special feature

The role of plants in evolutionary ecology

by Eric R. Pianka*

Conceived by R.A. Fisher in 1930, evolutionary ecology had a long gestation time and was not born until the early 1960s (MacArthur, 1961; Mayr, 1961; Orians, 1962; Ehrlich and Raven, 1964). In the past 25 years, it has blossomed into a massive discipline that has assimilated and largely replaced other ecological subdisciplines. Although a few people continue to use the terms 'animal ecology' and 'plant ecology', the distinction between these two fields has all but disappeared under the rubric of evolutionary ecology.

Plant biology and evolutionary biology have each greatly enriched one another in a two-way flow of concepts and information. Although Darwin (1859, 1862) had certainly adopted it, the evolutionary approach was not imported into plant biology until modern times (Harper, 1961b, 1967, 1977). Since then the concept of plant-animal coevolution, in particular, has greatly enriched evolutionary thinking.

Perhaps because of the very vastness of their subject matter, ecologists until recently have confined themselves to understanding ecological processes in 'now' time, or ecological time. Consideration of such processes over an evolutionary timescale has proven profitable and has greatly increased our understanding of many ecological phenomena (Pianka, 1986, 1988). Rigorous application of the theory of natural selection in population biology was first attempted by Fisher (1930), who can be considered the founder of evolutionary ecology. So-called 'selection thinking' has expanded the dimensions of our understanding: in addition to the traditional mechanistic approach, a long-term or strategic perspective exists (these two complementary approaches have been called the 'how?' versus 'why?' questions of biology by Mayr, 1961). The evolutionary approach has opened up whole new areas of endeavor such as optimal foraging, life history tactics, and coevolution, each of which became an instant subdiscipline, and then quickly exploded into a field in its own right.

Plants have played a pivotal role in this transformation of ecological thinking. The focal area of greatest interest to evolutionary ecology is plant/animal coevolution (Brues, 1920, 1924; Lippik, 1957; Mode, 1958; Ehrlich and Raven, 1964; Gilbert and Raven, 1975; Thompson, 1982, 1986; Futuyma and Slatkin, 1983; Nitecki, 1983; Stone and Hawksworth, 1986; Rausher, 1988). Coevolution has now fragmented into a diverse array of subdisciplines of its own (chemical ecology, insect host range, the impact of parasitoids and predators, seed dispersal and flowering tactics, to mention a few).

Coevolution refers to the joint evolution of two (or more) taxa that have close ecological relationships but do not exchange genes and in which reciprocal selective pressures operate to make the evolution of either taxon partially dependent on the evolution of the other (Ehrlich and Raven, 1964). Coevolution includes most of the various forms of population interaction, from competition to predation to mutualism, but the term is often used in a more restricted sense to refer primarily to the interdependent evolutionary interactions between plants and animals, especially their herbivores, pollinators, and dispersal agents (Janzen, 1980). Plants have invented and evolved an incredibly wide variety of chemical defenses against herbivores, including various oils, resins, alkaloids, nicotine, terpenes, terpenoids, sesquiterpenes, cardiac glycosides, cyanogenic (cyanide-based) compounds, mustard gases, nerve gases, hormone mimics, and tannins. This constitutes one of the best examples of 'aspect diversity' (Rand, 1967). A plant may evolve a secondary chemical substance that deters the vast majority of predators, but if a particular herbivore can in turn evolve a metabolic pathway to detoxify this chemical deterrent, it can thereby obtain an uncontested food supply. Through this kind of coevolution, many herbivores have become strongly specialized on a single species or a few closely related species of plants (Ehrlich and Raven, 1964; Benson et al., 1975). In some cases such specialized herbivores even use a plant's toxic chemicals (often quite volatile and/or pungent) as cues in locating and/or selecting their host plants. Certain herbivores actually sequester plant poisons that in turn make the herbivore unpalatable or even poisonous to its own potential predators. Monarch butterflies sequester cardiac glycosides from milkweed food plants, which make these insects distasteful to their own avian predators.

