary, the combination of long-distance pollination and long-distance biotic dispersal proposed by Regal (1977) did not exist during the Cretaceous radiation of the angiosperms.

3. THE IMPORTANCE OF MATE CHOICE

This hypothesis argues first that reproductive innovations of angiosperms result in rapid selection and, second, implies that this generates diversity ('plasticity') that accounts for angiosperm success (Mulcahy 1979). Mulcahy (1979) contended that pollen in gymnosperms arrives singly with the first arrival having a 'head start'. In insect-pollinated angiosperms, in contrast, pollen would arrive *en masse* and simultaneously. Pollen competition on the stigma and style might then result in more vigorous, competitively superior offspring (Mulcahy 1979). Animal pollination, in combination with the stigma and style arising from carpel closure, should thus speed up natural selection giving 'the angiosperms an evolutionary plasticity that fuelled their dramatic rise to dominance in the world flora' (Mulcahy 1979).

There are very few direct studies of microgametophytes per ovule to test Mulcahy's arguments. From the limited data that exists, ovules of wind-pollinated plants actually have more microgametophytes from which to choose (table 1). In *Ginkgo*, several male gametophytes may occur in the pollen chamber, each producing two spermatozoids, resulting in competition for fertilization at the two archegonia (Favre-Duchartre 1958). Indeed *Ginkgo*'s flagellated sperm has been interpreted as a device to win the competitive race across the pollination chamber (Haig & Westoby 1989). There are also few studies on the simultaneity of pollen deposition in wind-pollinated plants. The long delay between pollination and fertilization in wind-pollinated gymnosperms and some angiosperms (e.g. *Quercus*) has been interpreted as a mechanism for sampling more pollen for gametophytic selection (Willson & Burley 1983). If wind-pollinated plants use long pre-fertilization times to sample pollen mates, then pollination mode may influence rates of reproduction more than the diversity of pollen parents. Clearly more work is needed on wind-pollinated plants to test Mulcahy's assumptions of small microgametophyte or ovule ratios and 'first come first served'.

Mulcahy's argument ignores the significance of multiple paternity as a mechanism for generating genetic diversity. Many zoophilous taxa disperse pollen in polyads as opposed to the monads of anemophiles. Because of this and the higher probability of pollen from different donors arriving at wind-pollinated flowers, Kress (1981) argued that the potential for multiple paternity is actually highest in wind-pollinated taxa. Thus Kress (1981) argued that the low numbers of ovules per ovary which characterize wind-pollinated taxa may be the product of potentially higher levels of kin selection.

It has long been recognized that angiosperms have a high potential for discarding unwanted genotypes without proportionate loss of reproductive capacity (Buchholz 1922). However the relative importance of pre- versus post-zygotic selection in either controlling mate choice or costs of reproduction is still poorly understood. While pre-zygotic choice through pollen competition may be important, the evidence is still controversial (Snow & Mazer 1988; Charlesworth 1988; Stephenson *et al.* 1988). Mate choice does exist in gymnosperms (e.g. polyembryony, delayed fertilization (Wilson and Burley 1983); selective ovule abortion (Haig & Westoby 1989) but pre-zygotic mechanisms

Table 1. *The size of microgametophyte populations per ovule and pollination mode*

(Data from Snow (1986), *Epilobium*; Levin (1990), *Phlox* and *Polemonium*; M. Honig (personal communication, 1990), *Staberoha* (Cape fynbos Restionaceae).)

species	pollination	microgametophytes per ovule
Epilobium canum	insect	2
Phlox drummondii	insect	4.7
Polemonium viscosum	insect	3
Staberoha stokoei	wind	5.2

are poorly developed. Gymnosperms may be selective, but their selection may cost them dearly in terms of reproductive rates (see, for example, Stebbins (1974); Bond (1989)).

