Ecology and Evolution of Flowering Plant Dominance

Interplay of seed and pollen dispersal systems may explain angiosperm versus gymnosperm dominance.

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As a result of an ecological revolution 113 to 85 million years ago in the Cretaceous, angiosperms now dominate much of the earth's land surface. The question of why this displacement of the previously dominant tree ferns, horsetails, and gymnosperms occurred relatively late in geological history—Darwin's "abominable mystery" (*1*)—has prompted much speculation (*2*). Yet, "The problem of why this dramatic change in the world's flora occurred at this time is still completely unsolved" (*3*, p. 209).

Angiosperms typically have broad leaves, vessel elements for fluid conduction, and alkaloids (which may be defensive compounds). It has been suggested that these are superior features and that as one or more of them evolved the flowering plants were able to outcompete gymnosperms. However, broad leaves have evolved in gymnosperms such as *Ginkgo*, *Gnetum*, and *Podocarpus*. Vessel elements are absent in some primitive angiosperms but are found in the gymnosperms *Ephedra*, *Gnetum*, and *Welwitschia*. Therefore, since both groups had the potential to evolve these features the question remains, "Why did vascular systems and broad leaves become highly specialized in most angiosperm but not in most gymnosperm groups?" Likewise, the presence of alkaloids in many angiosperms does not provide a simple explanation for the ecological revolution. It is not clear that the alkaloids used as defensive compounds are superior to those resins, phenolics, and tannins that are found in gymnosperms and that are, in fact, retained in many angiosperms.

The unique adaptations of angiosperms are reproductive. The ovules are protected by a closed carpel. A stigma and style allow fertilization soon after pollination. Floral parts have evolved that attract pollinating insects, while the ovules are protected from these same potential "seed predators" (*4*). Double fertilization and a triploid endosperm may allow the rapid growth of propagules from essentially primordial ovules (*5*); this would be advantageous in ecological situations favoring a rapid life cycle (*5, 6*) and perhaps also an advantage in reducing the nutritive value of the ovules at the time when the flower is attracting insects.

Flowering plants are widely involved not only with insects, bats, and birds as pollen vectors (carriers), but with birds and mammals as the major seed vectors. A great variety of fleshy as well as hooked and barbed fruits and seeds among flowering plants illustrates this fact. It is not surprising, then, that one view has been that the evolution of birds, mammals, and particularly pollinating insects caused the revolution. However, mechanisms that could explain how this might have occurred have not been explicitly proposed, largely because of the formidable difficulties involved.

If the appearance of pollinating insects explains the success of the angiosperms, then why the late date of the revolution? Flying insects and land plants were present in the Paleozoic. The highly specialized Lepidoptera and Hymenoptera probably diversified as a result of the angiosperm revolution, but even several groups to which today's important pollinating insects belong are ancient: Diptera, Coleoptera (Permian), and certain Hymenoptera (Triassic) (*7*). Why did the far-reaching ecological merger between insects and plants not take place long before the mid-Cretaceous if insects were the limiting factor?

On the other hand, if birds and mammals were the limiting factor, then why should their arrival have favored insect-pollinated angiosperms over wind-pollinated plants? After all, birds and mammals disperse the seeds of both groups today. Several gymnosperms, among them *Juniperus*, *Torreya*, *Taxus*, *Podocarpus*, *Ginkgo*, and certain cycads and Gnetales, even have fleshy and often colorful seed coverings as adaptations that promote animal dispersal of seeds.

I shall argue that a mechanism exists whereby the appearance of birds and mammals could indeed have favored insect-pollinated plants. A complex set of principles underlying the exploitation of animals as reproductive vectors for plants is emerging from recent studies, particularly in the tropics where angiosperm forests first appeared (*8*) and today are essentially dominant. The new information and new interpretations of well-known facts suggest that there is a potential interplay between seed and pollen dispersal systems that may be of importance in understanding the dominance of angiosperms.

After presenting my hypothesis and discussing the principles on which the argument is based, I will suggest ecological conditions that may have allowed survival of forests dominated by gymnosperms. In the United States, at least, the distribution of gymnosperms is paradoxical. The phylogenetically old coniferous trees typically are dominant in some of the more severe and rigorous environments. Yet it is commonly assumed that the phylogenetically younger angiosperms have been "victorious" in evolution because they are more adaptable than gymnosperms.

To shorten the discussion and to facilitate comparisons with coniferous forests I will refer to angiospermous trees throughout the article, even though the first angiosperms were probably not canopy trees (*6*), and the argument actually applies more forcefully to subcanopy plants. Except where noted, moist, tropical lowland forests are in mind. The principles can easily be qualified to apply to shrubs and herbs; with some caution they can also be applied to xeric or cool climates.

The Hypothesis

1) Insect pollination may allow a plant to produce outcrossed offspring when it belongs to a population of widely dispersed individuals or of small clusters of individuals, where wind pollination would be unreliable.

2) This capacity gained significance only when widely foraging seed vectors (initially birds) came into existence; such vectors could carry large numbers of seeds to new areas for colonization, to

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small widely scattered safe-sites (*9*), and beyond populations of specialized seed predators. Thus, in the last two examples, efficient seed dispersal allowed the adult plants to occupy and become specialized for microhabitats where the spacing patterns made the plants dependent on animal pollen vectors.

3) Plants offering nectars and fruits to animals then proliferated, creating niches for nectivores and frugivores. This diversification in turn created new evolutionary possibilities for the plants. Such positive feedback loops generated additional evolutionary momentum.

4) With the addition of many new, diverse angiosperms to ecosystems, many of the preexisting gymnosperm populations were eventually forced by competition to become so sparse that wind pollination (and primitive insect pollination) was a liability.

5) Changing climatic conditions or other widespread ecological alterations could have accelerated the diversification of animal-pollinated plants. For example, if the warming mid-Cretaceous climate, epidemics, or introductions of alien competitors caused mortality to increase for a hypothetical conifer and angiosperm, through insect pollination the angiosperm might maintain genetic variability at a low density "bottleneck" more readily than the wind-pollinated conifer so that it could continue to occupy widely scattered safe-sites. Hence the angiosperm would stand the better chance of evolving adaptations to the new conditions.

Selection for rapid growth strategies (and consequently large leaves and advanced vascular systems), new systems of chemical defense, and a diversification of life forms can be viewed as resulting from the new ecological and genetic opportunities and the increased variety of competitive interactions involving primarily the flowering plants (*10–17*).

I shall assume that the highly complex flower organization of angiosperms represents a more sophisticated system for insect pollination than the systems developed in Gnetales, cycads or Bennettitales. So when animal pollination became of widespread advantage in ecosystems, it was largely angiosperms that were favored in competition.

Spatial Distributions and Sex

There may be advantages to animal pollination over wind pollination in several situations: for example, where air is still, winds unidirectional, wetness constant, or conceivably where the production of large amounts of pollen would be an unbearable metabolic expense. I suggest, though, that the critical advantage of animal pollination in the Cretaceous was to allow genetic exchange between widely spaced individuals or small populations. This advantage may be significant in several ecological situations. Paradoxically, some of these (see paragraphs 3 to 5 below) involve species that we may see as common and closely spaced.

1) A heterogeneous habitat may be subdivided by specialists. Plant species may utilize different conditions of temperature, soil, sunlight, moisture, and wind exposure. Populations that can outcross as widely dispersed individuals may often have an advantage in that they can adapt to a network of small, scattered, safe-sites. Predation and competition acting on such specialists could confine the populations to even lower densities than would result from the mosaic of resources alone.

2) A uniform habitat may be shared. Particular habitats might exist that are characterized by conditions of soil, moisture, temperature, and light so congenial to plant growth that a great variety of plants might grow equally well. Why does competitive exclusion not result in an elimination of species richness? Predation or climatic variability might keep the abundance of species low so that competition would be greatly reduced, as studies on intertidal invertebrates seem to show (*18*). Janzen and Connell (*19, 20*) have argued that herbivore and seed-predator pressure can maintain the diversity of tropical trees. This would mean that a species of plant would become uncommon in an area as specialized predators evolved. The more widely spaced were conspecific plants, the more difficulty the insects would have in locating their prey and in establishing populations on their hosts. So at low densities, young plants would essentially have enough room to "hide" from the pests that are seeking them (*19, 20*).