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Other Danaid butterflies and certain moths make double use of polyuridine alkaloids, which noxious chemicals are not only sequestered by larvae and/or adults and used for antipredator purposes, but are also exploited as chemical precursors in the synthesis of pheromones used in mate attraction. An arginine mimic, 1-canavanine, present in many legumes, ruins protein structure in most insects; however, a bruchid beetle has evolved metabolic machinery that enables it to utilize plants containing canavanine.

Attempts have been made to generalize about the coevolution of herbivores and plant antiherbivore tactics (Cates and Orians, 1975; Feeny, 1975, 1976; Rhoades and Cates, 1976). Rare or ephemeral plant species are hard for herbivores to find and hence are protected by escape in time and space (Feeny, 1975, 1976); moreover, Feeny asserts, such plant species should evolve a diversity of qualitatively different, chemically inexpensive, defenses that should constitute effective evolutionary barriers to herbivory by nonadapted generalized herbivores that are most likely to find such 'cryptic' plants. However, these same secondary chemicals will be only minimal ecological barriers to adapted specialized herbivores, against which the plant's primary anti-herbivore tactic is escape in time and space (i.e. not being found). In contrast, Feeny reasons that abundant and/or persistent plant species cannot prevent herbivores from finding them either in ecological or evolutionary time. Such 'apparent' plant species appear to have evolved more expensive defenses, including spines, hairs, hooks, and tough leaves of low nutrient or water content containing large amounts of relatively nonspecific chemicals such as tannins. These kinds of chemicals constitute so-called 'quantitative' defenses, because their effects on herbivores are dose-dependent. Such plant defenses should pose a significant ecological barrier to herbivores, although perhaps only a weak evolutionary barrier unless supplemented with qualitative chemical defenses (some plants have both).

Cates and Orians (1975) develop related predictions for early versus late successional plant species. Because early successional plants escape from herbivores in space and time, Cates and Orians reason that such plants should allocate fewer resources to chemical antiherbivore defenses than the more apparent plants of later stages in succession. Thus, early successional plant species should make better foods for generalized herbivores than later successional and climax plant species. Indeed, experimental studies on slug feeding indicate that early successional annuals were significantly more palatable than later successional species (Cates and Orians, 1975). Similar experiments with grasshoppers produced the opposite result (Otte, 1975); these generalized herbivores accepted more later successional plant species than early

ones. Otte suggest that this difference may arise from the difference in mobility between slugs and grasshoppers. Other exceptions and problems with the plant-apparency model are noted by Hay and Fenical (1988). Although generalizations are difficult to come by and must allow for exceptions, we need generalizations even if they are imperfect (Pianka, 1987).

In some cases plants have actually formed cooperative relationships with animals that result in their protection from certain herbivore species. By means of ant removal experiments, Janzen (1966, 1967) showed that some species of Acacia deprived of their normal epiphytic ant fauna are highly palatable to herbivorous insects, whereas species that do not normally have ants for protection from herbivores are far less palatable. Acacias that benefit from ant protection possess nectaries, pithy swollen thorns, and nodules (Beltian bodies) that produce nutritious proteins (see cover illustration). The thorns are hollowed out by the ants and used as nesting chambers. These Acacias thus attract and in turn benefit the ants, providing them with both food and living space. These plants put matter and energy into attracting ants to defend their leaves, rather than into more direct chemical warfare. This antiherbivore ploy is effective against a broad range of herbivores, since the ants ferociously attack a wide variety of both invertebrate and vertebrate herbivores. Ant protection may also reduce competition with other plants, as well as provide a measure of protection from fire, because the ants keep the ground surface clear immediately around their acacia plant.