In summary, critical evidence is lacking for the importance of biotic pollination in Mulcahy's mate choice hypothesis for the generation of angiosperm diversity. However, other structural features (the style, tectate pollen, reduced embryo sac, double fertilization, etc.) certainly do influence the capacity for mate choice without risking reproductive capacity. It is still not at all clear, though, whether the undoubted plasticity of angiosperm form springs from mate choice (Mulcahy 1979) or physiological attributes regulating organ growth such as rates of solute supply, the fine network of leaf veins, novel intercalary meristematic tissue (Halle *et al.* 1978; Bond 1989) or some combination. Plants have a remarkable capacity for macromutational change (Gottlieb 1984). The implication is that growth form diversity may depend more on regulation and flexibility of growth processes than soft selection acting on multiple alleles.

4. THE IMPORTANCE OF SPECIATION RATES

Could biotic gene dispersal increase speciation rates and would speciation rates (there being no doubt about the superior speciation rates of angiosperms) alone explain the rise to dominance of the angiosperms? Crepet (1984) and Crepet & Friis (1987) linked angiosperm diversification with the appearance of constant pollinators (Apoidea and Lepidoptera) in the late Cretaceous and early Tertiary. He argued that Coleoptera and Diptera, which had been present throughout the Mesozoic, 'do not have the ethologies associated with heightened promotion of speciation events' (Crepet 1984). However Coleoptera are the major pollinators of the highly speciose Asteraceae. In the rich Cape flora of South Africa, there is no strong evidence that speciation depends on the pollinator type and even less to suggest that speciation rates are a product of coevolution with constant pollinators (Midgley & Bond 1991). Contrary to Crepet's generalization, important pollinators of the Cape flora are Coleoptera, Diptera and birds (Johnson 1991).

Many wind- and insect-pollinated angiosperm lineages are almost equally speciose (Midgley & Bond 1991). It would be instructive to compare geographic differences in the scale of speciation between wind-pollinated and zoophilous taxa. A preliminary assessment of the Cape flora indicates little difference. Thus centres of endemism of important wind-pollinated (Restionaceae) and (mainly) animal-pollinated taxa (Proteaceae, Ericaceae, Rutaceae, Fabaceae) coincide (Oliver *et al.* 1983). Using the data in Oliver *et al.* (1983) species of Restionaceae occupy a mean of 4.5 quarter degree grid squares. Mean numbers of quarter degree squares occupied by species of the Proteaceae, Ericaceae, Penaeaceae and Bruniaceae (all zoophilous taxa) are all more than for the Restionaceae, and the Diosmeae (Rutaceae) are less. In other words the distribution patterns of zoophilous taxa does not indicate limited distributions. Finally, despite there being very few species with fleshy fruits, the Cape flora is exceptionally species rich (Bond & Goldblatt 1984). Our impression is that pollination syndromes (and fleshy fruits, for example, see Herrera (1989)) are not correlated with speciation rates or the sizes of distributions.

Coevolution thus appears less important than a series of morphological traits which promote speciation in angiosperms whether they are animal or wind pollinated or dispersed. Closure of the carpel, development of a stigma, style, and tectate pollen all lead to development of sporophytic and gametophytic reproductive barriers (Burger 1981; Zavada & Taylor 1986). Tectate pollen is absent in gymnosperms with the exception of an extinct group of conifers, the Cheirolepidiaceae (Alvin 1982; Watson 1988). Cheirolepids included extremely diverse growth forms ranging from stem succulents to cypress-like trees (Watson 1988). As in the angiosperms, this diversity has been attributed to the potential benefits of enhanced mate choice (Alvin 1982). It remains to be seen whether diversification of these conifers was also associated with biotic, rather than wind, pollination (Watson 1988).

5. ALTERNATIVES: A COMPETITION HYPOTHESIS

We believe that the importance of reproductive superiority has been over-emphasized whereas rapid growth rates and their attendant ecological effects, based on vegetative and reproductive structures (Bond 1989), have been neglected.