3) New habitats may be invaded. It is well understood that in a breeding population of a few dozen individuals, genetic variability may be lost through random processes. Populations passing through such a genetic bottleneck (*21*) may be at a disadvantage in competition with genetically more variable populations (*22, 23*). Invasions outside of a species' range may begin with a few scattered individuals. Given the invasion of a new habitat by small numbers of two ecologically similar species, the one that can maintain genetic variability in the first few critical generations has a competitive advantage. Insect pollination between colonizers could moderate bottleneck effects when colonization begins with a few or scattered individuals.

4) There may be a succession of plant communities. Habitats are typically in a state of flux. The growth of one plant community alters conditions and creates a new habitat for a second. Tree falls, fires, hurricanes, flooding, disease, landslides, and lava flows all open up new habitat even within dense, mature forests. A minority species may become abundant or a new species may disperse into the area. In either case there may sometimes be a genetic bottleneck that a few scattered individuals pass through. In this case, or in the cases discussed in paragraphs 3 and 5, we might see a very common and closely spaced species that can trace its original establishment in the area to having passed successfully through a genetic bottleneck.

5) Some species may have "waited" for appropriate climatic conditions before they became abundant. Only a small number of species can be common in any one time and place. Many species now abundant may have passed through genetic bottlenecks during climatic alterations [or "taxon" cycles (*24*)].

The scattered, unstable, stream margin habitats reconstructed for early angiosperms (*6, 25*) are relevant in terms of the situations described in paragraphs 1, 3, or 4.

Could some of the above functions also be accomplished by wind pollination? The air that we breathe is often full of pollen which under certain atmospheric conditions may disperse thousands of kilometers and may even fertilize ovules of plants up to tens of kilometers from a forest (*26, 27*), but this is essentially a residue that reflects the vast amounts of pollen released from forests or fields. It is not thought to reflect a strategy of reliable genetic exchange between individuals at great distances. Fertilization may require a pollen "rain" of, say, 10^6 grains per square meter over the recipient plant, since a 1-mm^2 stigma is a small target. Thus, counterintuitively, the individual pollen donor has a low probability of pollinating by wind except when it is surrounded by other individuals (*13, 26–29*).

Wind pollination is rare in the tropics except possibly in habitats such as savannahs and marshes dominated by dense stands of a few common herbaceous species (*13*). It becomes common, even among angiosperms, in the temperate zones (*30*) where extensive habitats dominated by a few species are usual. These ecological and geographic patterns offer important insights and will be discussed in the last section.

Some ecologists once claimed that insect pollination is also unreliable for widely spaced plants, and that the trees in many tropical forests where individuals of a given species are typically separated by 50 to 100 m must be self-pollinated. It is true that, if possible, insects tend to forage in small areas, but through modifications of nectar flow, blooming times, and even the quality of nectar or pollen, a plant can affect the behavior of insects so that outcrossing is maximized (*26, 29, 31–35*). Recent studies in Central America reveal that a large fraction of the rare trees are in fact obligate outcrossers (*32*). In some cases tropical pollinators patrol or "trap-line" long, regular routes through the forest. Janzen discussed the importance of this behavior and demonstrated that marked euglossine bees would return to a nest from as far away as 23 km in a tropical rain forest (*33*). In other cases, aggressive behavior results in individual pollinators being driven from one plant to another (*34*). Frankie calculated that even a low rate of pollination by such displaced individuals will account for fruit-set in tropical trees (*35*).

The costs of nectars, scents, and flowers, and the great diversity of complex pollination systems among plants, suggest that the advantages of animal-maintained sexuality are great. But is the sexual process necessary? The answer must be yes, but not an unqualified yes. The exact advantages of recombination and heterozygosity are being debated (*36, 37*). Inbreeding does not always reduce genetic variability (*38*). Many plants, particularly weedy and pioneering annual herbs, are self-fertilizing (*27, 38–40*). However, since obligate outcrossing plants cannot produce seeds except as a result of genetic exchange, self-fertilization is probably an adaptation for temporary niches where short life cycles and very rapid reproduction have a strong competitive advantage (*40, 41*). In other cases, restricted outcrossing may preserve adaptations to local or marginal conditions against genetic swamping from the species as a whole. In any event, while cross-fertilization is commonly obligate, self-fertilization is at best only rarely obligate (*40*). Since selfing populations usually retain the capacity to outcross at some low rate, I argue that, in appreciating the very real advantages of self-fertilization in some situations, we must not lose sight of the potentially enormous advantages of retaining some degree of outcrossing in the vast majority of situations (*22, 23, 37, 40–42*). So sexual processes may provide a competitive advantage in the wide variety of ecological situations outlined above.

However, if animal pollination offers such profound advantages, why did not angiosperms become dominant much earlier? The occupation of networks of small, scattered safe-sites over many generations requires more than a system for maintaining sexuality. It requires an efficient means of dispersing offspring to new safe-sites and those vacated following infestations of pathogens or herbivores, or climatic fluctuations (*43–45*). In other words, animal vectors of plant gametes and zygotes must work together to allow species of angiosperms to evolve "coarse-grained" responses to the environment. This term refers to organisms that in effect can select a class of resources or "grains" out of the environment in a nonrandom fashion (*46, 47*). This point, and the significance (for the evolution of new plant types) of long-distance dispersal of seeds by birds, are discussed in the following sections.

Birds Enter the Ecosystem

Feathers allow the functional differentiation of the avian wing into a propelling outer portion and an inner surface that provides lift (*48*). This is also true of bats where the outer portion of the wing is supported by the modified "fingers" (*49*). These types of wings were unprecedented in evolutionary history and offered unique possibilities for adaptive radiation into a wide variety of niches for agile fliers (*48*). Pterosaurs were probably not counterparts of agile birds moving through foliage or feeding off the ground. The wing membrane was borne upon a single "finger" and the small peculiar feet were not obviously adapted for perching or running. The bones were extraordinarily thin. Because of these limitations there has been much speculation on pterosaurs' way of life. Aerodynamically they may have functioned as modified, powered, Rogallo kites, and the largest perhaps depended on sea breezes (*50*).

Archaeopteryx of the upper Jurassic already had the basic avian wing elements, and there were aquatic birds of diverse modern groups worldwide dating from early and particularly late Cretaceous marine deposits. Even the "primitive" *Hesperornis* and *Ichthyornis* were advanced in general construction. There is little direct fossil evidence that Cretaceous terrestrial birds existed. But fossils of small terrestrial animals, including arthropods, are poorly represented in the Cretaceous. And since the aquatic avifauna were well developed early, *Archaeopteryx* was a land bird, and a diverse representation of modern terrestrial birds "appeared suddenly" in the early Tertiary, the conclusion is virtually inescapable that there was a major radiation of land birds during the Cretaceous (*51*). On the other hand, the first bat fossil appears in the Eocene (*52*), and so I shall say little about the role of bats in the early evolution of flowering plants. How could birds have had a major impact on plant communities?

With the adaptive radiation of birds, the world of a plant must have changed significantly as a result of the introduction of two new factors: a large increase in the incidence of long-distance dispersal and new patterns of local dispersal.

Flapping or gliding flight allow a bird to travel any given distance at a much lower metabolic cost than a terrestrial animal can and, of course, to travel the distance much more quickly (*53*). Many birds consequently forage daily over broad areas of several kilometers (*54*) and over distances of thousands of kilometers during migration. Recent studies show that seeds may be carried in the gut of some migrants much farther than once thought: up to 200 to 300 hours (*55*). High proportions of bird-dispersed plants on oceanic islands show the effectiveness of birds in long-distance dispersal (*56*).

Endothermy, with its high metabolic demands, probably evolved in conjunction with flight, if not earlier for some other reason (*57*), and so the flight capabilities, high-energy requirements, and hence the foraging patterns of early birds probably had basic similarities to those of modern birds. This could mean that early in the Cretaceous, the seeds of many plants—not simply those specialized for local dispersal by animals—were being carried to locations well outside of their traditional ranges in the guts (and on the surfaces) of birds, and were being deposited in envelopes of fertilizer.