Many plants protect their seeds either by enclosing them in a toxic matrix and/or by means of a hard shell. Some seeds are poisonous. Nevertheless, the high nutrient content of seeds has resulted in the evolution of effective seed predators. Predation on seeds may often be heaviest where they occur in greatest concentrations (such as acorns underneath a parent oak) because seed predator populations will generally be largest where the most food is available (Janzen, 1970, 1971b). As a result, the probability of an individual seed's surviving to establish itself as a plant may often vary inversely with seed density (actual data on this remain scant and are contradictory). In many trees, most seeds fall to the ground near the parent tree, with a continually decreasing number of seeds ending up at distances farther from the parent tree. As a result of these opposing processes, recruitment will be maximized at some distance from the parent tree (Janzen, 1971b), and seedlings will establish themselves in a 'ring' around the parent tree at some distance from the tree. Janzen's model of seed predation and recruitment may help to explain the high species diversity of tropical trees, which suffer heavy seed losses to specialized seed predators that eat the seeds of particular tree species (it neglects the question of why there are so many specialized

seed predators in the tropics in the first place). Such rings of seedlings have actually been demonstrated for a few tree species in a dry tropical forest in Costa Rica by plotting the spatial distribution of seedlings with respect to adult trees (Hubbell, 1979, 1980).

Intricacies of coevolutionary relationships between pine squirrels (*Tamiasciurus*) and their coniferous food trees were studied in the pacific northwest by Smith (1970). Conifer seeds constitute the staple food supply of these squirrels; they can effectively strip a tree of most of its cones. Trees reduce the effectiveness of squirrel predation in many different ways: (1) by producing cones that are difficult for the squirrels to reach, open, and/or carry; (2) by putting fewer seeds into each cone (squirrels eat only the seeds themselves and must 'husk' cones to get them); (3) by increasing the thickness of seed coats, requiring that the squirrels spend more time and energy extracting each seed; (4) similarly, by putting less energy into each seed (a drawback is that seedlings from smaller seeds have fewer resources at thier disposal and are presumably poorer competitors than seedlings from larger seeds); (5) by shedding seeds from cones early, before the young squirrels of the year begin foraging; and (6) by periodic cone 'failures' that decimate the squirrel population, thereby reducing the intensity of predation during the next year. Squirrel predation has had profound evolutionary influences upon various reproductive characteristics of conifers, including details of cone anatomy and location, the number of seeds per cone (and the variability in the number per cone), the time at which the cones shed their seeds, the thickness of seed coats, and annual fluctuations in the size of cone crops (another nice example of aspect diversity). Evolution of these defense mechanisms by the conifers has in turn forced squirrels to adapt in various ways, such as choosing cones carefully and stockpiling them.

Because most land plants cannot move, they often exploit animals both for pollination and for seed dispersal (some rely on wind, too). Seeds of many fruits pass unharmed through the intestines of herbivores and germinate to grow a new plant from the droppings of the animal dispersal agent. Colorful flowers with nectar and brightly colored fruits can only be interpreted as having been evolved to attract appropriate animals. Here, as in plant herbivore interactions, a high degree of plant/animal specificity has sometimes arisen. Animals that pollinate a particular plant are referred to as pollen vectors. As an example, in Central America different species of male euglossine bees are highly specific to particular species of tiny epiphytic orchids; male bees travel long distances between orchids (Dressler, 1968). Different bee species are attracted by different orchid fragrances, as can be shown by putting out 'baits' of artificially synthesized orchid 'fragrances'. Male bees do not obtain nectar from the orchids they visit, but only obtain orchid products that the insects use for production of their own pheromones to attract females (Feinsinger, 1983). These bees are probably necessary for, and may have allowed the evolution of, the great diversity of tropical orchids, many of which are evidently quite rare and far apart (Janzen, 1971a). Such specificity of pollinating vectors assures that the plant's pollen is transmitted to the ovules of its own species. Whereas female euglossine bees are not as specific to the plant species they pollinate as males, individual females travel distances up to 23 kilometers (Janzen, 1971a) and regularly move long distances between sparsely distributed plants in gathering nectar and pollen; thus, they probably promote outcrossing among tropical plants at low densities. Indeed, such 'traplining' by female bees may actually permit the very existence of plant species forced to very low densities by factors such as diffuse competition and predation on their seeds and seedlings.