The capacity for rapid vegetative growth and fast reproduction allows angiosperms to colonize disturbed areas and rapidly occupy space: Grime's (1979) ruderal and competitive strategies respectively. In productive environments, angiosperms can outcompete gymnosperm seedlings, outgrow gymnosperm canopies in forests, and reproduce earlier than gymnosperms to survive disturbance such as fire (Bond 1989).

Angiosperms have been able to diversify into a wide variety of growth forms (annuals, broad leaves), architecture (*sensu* Halle *et al.* 1978) and regeneration strategies (rhizomes) which gymnosperms have not. This plasticity can be attributed to vegetative traits such as the more efficient transport system (see, for example, Halle *et al.* (1978); Bond (1989)) and a different meristematic organization (Klekowski *et al.* 1985). Many conifers lack regular axillary meristems (Burrows 1987), which may severely constrain flexibility of tree architecture.

The problem of the peculiar biogeography of the gymnosperms and their persistence over large areas is not addressed by either the mate choice or speciation hypotheses. However the biogeography of non-angiosperms is interpretable in terms of their retreat into environments where fast-growing angiosperms are restrained (Bond 1989). The absence of conifers in tropical lowland forests has been explained in terms of the limitations of wind pollination in species-rich communities (Regal 1977). It seems to us an equally plausible solution is that conifers cannot successfully compete in these productive environments. Rundel *et al.* (1991) have used stable isotopes to compare water-use efficiency between angiosperms and gymnosperms. Semi-arid gymnosperms have water-use efficiencies comparable to woody angiosperms. In this environment the low evaporative flux of gymnosperms is not a handicap. However tropical conifers depart markedly from angiosperms with lower water-use efficiency, consistent with lower maximum conductance values and reduced carbon uptake. Rundel *et al.* (1991) conclude that their results are consistent with the growth-rates hypothesis (based on low conductive efficiency) and help explain the scarcity of conifers in the tropics.

Wolfe (1990) showed strong correlation of leaf physiognomy and climate in most extant vegetation types. Tropical angiosperm forests have large leaves. Arborescent conifers may be excluded from these environments simply because they do not have large leaves.

Rapid reproductive rates in angiosperms has been attributed to the reduced embryo, double fertilization, acceleration of pollen tube growth by the style and the lower cost of insect pollination (Stebbins 1976, 1981). There still are no clear data on the costs of reproduction for different pollination syndromes, i.e. whether the insect pollination of the angiosperms represented a saving. Anemophiles produce vast quantities of pollen and this has traditionally been taken to indicate its inefficiency and high cost. An alternate explanation for this increase in pollen production is that it is due to intramale competition (Lloyd 1984; Bond & Midgley 1988), rather than evidence of inefficiency. Zoophilous taxa gain no advantage in producing more than a certain amount of pollen because their vectors get saturated. This trade-off does not apply to wind-pollinated taxa. As far as the costs are concerned, the pollen of anemophiles is energetically cheaper to produce than that of zoophilous species (Petanidou & Vokou 1990). Further work is needed to clear up the overall costs of reproduction of wind versus insect pollination.

(*a*) *Implications of the growth-rates hypothesis*

We believe the growth-rates hypothesis can be expanded to include other groups besides the conifers. Ferns for instance should be found in dark nutrient-poor and cold environments or in growth forms that angiosperms cannot exploit. Thus in productive environments we hypothesize that angiosperm epiphytes (e.g. Brommeliaceae, Orchidaceae) exclude pteridophytic epiphytes. We expect parallels in distribution patterns between ferns and conifers despite their different 'pollination systems'. Cycad biogeography remains unsynthesized. We suggest competition in regeneration niche, especially from grasses, as crucial. We expect them to be vulnerable to frequent disturbance (e.g. fire) and to be more common in stressful (micro)sites (e.g. nutrient-poor, shallow soils and shady). We predict that non-angiosperms (e.g. Bennetitaleans) persisted longer on nutrient-poor (arenaceous) than on nutrient-rich (argillaceous) substrates.