Long-Distance Dispersal

We can assume that with the adaptive radiation of birds, numerous plant species were being repeatedly tested by selection in new habitats. It may have been largely the insect-pollinated species that benefited from a high rate of "experimentation" because of their presumed ability to preserve and generate genetic variability in founder populations of scattered individuals. These are the sorts of circumstances under which species might enter new adaptive zones and from which "large evolutionary events" might result (*58*).

The dispersal of plants beyond the ranges of coadapted predators, herbivores, and diseases could facilitate the establishment of new populations (*59, 60, 61*). "Previously unoccupied habitats are very important in the production of new populations because an invading species often leaves its predator and pest populations behind, allowing it to enter a new habitat more readily than a resident species can expand its population to use the same resources" (*19*, p. 521). On a broad geographic scale we may recall the often dramatic (and often tragic) success of plants and animals once they gain a foothold on new continents free from disease, predators, or effective competition (*61*). New adaptive plant types so generated might then be dispersed by birds into still other habitats, not only increasing the species variety within communities but with potentially profound alterations of these, with competition possibly forcing residents into low-density bottlenecks (*62*).

Man's history of transporting wild animals shows that attempts to introduce species had often, though not always, to be repeated (at considerable expense) even though the final attempt sometimes resulted in the species swarming over islands or continents (*63*). I picture birds as having played a similar role with plants because of the birds' stereotyped habits and tendency to travel rapidly over great distances. Birds repeatedly transported moderately large seeds from marshes, tree falls in forests, xeric rain shadow habitat mosaics, in one region to similar habitats in other regions. These points are particularly important. It is critical not to confuse the issue of the evolution of ecological dominance by angiosperms with the question of their actual origin. The major problem now is to explain the replacement of gymnosperms by angiosperms as elements of mature and stable ecosystems where "phenotypic" competition is great (K selection) and open genetic recombination and moderately large seeds may be critical. In unstable, ecotonal situations, simply rapid reproduction (and sometimes self-fertilization)—selection for *r*—and wind dispersal of small seeds may be adaptive.

Wind may have carried seeds to new habitats in the Mesozoic. Safe-sites for seeds being larger than stigmas as sites for pollen, the haphazard nature of wind dispersal may not have been so serious for seeds as it was for pollen. Nevertheless, the density of seeds that reach a given site declines as a function of distance (and also depends on the wind patterns). Large seeds can generally not be carried as far as tiny, highly specialized seeds, such as those of orchids or cottonwoods (*Populus*). This is significant because large numbers of seeds with moderate food reserves for seedlings should, theoretically, favor a resident in competition with a few tiny seeds from a foreign invader. Without minimizing the importance of occasionally successful introductions of plants with wind-dispersed seeds over long distances, we should clearly distinguish between the success that a plant may have in invading a local habitat for which it is adapted, by blanketing the region with seeds, and the relative difficulty that only a few of its seeds may have in invading a new area with a spectrum of indigenous competitors (*23*, *63*).

In short, birds may have substantially increased the rate at which moderately large seeds were transported into new areas (*64*), and the evolutionary consequences could have been profound if new species of angiosperms were added to ecosystems faster than gymnosperms were. Obviously, the model is based on today's typical and somewhat generalized pollinating animals, not the host-specific types where the plants cannot establish themselves beyond the range of a particular pollinator (for example, some orchids).

Efficient Local Dispersal

Birds and, later, bats and also terrestrial mammals must have increased the efficiency of many local dispersal functions such as transport beyond concentrations of seed predators and to widely scattered safe-sites, for which only reptiles, wind, and water were previously available as vectors. We can imagine that birds and mammals began to feed on large fleshy (or nutlike) fruits and seeds adapted for dinosaur dispersal. Possibly the very first angiosperms were habitat specialists with patchy (*65*) distributions (not necessarily trees in tropical forests) that remained low in abundance and diversity for millions of years because of the low efficiency of reptilian dispersal of seeds. Alternatively, birds and mammals began feeding upon seeds, possibly of species adapted for disturbed (or "weedy") situations (*5*, *6*), that were previously distributed by wind or water. Adaptations, particularly for avian dispersal, might have evolved in either case because of the advantages of birds in transporting moderately large seeds within minutes, and reliably, to safe-sites hundreds of meters and even several kilometers away from the parent plant.

It should be to the plant's advantage to distribute its annual seed crop in, say, several hundred bird droppings rather than in the feces of a handful of "small" dinosaurs. Also, the agility, coordination, and size of birds allow them often to take seeds and fruits directly and selectively from branches with minimal damage to the plant, and for some seeds and fruits to bypass potential fungal disease or insect attacks on the ground.

The ecology of local seed dispersal is a deceptively complex subject (*45*, *66*, *67*). Because of space limitations I have only touched superficially upon some aspects of bird and mammal dispersal of seeds (*68*). Birds and mammals have high metabolic demands and large brains relative to reptiles. These features make them potentially reliable yearly visitors to a fruiting tree or shrub once they have located it. Further, high metabolic rates may lead to relatively rapid passage of food through the guts of birds and mammals, providing "high quality seed treatment," by reducing the effects of harsh chemicals and mechanical action, and reducing the need for a hard seed coat. Since not all animals that eat fruits provide "quality dispersal" there may be intense competition for certain types of animal vectors, resulting in the diversity of fruit types and fruiting seasons in a community. Thus some fruits are highly specialized for dispersal by particular animals, while generalized strategies have been adequate for other species. Still others have apparently reverted to seed dispersal by wind even in the tropics (*66–69*).

We can do little more than wonder if the Mesozoic reptiles were reliable (*70*) visitors and sufficiently diverse (*71*) to provide "quality dispersal" to more than a few species of plants in any one area. If their behavior, physiology, size, or diversity did limit them, then the proportions of widely spaced specialists in communities may well have remained low simply because of this factor.

In any event, I see the ecological revolution as resulting from a combination of factors including (i) an accelerated rate of species formation in which angiosperms were favored, (ii) widespread ecological changes in plant community interactions resulting from this, and not least from (iii) an increase in the capacity of ecosystems to absorb many animal-maintained plants so that the gymnosperms were "diluted" and the reliability of their wind pollination was reduced to the point where many were unable to adapt to the changes as easily as angiosperm competitors were.

Modern Community Trends

Organisms have evolved many diverse ways of life and, not surprisingly, there are individual counterexamples to several generalities that I use in support of the hypothesis. Further, it is not simple to put species into categories. What is a species of widely spaced individuals? Perhaps most species which are common in some part of their range are rare in another: Which should we focus upon? Under which condition did reproductive patterns actually evolve? Which condition had the strongest influence on the evolution of a species that has "always" had both sparse and dense populations within its total range?

Yet the propositions may hold as trends and perhaps we may begin to approach tests of generality by focusing on geographic and ecological regularities. Studies in Costa Rica (*69*) indicate that in a 700-hectare wet forest, of the 185 species studied (65 to 75 percent of all tree species in the area) only 7 percent disperse their seeds by wind; in eight subsites of a 20,250-ha dry forest with 113 species studied (± 80 percent of all species), 32 percent of the trees disperse their seeds by wind. These and other studies (*67*) also show that the wind-dispersed tropical trees are apt to be among the emergent or secondary forest species and that animal dispersal characterizes the shorter trees (and shrubs) of climax forest. A correlation between wind dispersal and low species richness has been observed along a gradient in the Great Smoky Mountains (although not in Ohio) (*72*). Abiotic dispersal in very species-poor tropical habitats is thought to be common (*12, 66*).

These data raise the question of whether wind dispersal and low species richness are correlated in turn with a reduction in availability of animal vectors (*12, 66*), much wind (*13*), reduced seed-predator pressure or seed-predator satiation (*12, 13*), or with greater availability of safe-sites simply because of a reduced variety of interspecific competitors. Further studies of community patterns are needed to provide answers to these questions.