Some pollinators, such as *Heliconius* butterflies (Gilbert, 1972), obtain amino acids from the pollen of plants they pollinate. Because production of nectar and pollen (and fruit) requires matter and energy, attracting animal pollinators (and seed dispersers) has its costs to the plant. Nectar and fruits are usually rich in sugars and other carbohydrates but contain relatively little protein (many fruits are high in lipids, too); in contrast, pollen and seeds contain considerably greater amounts of nitrogen and other limiting materials. Due to the frequent scarcity of such vital nutrients, carbohydrates are presumably cheaper for a plant to produce than amino acids and proteins. Pollen-eating pollinators presumably cost a plant considerably more than strict nectar feeders. Returns from visiting a flower (or eating a fruit) must be great enough to an animal pollinator or seed disperser to make it worthwhile, yet small enough that the animal will travel the distance necessary to disperse the pollen or seeds (Feinsinger, 1987). This delicate energetic interplay between plants and their pollinators is reviewed by Heinrich and Raven (1972) and Feinsinger (1983).

Work described above deals with plant/animal interactions and is a decade or more old. Massive numbers of publications have been spawned since then in an overwhelming number of different directions, including plant–plant coevolution. The evolutionary approach has also proven to be fruitful in numerous other dimensions of plant biology, including various aspects of genetics and developmental plasticity (Bradshaw, 1965, 1972; Willson, 1973a; Quinn, 1987), self-pollination, inbreeding depression, and 'optimal outcrossing' (Bateson, 1978, 1980; Price and Wasser, 1979; Levin, 1984), sexual selection (Willson, 1979; Willson and Burley, 1983), energy budgets and resource allocation (Harper and Ogden, 1970; Willson, 1972a), survivorship (Harper and

White, 1974), interspecific competition (Harper, 1961a, 1961b, 1967; Willson, 1973b), life historical tactics (Harper, 1966, 1977; Harper and Ogden, 1970; Harper et al., 1970; Gadgil and Solbrig, 1972; Willson, 1972b), germination and seed tactics (Salisbury, 1942; Cohen, 1967; Harper et al., 1970; MacArthur, 1972; Venable and Lawlor, 1980; Wheelwright and Orians, 1982; Rathcke and Lacey, 1985), seed dispersal (Smith, 1970; Janzen, 1983), evolution of floral displays, flowering and fruiting tactics (Darwin, 1862; Wasser and Price, 1981; Feinsinger, 1983; Wheelwright, 1985; Stanton et al., 1986; Galen, 1989), leaf mimicry (Rausher, 1978; Gilbert, 1979), leaf tactics (Parkhurst and Loucks, 1971; Givnish and Vermeij, 1976; Orians and Solbrig, 1977), regulation of herbivore populations (Bryant, 1980a, 1980b; Bryant et al., 1983), effects on herbivore growth rates (Feeny, 1968, 1970), plant-herbivore interactions (Fisher, 1958; Gilbert, 1971, 1979; Willson, 1973c; Caughley and Lawton, 1981; Singer, 1983; Bernays and Graham, 1988; Hay and Fenical, 1988), the role of predation in vegetational diversity (Harper, 1969), diffuse coevolution (Fox, 1981, 1988; Gilbert, 1980; Janzen, 1980), growth form and succession (Horn, 1971, 1974, 1975a, 1975b, 1976), photosynthetic pathways (Evans, 1971), indirect interactions (Brown et al., 1986; Fox, 1988), tropical tree species diversity (Jones, 1956; Janzen, 1975; Hubbell, 1979, 1980), and community structure (Whittaker, 1965, 1967; Seifert and Seifert, 1976; Lawton, 1984, Armbruster, 1986).

Acknowledgements

References

Armbruster, W.S., 1986. Reproductive interactions between sympatric Dalechampia. species: are natural assemblages 'random' or organized? Ecology, 67: 522−533.