The growth-rates hypothesis is consistent with the fossil record with its steady-state take over, rather than a bumpy pattern correlated with the evolution of other animal lineages. According to the growth-rates hypothesis, the take-over by angiosperms is expected to have taken place first in productive environments (low palaeolatitudes). The rise of the angiosperms may have been facilitated by other factors such as advanced pollinators and vertebrate dispersers but was not dependent on them.

Finally, growing information on other physical and biological attributes of Cretaceous environments are consistent with the growth-rates hypothesis but are not addressed by the coevolution hypotheses. High oxygen levels during the Cretaceous may have led to more frequent fires (Robinson 1989) and changes in browsing levels of the dinosaur fauna (Bakker 1978), both favoured rapid growth and short generation time. Abiotic changes would also have promoted the necessary fast growth. Cretaceous climates were warm and latitudinal gradients were very weak, especially near the poles (Spicer & Chapman 1990). High oxygen levels would have produced a more oxidative soil environment rather than a reducing podzolic soil environment produced by cool wet gymnosperm dominated flora (Robinson 1989). The break-up of Gondwanaland in an erosional rather than depositional cycle would have favoured angiosperms by providing nutrient-rich substrates.

6. CONCLUSIONS

We have taken a particularly critical stance against arguments involving the importance of biotic gene dispersal. We do so to emphasize the weak evidence for several widely accepted hypotheses and the need to explain the many exceptions of diverse and successful taxa without animal pollination or dispersal.

What are the problems with the fast growth-rate hypothesis? First, although it can explain the great diversity of growth forms among the angiosperms, it has nothing to say on speciation within a growth form. Secondly, although the early success of the ephedroids (see Crane & Lidgard 1989) is compatible with the growth-rates hypothesis it does not explain their subsequent failure to match the angiosperms. Gnetalean vascular morphology may not produce the transport efficiency of modern angiosperms but we lack data. Finally the impact of environmental changes, especially if they are abrupt, needs further attention.

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Discussion

E. A. JARZEMBOWSKI (*Booth Museum of Natural History, Brighton, U.K.*). In the search for animal vectors in biotic pollination, it is tempting to generalize about insects, although they greatly outnumber vertebrates and angiosperms with diversities in major orders such as Diptera, Coleoptera and Hymenoptera exceeding 10^5 species. It is certainly true that these orders had appeared before the Cretaceous radiation of the angiosperms, but closer examination of the fossil data indicates a greater turnover of families at the Lower–Upper Cretaceous boundary than at the Cretaceous–Tertiary boundary. The radiation of angiosperms seem to have been more disruptive than the K/T catastrophe although the same data shows an increase in overall insect diversity during the Cretaceous implying insect–plant interaction.

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J. J. MIDGLEY. The problem is whether the radiation of associated animals (mainly insects and birds), especially pollinators and dispersers but also herbivores, preceded or followed that of angiosperms. We have argued that plant–animal interactions were less important than plant–plant interactions. We expect the radiation of the angiosperms to have preceded that of associated animal groups.

P. J. GRUBB (*Botany School, University of Cambridge, U.K.*). Gymnosperms do not dominate equally effectively all kinds of vegetation in which plants grow slowly. They commonly dominate in cold areas, on soils poor in nutrients, and in areas as dry as those with mediterranean climates but they are generally absent from semi-deserts, with the exception of *Welwitschia* and some *Ephedra* species. Most gymnosperms depend on maintaining several cohorts of long-lived leaves on the adult, which is not a viable option for shrubs that need to survive very long and severe droughts (often shedding most or all of their leaves) and then grow quickly when rain comes. *Welwitschia* and *Ephedra* effectively parallel succulents.

J. J. MIDGLEY. We agree with Dr Grubb's comments. In general gymnosperms appear to be relatively ineffective, especially in the regeneration niche, in any ecosystem where speed (rapid growth) rather than endurance is crucial. Also, present gymnosperms are morphologically fairly uniform. We need further information as to why so few seem to have converged on the succulence niche.