What limits for the parameters of height, mean crowding (*65*), patchiness, extensiveness of stands, mass of pollen produced per individual, will allow reliable outcrossing in a wind-pollinated population? At what threshold does a reduction in recombination become a handicap in competition? How much spatial "dilution" will a wind-pollinated species faced with competition tolerate? A number of gymnosperms and angiosperms are wind-pollinated and animal-dispersed (and others vice versa). Under what conditions might animal-promoted "seed flow" be able to compensate, despite a time lag, for a reduction in gene flow through ineffective pollen exchange? Values are not available for making estimations for particular species. There are, however, ecological and geographic patterns and these suggest some degree of regularity in the adaptations of species to their environments. For example, wind pollination is common in the temperate zones and uncommon in most tropical habitats (*13, 30*). A detailed study of spacing patterns and reproductive biology in whole communities along ecological gradients might provide insight into questions raised by my hypothesis.

Survival of Coniferous Forests

If only a few species of gymnosperms had survived in scattered refugia they would be no more remarkable than any other relict plant or animal group. However, many parts of the earth, particularly at high elevations and latitudes, are dominated by dense coniferous forests. Apparently there were limits to the rapid advances that the angiosperms were making some 100 million years ago. What were they?

Wind pollination may be of no particular disadvantage where individuals are closely spaced. Thus, in areas where species richness is low, wind pollination might be tolerated or even favored, and competitive superiority might be decided purely by features other than pollination. Severe ecological conditions combined with prior occupancy may act as a "filter" against invasion by all but a few select species (*73*). Thus we might expect gymnosperms to have survived in, and to be specialized for, geographically extensive habitats characterized by nutrient-poor substrates, acidic soils, waterlogged soils, drought, frequent fires, cold surface or soil climates, short growing seasons or, conceivably, conditions unfavorable for pollinating insects.

Why is it that in the United States conifers are dominant in some of the most severe and rigorous environments? The answer is, perhaps, that present-day conifers are adapted to rigorous conditions because these have characterized large "ecological islands" low in species richness and conducive to wind pollination for millions of years. [Indeed, the high densities under which many gymnosperm species may have originated might have themselves produced harsh soil conditions (*10*).] Thus, there is a common denominator to the great coniferous forests of cold and northern regions, the piñon-juniper forests that are extensive throughout areas of cool, relatively dry winters and hot dry summers, the frequently burned closed-cone and other pine forests, southern coniferous forests on sandy soils, and acidic bogs. (Several such habitats are geologically young and have been occupied only recently by *Pinus* and *Juniperus*.)

This hypothesis does not predict that gymnosperms will dominate all harsh or species-poor habitats: only that they may be able to survive somewhere within a range of conditions that would be regarded as stressful for elements of adjacent species-rich communities. Angiosperm-dominated mangrove, chaparral, and alpine habitats, for example, are harsh by most standards, but with 349 families and 12,334 genera of angiosperms (*3*) it is hardly surprising that many of these dominate in situations where exceptional adaptations are necessary. As angiospermous ecological counterparts of gymnosperms evolve, angiosperms may gradually replace gymnosperms today even in many species-poor situations. Wind-pollinated angiospermous trees such as alder, ash, aspen, beech, birch, elm, hazel, and oaks dominate many northern areas.

How the extensive coniferous forests of coastal Washington and Oregon conform to the prediction is not obvious. Indeed, the factors producing the vegetation in this area have long been a puzzle. The mild, wet climates here, as well as in Asia, may simply provide refuges for certain conifers as is commonly assumed. On the other hand, much of Washington and Oregon were affected by glaciation, and the soils are young and poor (*74, 75*). It has recently been argued that an unusual combination of mild winters and cool but dry summers (*74–78*) may allow conifers to compete successfully with angiosperms since conifers are both drought resistant and can also use the wet, cool fall, winter, and spring for photosynthesis (*75, 79*). Angiospermous trees in this area tend to dominate only along rivers, in hot habitats, and sometimes in early seral stages—where the rivers moderate the summer soil dryness, or where the heat excludes the local species of conifers, or where red alder or big-leaf maple sometimes become established until slower growing spruce or hemlock shade them out (*75*). More detailed studies both in the Pacific Northwest and in Asian temperate forests would help to resolve the different possibilities for the persistence of coniferous forests in these areas (*80–83*).

Paleoecological studies show that fire has been important in determining the dominance of conifers in some northern areas previously thought to be directly under climatic control (*84*). The southeastern United States has a generally warm, moist climate; however, studies in Florida show that the distributions of pines and cypress are controlled by fire, poorly drained soils, and flooding, rather than directly by climate (*85*).

I am not arguing that rainfall and mean annual temperature extremes are unimportant in plant distribution. Simple climatic data may be necessary but not sufficient to explain why many areas in the United States are dominated by conifers and others not (*86*). It follows that it is unsafe to view the habitats of gymnosperms in the rest of the world in only general climatic terms. The situation in most tropical areas is even more poorly understood than in the United States. Though the data are few, some generalizations can be made.

Pines have been relatively well studied in the tropics. In tropical Asia, Central America, and the Antilles pines dominate where fires occur every 5 to 20 years. More frequent burnings produce grassland; less frequent burnings permit angiosperm forest. Where annual precipitation is high, it may take a severe dry season to favor pine. The effects of fire are compounded by shallow, poor soils, acidic parent rocks, low precipitation, and low temperature. Extensive porous and well-drained soils may be poor in nutrients and these and shallow soils may have little water-holding capacity, thus exposing the vegetation to water stress when precipitation is reduced (*87*). So the many tropical species of *Pinus* form forest in rigorous situations and conform to predictions.

Havel (*88*) and Webb and Tracey (*89*) argued that araucarias are a common element of tropical and subtropical forest types where "broadleaves" are reduced in density and height because of unfavorable soil or climatic conditions (*90, 91*).

Species of conifers existing as scattered individuals in broad-leaved forest are a tangential issue to the question of why forests dominated by conifers continue to exist. Yet they are still of considerable interest to this discussion. Do they have special genetic, physiological, or other adaptations that allow them to function as community members?

The gymnosperms *Agathis*, *Dacrydium*, and *Podocarpus* are said to be found mixed with angiosperms in rich lowland tropical forests (*92*), although some are also found at higher elevations and latitudes and commonly in impoverished tropical heath forest (*17, 92, 93*). Since species richness declines in these last situations, we should focus the search for exceptions on the fertile lowlands. It has frequently been suggested, for these and other tropical conifers, that present-day mixed forests represent a stage in transition to complete angiosperm dominance (*93*), or alternatively, a successional stage following widespread disturbances or climatic change. For this reason among others discussed, more study is required before we can pinpoint individual exceptions to my generalizations among the lowland tropical forest conifers or among those of New Caledonia or southern China (*94*). I do expect some exceptions to predictions, but I have not yet found good examples.

The biology of nonconiferous low-latitude gymnosperms is also of interest. Animal dispersal of seeds is probably common in Cycadales and Gnetales (*67*) and circumstantial evidence suggests some insect pollination (*26*). Such plants lack obvious, complex specializations for insect pollination, but it would be instructive if (despite inferior specializations) insect pollination and seed dispersal by animals have contributed in any way to their survival and competitive potential.

Conclusions

It is obvious that different spacings of the members of a population of organisms can have profound, immediate, and long-term consequences for the individual and its offspring. However, only recently have ecologists begun to explore these in detail. The demographic and genetic implications are particularly intriguing for rooted plants when the typical individual is separated from sites favorable for the growth of seedlings and from other reproductive members of its population. Probably most species of higher plants have achieved some degree of "directed movement" through adaptations that cause animals to carry their reproductive cells. Efficient vectors of seeds may allow the evolution of specialist plant species that can exploit rare or patchily distributed resources. However, the genetic consequences of diffuse spacing patterns for a population must also be considered. Without an efficient means of pollen dispersal such a population could face reduction in sexual recombination. Then the potential to specialize for widely scattered resources would be counterbalanced by a decline in the genetic resources that we assume are important for the generation of new adaptations. In such examples the evolution of animal-dispersed pollen and seeds would ideally go hand in hand.