Bateson, P.P.G., 1978. Sexual imprinting and optimal outbreeding. Nature, 273, 273: 659−660.

Bateson, P.P.G., 1980. Optimal outbreeding and the development of sexual preferences in Japanese quail. Zeitschrift fur Tierpsychologie, 53, 231−244.

Benson, W.W., Brown, K.S. Jr. and Gilbert, L.E., 1975. Coevolution of plants and herbivores: Passion flower butterflies. Evolution, 29: 659−680.

Bernays, E. and Graham, M., 1988. On the evolution of host specificity in phytophagous arthropods. Ecology, 69: 886−892.

Bradshaw, A.D., 1965. Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics, 13: 115−155.

Bradshaw, A.D., 1972. Some of the evolutionary consequences of being a plant. Evolutionary Biology, 5: 25−47.

Brown, J.H., Davidson, D.W., Munger, J.C. and Inouye, R.S., 1986. Experimental community ecology: the desert granivore system. Chapter 3 (pp. 41−61) in Diamond, J. and T.J. Case (eds), Community Ecology. Harper & Row: New York.

Brues, C.T., 1920. The selection of food-plants by insects with special reference to lepidopterous larvae. American Naturalist, 54: 313−332.

Brues, C.T., 1924. The specificity of food-plants in the evolution of phytophagous insects. American Naturalist, 58: 127−144.

Bryant, J.P., 1980a. Selection of winter forage by subarctic browsing vertebrates: The role of plant chemistry. Annual Review of Ecology and Systematics, 11: 261−285.

Bryant, J.P., 1980b. The regulation of snowshoe hare feeding behavior during winter by plant antiherbivore chemistry. In K. Meyers (ed.), Proceedings of the First International Lagomorph Conference (pp. 69−98). Guelph University Press.

Bryant, J.H., Chapin, F.S. and Klein, D.R., 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos, 40: 357−368.

Cates, R.G. and Orians, G.H., 1975. Successional status and the palatability of plants to generalized herbivores. Ecology, 56: 410−418.

Caughley, G. and Lawton, J.H., 1981. Plant-herbivore systems. Chapter 7 (pp. 132−166) in R.M. May (ed.), Theoretical Ecology: Principles and Applications (Second ed.). Blackwell: Oxford.

Cohen, D., 1967. Optimizing reproduction in a randomly varying environment. Journal of Theoretical Biology, 16: 1−14.

Coley, P.D., Bryant, J.P. and Chapin, F.S., III, 1985. Resource availability and plant antiherbivore defense. Science, 230: 895−899.

Darwin, C., 1859. The Origin of Species by Means of Natural Selection (numerous editions). Murray: London.

Darwin, C., 1862. On the Various Contrivances by Which Orchids are Fertilized by Insects. Murray: London.

Dressler, R.L., 1968. Pollination by euglossine bees. Evolution, 22: 202−210.

Ehrlich, P.R. and Raven, P.H., 1964. Butterflies and plants: A study in coevolution. Evolution, 18: 586−608.

Evans, L.T., 1971. Evolutionary, adaptive and environmental aspects of the photosynthetic pathway: assessment. In M.D. Hatch, C.B. Osmond and R.O. Slayter (eds), Photosynthesis and Photorespiration. Wiley and Sons: New York.

Feeny, P.P., 1968. Effects of oak leaf tannins on larval growth of the winter moth Operophtera brumata. Journal of Insect Physiology, 14: 805−817.

Feeny, P.P., 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology, 51: 565−581.

Feeny, P.P., 1975. Biochemical coevolution between plants and their insect herbivores. In L.E. Gilbert and P.H. Raven (eds), Coevolution of Animals and Plants (pp. 3−19). Univ. of Texas Press: Austin.

Feeny, P.P., 1976. Plant apparency and chemical defense. Recent Advances in Phytochemistry, 10: 1−40.