Animal-dispersed and pollinated plants abound today in the subcanopy of moist tropical forests where reduced wind and the patchy availability of sunlight and other resources may interact to give great advantages to such systems. One could assume that the tripartite coevolutionary strategy proposed here (disperser-pollinator-angiosperm) matured and diversified first in the moist tropical subcanopy plant community. In that case, one derived evolutionary condition would be represented by the abiotically dispersed trees that are not poorly represented among emergent trees and particularly among trees of less species-rich tropical forests.

Additional derived conditions may have evolved as the angiosperms spread poleward into the temperate latitudes (or alternatively protoadapted forms spread poleward). Here extensive areas are dominated by only a few species. Several groups of angiosperms have reverted to wind pollination, others to abiotic seed dispersal, and some to both. Wind-pollinated conifers dominate vast areas as well. Although abiotic dispersal and pollination are major components of the temperate ecosystems with which many of us are most familiar, it is well to bear their special nature in mind.

Abstract

Birds and mammals are important seed dispersers and their diversification in the Cretaceous may have created niches for many plant specialists on scattered resources. Maintaining sexual recombination through wind pollination in such sparse populations is difficult, and so angiosperms with their sophisticated systems for insect pollination were favored in many critical situations.

References and Notes

1. Darwin saw the "sudden change" as conflicting with the view of evolution as a gradual process and suggested, in an 1879 letter to Hooker, "The rapid development so far as we can judge of all the higher plants within Recent geological time is an abominable mystery. I would like to see the whole problem solved. I have fancied that perhaps there was during long ages a small isolated continent in the S. Hemisphere which served as the birth place of the higher plants—but this is a wretchedly poor conjecture" [see F. Darwin and A. C. Seward, Eds., *More Letters of Charles Darwin* (Appleton, New York, 1903), vol. 2, pp. 20–22].
2. Some authors have argued that flowering plants evolved perhaps 60 million years before they appeared in abundance during the Cretaceous [D. I. Axelrod, in *Evolution after Darwin*, S. Tax, Ed. (Univ. of Chicago Press, Chicago, 1960), vol. 1]. If this is so, the problem remains: Why did flowering plants remain obscure in world ecology for at least 60 million years and then "suddenly" become abundant? It has been speculated that angiosperms spread from the uplands to the lowlands as warm, mild climates spread. It is not clear, however, that the mid-Cretaceous warming was unprecedented or that warm, mild climates had not existed regionally. Plausible mechanisms that would cause warming to favor flowering over nonflowering forms or that would explain the survival of gymnosperm forests in warm, mild climates have not been proposed.
3. G. L. Stebbins, *Flowering Plants: Evolution above the Species Level* (Harvard Univ. Press, Cambridge, Mass., 1974).
4. V. Grant, *Evolution* **4**, 179 (1950).
5. G. L. Stebbins, in *Origin and Early Evolution of Angiosperms*, C. B. Beck, Ed. (Columbia Univ. Press, New York, 1976).
6. J. A. Doyle and L. J. Hickey, in *ibid*.
7. E. F. Riek, in *The Insects of Australia* (C.S.I.R.O. and Melbourne Univ. Press, Carlton, Victoria, 1970).
8. G. J. Brenner, in *Origin and Early Evolution of Angiosperms*, C. B. Beck, Ed. (Columbia Univ. Press, New York, 1976).
9. Defined here as a patch of habitat meeting the germination and growth requirements of a particular species in terms of its particular adaptations for soil, moisture, and climate.
10. Several hypothetical scenarios could explain why broad leaves and advanced vascular systems evolved so early in so many angiosperm lineages. I focus upon lowland tropical forests here because angiosperm dominance of these is an outstanding problem. However, the very first angiosperms could have evolved as small plants in arid upland sites (*5, 11*). In early evergreen

tropical forests limited in species variety because of abiotic (or primitive animal) seed and pollen dispersal, the plants may have invested much of their productivity in chemical defenses (tannins, resins, phenolics?) and indigestible tissue as protection against outbreaks of specialized phytophagous insects or fungi in the dense stands (*12–14*). These secondary substances could also have been important for young plants growing slowly in the shade and competing with adults for water and nutrients, since nutrient deficiency or water stress can increase susceptibility to phytophagous insects [W. J. Mattson and N. D. Addy, *Science* **190**, 515 (1975)]. Secondary substances in the leaves may have slowed litter decomposition in early Cretaceous gymnosperm forests much as Janzen proposed for certain modern species-poor tropical forests such as those on high-porosity white sand soils and heath forests [additional studies are needed, but see references in (*12, 13*) and J. R. Gosz, G. E. Likens, F. H. Borman, *Ecol. Monogr.* **43**, 184 (1973)]. This situation might create nutrient stress in and of itself, regardless of the parent rocks from which the soils are derived.

One often sees small-leaved plants in xeric conditions and on nutrient-poor soils. Smaller leaves tend to be efficient in dissipating heat, and this reduces water loss. With smaller leaf dimensions and moderate resistance to water vapor diffusion, the efficiency of water use (ratio of CO_2 fixed to water expended) is great, but overall photosynthetic rates are low (*15*). With water scarcity or with a smaller root system, a smaller-leaved species might grow slowly but efficiently—not "wasting" water for heat dissipation and thereby exposing itself to dehydration. (Conversely, with abundant water and nutrients, a large-leaved form would have a competitive advantage, growing rapidly but "wastefully.") Givnish and Vermeij (*16*) recently argued that if growth is limited by nutrient scarcity, then the increased photosynthetic profits that larger warmer leaves are capable of cannot be realized and their cost in terms of structures and physiological processes associated with increased water loss becomes excessive. This may explain why small-leaved plants are often found on nutrient-poor soils.

Let us consider, then, a sequence of feedback effects: nutrient-poor conditions favor slow growth and low species richness. These in turn favor species accumulating large amounts of secondary compounds, which results in slow litter decomposition. This exacerbates the initial nutrient scarcity, placing a still greater premium on small leaves and making invasion by many competitors even less likely. Thus, many modern conifers may have been "protoadapted" for nutrient-poor or drought conditions by having originated in species-poor communities where slow, efficient growth and small leaves functioned as discussed.

On the other hand, if early angiosperms were readily able to colonize canopy gaps or other disturbed areas and to maintain outcrossing, both by means of animal vectors, perhaps they were able to specialize for rapid growth and reproduction. By occupying widely scattered safe-sites, thus "hiding" from specialized herbivores and seed predators and discouraging generalist herbivore and pathogen species with physical impediments or small amounts of toxins (*14*), perhaps angiosperms were relatively free to invest in the production of photosynthetic and reproductive tissues and to make a relatively small commitment to antiherbivore adaptations. Rapid mineral recycling after a tree fall or fire would also add to the feasibility of this strategy.

Broad leaves may function to shade out competitors by distributing a relatively small tissue mass into monolayers [(H. S. Horn, *The Adaptive Geometry of Trees* (Princeton Univ. Press, Princeton, N.J., 1971), pp. 56, 126]. Also, broad leaves in sunlight heat above air temperature and thus increase photosynthetic rate per unit leaf area (to an upper limit) (*15*). When heat absorption becomes excessive, evaporation dissipates heat (*15*). High photosynthetic rates also require water to bring nutrients from the roots to the leaves and both these last factors would favor advancement of vascular systems, particularly if growth were confined largely to short intervals during the day or year [(S. Carlquist, *Ecological Strategies of Xylem Evolution* (Univ. of California Press, Berkeley, 1975)]. In modern tropical rain forests many "nomadic" species have large leaves (at least when young), grow rapidly, have efficient means of seed dispersal, but cannot survive long in shade (*17*).