Feinsinger, P., 1983. Coevolution and pollination. Chapter 13 (pp. 282−310) in D. Futuyma and M. Slatkin (eds), Coevolution. Sinauer: Sunderland, Mass.

Feinsinger, P., 1987. Approaches to nectarivore−plant interactions in the New Word. Revista Chilena de Historia Natural, 60: 285−319.

Fisher, R.A., 1930. The Genetical Theory of Natural Selection. Clarendon Press: Oxford.

Fisher, R.A., 1958. Polymorphism and natural selection. Journal of Animal Ecology, 46: 289−293.

Fox, L.R., 1981. Defense and dynamics in plant−herbivore systems. American Zoologist, 21: 853−864.

Fox, L.R., 1988. Diffuse coevolution within complex communities. *Ecology*, 69: 906–907.

Futuyma, D.J. and Slatkin, M. (eds), 1983. *Coevolution*. Sinauer: Sunderland, Mass.

Gadgil, M. and Solbrig, O.T., 1972. The concept of *r* and *K* selection: Evidence from wild flowers and some theoretical considerations. *American Naturalist*, 106: 14–31.

Galen, C., 1989. Measuring pollinator-mediated selection on morphometric floral traits: bumblebees and the alpine sky pilot *Polemonium viscosum*. *Evolution*, 43: 882–890.

Gilbert, L.E., 1971. Butterfly-plant coevolution: Has *Passiora adenopoda* won the selectional race with Heliconiine butterflies? *Science*, 172: 595–596.

Gilbert, L.E., 1972. Pollen feeding and reproductive biology of *Heliconius* butterflies. *Proceedings of the National Academy of Sciences*, 69: 1403–1407.

Gilbert, L.E., 1979. Development of theory in the analysis of insect–plant interactions. Chapter 5 in D.J. Horn, R. Mitchell and G.R. Stairs (eds), *Analysis of Ecological Systems* (pp. 117–154). Ohio State University Press: Columbus.

Gilbert, L.E., 1980. Coevolution of animals and plants: a 1979 postscript. pp. 247–263 in L.E.Gilbert and P.H.Raven (eds), 1980. *Coevolution of Animals and Plants*. Second Edition. University of Texas Press: Austin.

Gilbert, L.E. and Raven P.H. (eds), 1975. *Coevolution of Animals and Plants*. University of Texas Press: Austin.

Givnish, T.J. and Vermeij, G.J., 1976. Sizes and shapes of liane leaves. *American Naturalist*, 110: 743–778.

Harper, J.L., 1961a. Approaches to the study of plant competition. *Society for Experimetnal Biology Symposium*, 15: 1–39.

Harper, J.L., 1961b. The evolution and ecology of closely related species living in the same area. *Evolution*, 15: 209–227.

Harper, J.L., 1966. The reproductive biology of the British poppies. In J.G. Hawkes, (ed.), *Reproductive Biology and Taxonomy of Vascular Plants*. (pp. 26–39). Pergamon & Botanical Society of the British Isles: Oxford.

Harper, J.L., 1967. A Darwinian approach to plant ecology. *Journal of Ecology*, 55: 247–270.

Harper, J.L., 1969. The role of predation in vegetational diversity. *Brookhaven Symposium Biology*, 22: 48–62.

Harper, J.L., 1977. *Population Biology of Plants*. Academic Press: New York.

Harper, J.L., Lovell, P.H. and Moore, K.G., 1970. The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*, 1: 327–356.

Harper, J.L. and Ogden, J., 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris*. L. *Journal of Ecology*, 58: 681–698.

Harper, J.L. and White, J., 1974. The demography of plants. *Annual Review of Ecology and Systematics*, 5: 419–463.

Hay, M.E. and Fenical, W., 1988. Marine plant–herbivore interactions: The ecology of chemical defense. *Annual Review of Ecology and Systematics*, 19: 111–145.

Heinrich, B. and Raven, P.H., 1972. Energetics and pollination ecology. *Science*, 176: 597–602.