11. My hypothesis is compatible (though I illustrate it with wet-forest communities) with the major theme of D. Axelrod [*Am. Nat.* **106**, 311 (1972)] and of Stebbins (*3, 5*) that angiosperms first pioneered ecotonal situations near "rain forests," but it differs in certain respects. Stebbins visualized species formation as the result of a "species pump" (*3*, p. 195) where the range of widespread species contracts and leaves behind isolates, some of which differentiate and later come into sympatry with the parental population. This results in a more diverse species pool following each climatic cycle. I visualize the isolates as being established by birds independently of climatic cycles. Immigrant rather than relict populations may be more likely to enter new adaptive zones as a result of escape from natural regulating agents in the parent communities.
12. D. H. Janzen, *Biotropica* **6**, 69 (1974).
13. ______, *Ecology of Plants in the Tropics* (Arnold, London, 1975).
14. Plants (particularly trees) in species-poor stands are likely to be found by or *apparent* to pathogens and herbivores. Such plants may decrease their edibility by having tough leaves low in nutrients, and by developing relatively large quantities of chemicals such as tannins or resins which are difficult to deactivate. On the other hand, early successional plants (and perhaps many climax species in the species-rich tropics) often escape attacks by certain pathogens and herbivores. Such *unapparent* plants may contain low concentrations of toxins such as alkaloids as "cheap" or "qualitative" defenses against generalists [P. Feeny, *Rec. Adv. Phytochem.* **10**, 1 (1976); D. F. Rhoades and R. G. Cates, *ibid.*, p. 168; D. A. Levin, *Annu. Rev. Ecol. Syst.* **7**, 121 (1976); R. G. Cates, *Ecology* **56**, 391 (1975)]. R. G. Cates and G. H. Orians [*Ecology* **56**, 410 (1975)] predicted that early successional plants would be relatively more palatable to generalists, and this was true for slugs in the state of Washington. But D. Otte [*Oecologia* **18**, 129 (1975)] found no relationship using Texas grasshoppers. Be that as it may, the commonness of alkaloids in angiosperms agrees with my argument that animal pollination and seed dispersal have commonly allowed flowering plants to exist as "unapparent" species throughout their evolution.
15. D. M. Gates, *Ecology* **46**, 1 (1965); S. E. Taylor, in *Perspectives of Biophysical Ecology*, D. M. Gates and R. B. Schmerl, Eds. (Springer-Verlag, New York, 1975); D. F. Parkhurst and O. L. Loucks, *J. Ecol.* **60**, 505 (1972).
16. T. J. Givnish and G. J. Vermeij, *Am. Nat.* **110**, 743 (1976).
17. T. C. Whitmore, *Tropical Rain Forests of the Far East* (Oxford Univ. Press, London, 1975).

→ J. H. Connell, *Ecol. Monogr.* **31**, 61 (1961); R. T. Paine, *Am. Nat.* **100**, 65 (1966); *Oecologia* **15**, 93 (1974); B. A. Menge and J. P. Sutherland, *Am. Nat.* **100**, 351 (1976); J. L. Menge, *ibid.*, in press.

19. D. H. Janzen, *Am. Nat.* **104**, 501 (1970).

→ ______, *ibid.* **105**, 97 (1971); *Annu. Rev. Ecol. Syst.* **2**, 465 (1971); *Ecology* **53**, 350 (1972); J. H. Connell, in *Dynamics of Populations, Proceedings of the Advanced Studies Institute on Dynamics of Numbers in Populations, Oosterbeek, 1970*, P. J. den Boer and G. R. Grandwell, Eds. (Center for Agricultural Publications and Documentation, Wageningen, Netherlands, 1970); D. E. Wilson and D. H. Janzen, *Ecology* **53**, 954 (1972). This hypothesis is reasonable, but even more empirical tests are needed because it has become critical in recent discussions; it is relevant, but not critical, to my hypothesis. See J. J. Burdon and G. A. Chilvers [*Oecologia* **23**, 17 (1976)] for the effect of clumped planting patterns on epidemics. Some tropical habitats do have plant species at relatively high densities (*12, 13, 17*), and Janzen argues that most of these have seeds protected either by mast fruiting (saturating seed predators with great numbers of unpredictable intervals) or by having a few very toxic large seeds and by having foliage that is exceptionally rich in secondary compounds (*12*). These forests are typically limited to low-fertility soils [see (*12, 13, 17*)]. [P. R. Ehrlich and P. H. Raven, *Evolution* **18**, 586 (1964) argued that as each angiosperm lineage escaped herbivores not spatially but through biochemical mutations the angiosperms rose to dominance and their species diversity also increased.]

21. M. Nei *et al.*, *Evolution* **29**, 1 (1975).
22. E. Mayr, *Populations, Species and Evolution* (Harvard Univ. Press, Cambridge, Mass., 1970).
23. D. B. Mertz, D. A. Cawthon, T. Park, *Proc. Natl. Acad. Sci. U.S.A.* **73**, 1368 (1976).
24. R. E. Ricklefs and G. W. Cox, *Am. Nat.* **106**, 195 (1972).
25. R. L. Pierce, *Bull. Minnesota Geol. Surv.* **42**, 1 (1961).
26. K. Faegri and L. van der Pijl, *Principles of Pollination Ecology* (Pergamon, New York, 1971).
27. V. Grant, *Cold Spring Harbor Symp. Quant. Biol.* **23**, 337 (1958).
28. K. Faegri and J. Iversen, *Text-book of Modern Pollen Analysis* (Hafner Press, New York, 1975); A. Cronquist, *The Evolution and Classification of Flowering Plants* (Houghton Mifflin, Boston, 1968).
29. M. Procter and P. Yeo, *The Pollination of Flowers* (Taplinger, New York, 1972).
30. D. R. Whitehead, *Evolution* **23**, 28 (1969); B. Heinrich and P. Raven, *Science* **176**, 597 (1972); V. A. Krasilov, *Paleoecology of Terrestrial Plants* (Wiley, New York, 1975), p. 134.
31. B. Heinrich, *Annu. Rev. Ecol. Syst.* **6**, 139 (1974).
32. K. S. Bawa, *Evolution* **28**, 85 (19 → K. S. Bawa and P. A. Opler, *ibid.* **29**, 167 (1975).
33. D. H. Janzen, *Science* **171**, 203 (1971); *Nat. Hist.* **83**, 49 (1974).
34. G. W. Frankie and H. G. Baker, *An. Inst. Biol. Univ. Nat. Aton. Mexico Ser. Botanica* **45**, (1), 1 (1974); L. K. Johnson and S. P. Hubbell, *Ecology* **55**, 120 (1974).
35. G. W. Frankie, in *Variation Breeding and Conservation of Tropical Forest Trees*, J. Burley and B. T. Stiles, Eds. (Academic Press, New York, 1976).
36. G. C. Williams, *Sex and Evolution* (Princeton Univ. Press, Princeton, N.J., 1975); B. Wallace, *Evolution* **29**, 193 (1975). For responses see (*37*).
37. The advantages of sex for adaptation to changing conditions have been well discussed; for example, see Mayr (*22*); and D. A. Levin, *Am. Nat.* **109**, 437 (1975). See also D. Nyberg, *J. Theor. Biol.* **50**, 429 (1975); T. Nagylaki, *ibid.* **58**, 55 (1976); J. M. Smith, *ibid.* **63**, 245 (1976); M. Treisman and R. Dawkins, *ibid.*, p. 479; R. R. Glesener and D. Tilman, in preparation. D. Nyberg [*Evolution* **28**, 367 (1974)] reports that resistance to experimentally imposed stress increases with increasing sexuality among strains of *Paramecium* and *Tetrahymena* ranging from extreme inbreeders to extreme outcrossers.
38. R. W. Allard, S. K. Jain, P. L. Workman, *Adv. Gen.* **14**, 55 (1968).
39. R. W. Allard, in *The Genetics of Colonizing Species*, H. G. Baker and G. L. Stebbins, Eds. (Academic Press, New York, 1965).
40. G. L. Stebbins, *Am. Nat.* **91**, 337 (1957); *Cold Spring Harbor Symp. Quant. Biol.* **23**, 337 (1958).
41. A seasonal shift each year from parthenogenesis and *r* selection in the summer to sexuality as conditions become more severe in the fall is well known for animals such as aphids, *Cladocera*, and rotifers [for example, see R. K. Shan, *Hydrobiologia* **34**, 513 (1969)].
42. Grant (*27*) cites experimental studies on freely self-fertilizing species showing that foreign pollen is clearly favored over "self" pollen.
43. Efficient dispersal is obviously important in the simple persistence of populations in progressively more heterogeneous spatial environments, and this has been detailed in mathematical models for animals [D. A. Roff, *Oecologia* **15**, 245 and 259 (1974); **19**, 217 (1975)]. S. H. Bullock [*Oecologia* **24**, 247 (1976)] has modeled local seed dispersal in annual plant populations. See also S. A. Levin, *Annu. Rev. Ecol. Syst.* **7**, 287 (1976).
44. It follows from (*43*) that high species richness could be limited entirely by the richness of seed-dispersing animals. I could even argue that when these animals appeared, angiosperms were favored merely by their ability to produce large appealing seeds and fruits rapidly by means of double fertilization and a triploid endosperm so that the pollination considerations are only part of the answer. Is it possible that seasonally imposed constraints upon the variety of frugivores (*45*) results in the reduced species richness of trees at high latitudes? Could this reduced species richness in turn sponsor the trend toward wind pollination in high latitudes? I believe that such hypotheses are reasonable but difficult to assess critically at present.
45. D. W. Snow, *Ibis* **113**, 194 (1971); *The Web of Adaptation* (Quadrangle–New York Times Book, New York, 1976); E. S. Morton, *Am. Nat.* **107**, 8 (1973).
46. See J. A. Wiens [*Annu. Rev. Ecol. Syst.* **7**, 81 (1976)] for a review of the concept.
47. R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography*, (Princeton Univ. Press, Princeton, N.J., 1967).
48. D. B. O. Savile, *Evolution* **11**, 212 (1957); *Am. Zool.* **2**, 161 (1962).
49. T. A. Vaughn, in *Biology of Bats*, W. A. Wimsatt, Ed. (Academic Press, New York, 1970).
50. A. S. Romer, *Vertebrate Paleontology* (Univ. of Chicago Press, Chicago, 1966); C. J. Pennycuick, *Animal Flight* (Arnold, London, 1972). See R. S. Stein and J. H. McMasters [*Science* **191**, 898 (1976)] for a discussion of a giant pterosaur; the references therein lead to the scant literature on the smaller ones.

51. P. Brodkorb, in *Avian Biology*, D. Farner and J. King, Eds. (Academic Press, New York, 1971), vol. 1; *Smithsonian Cont. Paleobiol* **27**, 67 (1976); J. Cracraft, *J. Zool. (London)* **169**, 455 (1973).
52. G. L. Jepsen, in *Biology of Bats*, W. A. Wimsatt, Ed. (Academic Press, New York, 1970).
53. V. A. Tucker, *Am. Sci.* **63**, 413 (1975). Gliding is even cheaper than flapping flight [K. V. Baudinette and K. Schmidt-Nielsen, *Nature (London)* **248**, 83 (1974)]. Some birds such as wood storks may synchronize daily foraging movements with the development of thermals, and observations from light airplanes show that they may travel 40 km to feeding areas without flapping at all [M. P. Kahl Jr., *Ecol. Monogr.* **34**, 97 (1964)].
54. The literature is fragmentary and is biased toward relatively sedentary or territorial breeding birds because they are easy to study. Further, tropical birds that exploit scattered food sources have been poorly studied because it is difficult to work in and move through forests. Yet experienced ornithologists agree (D. Warner and H. B. Tordoff, personal communication) that tropical parrots and icterids, for example, seem to forage easily over several tens of kilometers each day (± 40 to 100 km for larger species). Recent studies with banded passerines in southern Mexico show that many individuals are sedentary and territorial, but others of the same species form flocks of "floaters" with large fat reserves and these may forage widely through the rain forests [J. H. Rappole, thesis, University of Minnesota (1976)]. Bats may commonly disperse seeds at least 1 km or more [E. R. Heithaus, T. H. Fleming, P. A. Opler, *Ecology* **56**, 841 (1975)].
55. V. Proctor, *Science* **160**, 321 (1968); V. Vlaming and V. Proctor, *Am. J. Bot* **55**, 20 (1968). However, R. W. Cruden [*Evolution* **20**, 517 (1966)] had argued that long-distance dispersal by birds is apt to be a stepwise process. M. E. Gillham [*J. Ecol.* **44**, 429 (1956)] and P. R. Grant, J. N. M. Smith, B. R. Grant, I. J. Abbott, and L. K. Abbot [*Oecologia* **19**, 239 (1975)] report significant seed dispersal by gulls and owls over seawater.
56. S. Carlquist, *Island Biology* (Columbia Univ. Press, New York, 1974).
57. P. J. Regal, *Quart. Rev. Biol.* **50**, 35 (1975).
58. E. Mayr, in *Evolution after Darwin*, S. Tax Ed. (Univ. of Chicago Press, Chicago, 1960).
59. H. N. Ridley, *The Dispersal of Plants Throughout the World* (Reeve, Ashford, Kent, 1930).
60. J. A. Bullock, *J. Indian Bot. Soc.* **46**, 323 (1967); J. B. Gillet, *Syst. Assoc. Publ. No. 4*, 37 (1962).
61. C. S. Elton, *The Ecology of Invasions by Animals and Plants* (Methuen, London, 1958).
62. Similarly, an increase in the rate of transport of pathogens such as fungi may have caused waves of mortality which the angiosperms were best able to survive.
63. G. Laycock, *The Alien Animals* (Natural History Press, Garden City, N.Y., 1966). R. M. Schuster [in *Origin and Early Evolution of Angiosperms*, C. B. Beck, Ed. (Columbia Univ. Press, New York, 1976), p. 65], argues, too, that plant "communities tend to repel invaders." The difficulty might be less, of course if an island with a depauperate flora were the target, or if the invader had extraordinary protoadaptations.
64. Large mammals, such as caribou, migrate, and some dinosaurs may have migrated if the environment was highly seasonal and if they were unable to become dormant. However, they could not have moved as fast as flying animals. To estimate the importance of dinosaurs as long-distance dispersal agents, we would have to know not only *if* they migrated, but how fast their guts emptied in relation to the distance traveled each day. (Or what the probability was each day of mud and other clinging matter being brushed off the body.)
65. Mean crowding is the number of other individuals within the ambit of a given individual (for occupied quadrats). Patchiness is the ratio of mean crowding to mean density for all quadrats [M. Lloyd, *J. Anim. Ecol.* **36**, 1 (1967)]. Small, widely separated populations (with patchy distributions), or widely separated individuals would both particularly benefit from insect pollination.
66. D. McKey, in *Coevolution of Animals and Plants*, L. E. Gilbert and P. H. Raven, Eds. (Univ. of Texas Press, Austin, 1975).
67. L. van der Pijl, *Principles of Dispersal in Higher Plants* (Springer-Verlag, New York, 1972). H. F. Howe, R. B. Primack, *Biotropica* **7**, 278 (1975).
68. See McKey's analysis of "quality dispersal" (*66*).
69. G. W. Frankie, H. G. Baker, P. A. Opler, *J. Ecol.* **62**, 881 (1974).
70. Most dinosaurs had the same brain-to-body ratios as modern reptiles. The enlarged mental capacities of mammals and birds may reflect abilities to forage widely and efficiently in highly heterogeneous habitats (P. J. Regal, in *Behavior and Neurology of Lizards*, N. Greenberg and P. McLean, Eds. (National Institute of Mental Health, Washington, D.C., in press).
71. About 10 to 25 species of dinosaurs are known from any particular fossil community. While we cannot know how many have escaped preservation, paleontologists believe that the numbers reflect a low variety of dinosaurs in any one community relative to contemporary birds and mammals (R. Sloan, personal communication).
72. W. N. Beyer's [*Am. Nat.* **109**, 103 (1975)] interpretation of his data was that, "Trees which are capable of becoming strongly dominant in a community tend to have seeds that are primarily wind dispersed," but other explanations are available. E. J. Tramer, D. E. Suhrweir, and W. F. Straker [*Am. Nat.* **110**, 500 (1976)] present a counterexample.
73. A. Danin [*Oecologia* **22**, 251 (1976); and references therein] document this common observation. I have oversimplified its probable causes: see J. Terborgh, *Am. Nat.* **107**, 481 (1973).
74. R. M. Highsmith, *Atlas of the Pacific Northwest* (Oregon State Univ. Press, Corvallis, 1973).
75. J. F. Franklin and C. T. Dryness, *Natural Vegetation of Oregon and Washington* (U.S. Department of Agriculture Forest Service Tech. Rep. PNW-8, Washington, D.C. 1973).
76. Since the area looks so green and mesic, the annual rainfall is high, and light rain and fog are present in summer, the summer dry soil conditions may go unappreciated even among some residents.
77. M. J. Schroeder and C. C. Buck, *Fire Weather* (U.S. Department of Agriculture, Forest Service, Washington, D.C. 1970).
78. H. Walter, E. Harnickell, D. Mueller-Dombois, *Climate-diagram Maps* (Springer-Verlag, New York, 1975).
79. The point is illustrated by recent physiological studies on *Juniperus virginiana* in Virginia which show that photosynthesis is carried on under low soil moisture in the summer and during the winter even at 0°C [P. Ormsbee, F. A. Bazzaz and W. R. Boggess, *Oecologia* **23**, 75 (1976)]. The winters in the Pacific Northwest are not severe, yet 300 freeze-free days per year may be a maximum (*74*, p. 44).
80. A. W. Küchler [*Ann. Assoc. Am. Geogr.* **36**, 122 (1946)] had previously stressed historical factors (which must also be important here) rather than climate.
81. Li (*82*, p. 257) reviewed the scanty data for the habitats of all conifers and taxads. "(1) Most of the genera grow in mountainous situations; (2) Most of these genera occur in warm temperate regions, especially in areas with equable climate; (3) Most of these genera show definite preference to moist situations." Unfortunately, such gross climatic correlates can be misleading as they give no insight into historical, edaphic, microclimatic factors, and competition. For example, Li described *Sequoia* as, "Forming pure forest . . . on the sides of ravines and the banks of streams. This is a lover of moisture and a characteristic tree of the coastal fog belt." Some authors have argued instead that the critical factors allowing the redwood to dominate in the face of potential competition are probably the abilities to withstand both fire and flooding (*83*). Again, more studies are needed to resolve the disagreement.
82. H. Li, *Evolution* **7**, 245 (1953); R. Florin, *Acta Horti Bergiani* **20**, 121 (1963).
83. E. C. Stone and R. B. Vasey, *Science* **159**, 157 (1968); G. Namkoong and J. H. Roberds, *Am. Nat.* **108**, 355 (1974).
84. See references in H. E. Wright, Jr., *Science* **186**, 487 (1974); T. T. Kozlowski and C. E. Ahlgren, Eds., *Fire and Ecosystems* (Academic Press, New York, 1974); see also (*77*).
85. C. C. Monk, *Ecology* **47**, 504 (19[illegible] *Am. Midl. Nat.* **79**, 441 (19[illegible] E. Quarterman and C. Keever, *Ecol. Monogr.* **32**, 167 (1962); F. C. Craighead, Sr., *The Trees of South Florida* (Univ. of Miami Press, Coral Gables, 1971), vol. 1.
86. To illustrate the point in another way: in the Diablo Range of San Benito County, California, the climate would seem not to support forest but rather chaparral and a grassy woodland. In the midst of this, though, a large area of exposed serpentine rock supports a distinctive flora and vegetation: a very thin forest of four conifer species with some 20 shrubby species as well. A remarkable proportion of the plants are disjunctions or endemics [(J. R. Griffin, *Fremontia* **2**, 11 (1974)]. We may speculate that the extremely poor soil conditions "filter out" the native chaparral and allow a few unlikely forest species to persist in the "unfavorable" climate because of reduced competition from the native plants.
87. See reference [illegible] N. E. Kowal, *Ecol. Monogr.* **36**, 389 (1966); E. N. G. Cooling, *Pinus merkusii* (Commonwealth Forestry Institute, Oxford, 1968); A. F. A. Lamb, *Pinus caribae* (*ibid.*, 1973); (*17*).
88. J. J. Havel, *J. Ecol.* **59**, 203 (1971).
89. L. J. Webb and J. G. Tracey, *Aust. Forestry* **31**, 224 (1967).
90. For additional information on araucarias see, O. O. Ntimia, *The Araucarias* (Commonwealth Forestry Institute, Oxford, 1968); B. Gray, *J. Ecol.* **63**, 273 (1975). Compare the low species richness of trees reported for *Araucaria* forest in Paraná, Brazil (p. 114), with tropical broadleaf forest (p. 58) in S. A. Cain and G. M. de Oliveira Castro [*Manual of Vegetation Analysis* (Harper, New York, 1959)]; also E. F. Brünig, *Amazoniana* **4**, 293 (1973); (*17*).
91. *Araucaria husteinii* is found on mountain slopes and ridges in New Guinea. Here we may expect that the nutrient content, water-holding capacity, and stability of the soil are reduced. At elevations above and below *A. husteinii* is *A. cunninghamii*, and this "disjunction" would seem strange if only climate directly determined its distribution. Of course, at higher altitudes cold should compound soil and moisture problems [(*17*); H. Walter, *Vegetation of the Earth* (Springer-Verlag, New York, 1973)] and so gymnosperms are not expected, but what of the lowland sites? "It has a very wide ecological range at lower elevations and has been recorded on ultrabasaltic rocks, in swampland (supposedly), and (at Daribi) on limestone. This last locality is the only place where pure stands have been found" (*17*, p. 175). In Australia the same species are primarily found in areas of lower soil fertility and/or moisture (*89*).

    The *Araucaria* forest of southern Brazil are in a wet, temperate climate with no drought [H. Pimenta Veloso, *Atlas Forestal do Brazil* (Ministry of Agriculture, Rio de Janeiro 1966); (*78*)]. However, the soils are humic ferralsols most of which require treatment, including neutralization of free aluminum with lime, for intensive agriculture. Without treatment even plantation planting of the native *Araucaria* is not profitable [FAO-Unesco, *Soil Map of the World,* vol. 4 (Paris, 1971), pp. 100, 111]. These forests will require further analysis since soil results from interactions of parent rock, vegetation, and climate, and I have not isolated the ruling factor here.
92. T. C. Whitmore, *J. Ecol.* **54**, 285 (1966).
93. R. G. Robbins, *Trans. R. Soc. N. Zealand Bot.* **1**, 33 (1962).
94. Whitmore (*92*), showed that *Agathis macrophylla* on Vanikoro Island is a normally reproducing part of the community: not a successional species. For our purposes, however, several points must be made. Vanikoro has very highly leeched soils because of high rainfall. Beyond this, Vanikoro is 2600 km due east of northernmost Queensland (*Agathis* are mostly island forms). On small remote islands there are apt to be fewer species than one might predict ("undersaturation" as the distance from colonizing sources increases) (*47*). Species richness is low here perhaps due simply to insularity. A poor variety of herbivorous, pollinating, and seed-dispersing animals on islands could also interact to keep plant species richness low (*13*).

    The island of New Caledonia is famed for its richness in conifers and other primitive and endemic plants. The climate is mostly mild and not very moist with a marked drier season, destructive cyclones, extensive areas of serpentines and other peculiar soils. [(*56*); R. F. Thorne, *U. Iowa Stud. Nat. Hist.* **20**, No 7, 1 (1965).] There are no native land mammals and insularity has had some effects on the bird and insect faunas as well as plants. Because of insularity, and particularly the extensive deposits of peculiar soils, the rich variety of conifers here cannot be considered an exception to my predictions without a careful ecological analysis.

    There are 17 genera of conifers in the vast Evergreen Broad-Leaved Forest Formation of Asia [C. Wang, *The Forests of China* (Maria Moors Cabot Foundation Publ. 5, Cambridge, Mass., 1961)]. It is for these forms along with the lowland tropical podocarps that ecological, historical, and genetic studies would be of utmost interest.

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