Horn, H.S., 1971. *The Adaptive Geometry of Trees*. Princeton University Press: Princeton, N.J.

Horn, H.S., 1974. The ecology of secondary succession. *Annual Review of Ecology and Systematics*, 5: 25–37.

Horn, H.S., 1975a. Forest succession. *Scientific American*, 232 (May): 90–98.

Horn, H.S., 1975b. Markovian properties of forest succession.

In M.L. Cody and J.M. Diamond (eds), *Ecology and Evolution of Communities* (pp. 196–211). Harvard University Press: Cambridge, Mass.

Horn, H.S., 1976. Succession. Chapter 10 (pp. 187–204) in R.M. May (ed.), *Theoretical Ecology: Principles and Applications*. Blackwell: Oxford.

Hubbell, S.P., 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, 203: 1299–1309.

Hubbell, S.P., 1980. Seed predation and the coexistence of tree species in tropical forests. *Oikos*, 35: 214–229.

Janzen, D.H., 1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution*, 20: 249–275.

Janzen, D.H., 1967. Fire, vegetation structure, and the ant-acacia interaction in Central America. *Ecology*, 48: 26–35.

Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist*, 104: 501–528.

Janzen, D.H., 1971a. Euglossine bees as long-distance pollinators of tropical plants. *Science*, 171: 203–205.

Janzen, D.H., 1971b. Seed predation by animals. *Annual Review of Ecology and Systematics*, 2: 465–492.

Janzen, D.H., 1976. *Ecology of Plants in the Tropics*. Arnold: London.

Janzen, D.H., 1980. When is it coevolution? *Evolution*, 34: 611–612.

Janzen, D.H., 1983. Dispersal of seeds by vertebrate guts. Chapter 11 (pp. 232–262) in D. Futuyma and M. Slatkin (eds), *Coevolution*. Sinauer: Sunderland, Mass.

Jones, E.W., 1956. Ecological studies on the rain forest of southern Nigeria. *Journal of Ecology*, 44: 83–117.

Lawton, J.H., 1984. Non-competitive populations, non-convergent communities, and vacant niches: The herbivores of Bracken. In D.R. Strong, D. Simberloff, L.G. Aberle and A.B. Thistle, (eds), *Ecological Communities: Conceptual Issues and the Evidence* (pp. 67–95). Princeton University Press: Princeton, N.J.

Levin, D.A., 1984. Inbreeding depression and proximity-dependent crossing success in *Phlox drummonida*. *Evolution*, 38: 116–127.

Lippek, E.E., 1957. Evolutionary relationship between entomophilous plants and anthophilous insects. *Evolution*, 11: 466–481.

MacArthur, R.H., 1961. Population effects of natural selection. *American Naturalist*, 95: 195–199.

MacArthur, R.H., 1972. *Geographical Ecology: Patterns in the Distributon of Species*. Harper & Row: New York.

Mayr, E., 1962. Cause and effect in biology. *Science*, 134: 1501–1506.

Mode, C.J., 1958. A mathematical model for the coevolution of obligate parasites and their hosts. *Evolution*, 12: 158–165.

Nitecki, M.H., (ed.), 1983. *Coevolution*. University of Chicago Press: Chicago.

Orians, G.H., 1962. Natural selection and ecological theory. *American Naturalist*, 96: 257–263.

Orians, G.H. and Solbrig, O.T., 1977. A cost-income model of leaves and roots with special reference to arid and semiarid areas. *American Naturalist*, 11: 677–690.

Otte, D., 1975. Plant preference and plant succession. A consideration of evolution of plant preference in *Schistocerca*. *Oecologia*, 18: 129–144.

Parkhurst, D.F. and Loucks, O.L., 1971. Optimal leaf size in relation to environment. *Journal of Ecology*, 60: 505–537.

Pianka, E.R., 1986. Ecological phenomena in evolutionary perspective. Chapter 16 (pp. 325–336) in: 'Ecosystem Theory and Application' Polunin, N. (ed.). Wiley and Sons, London.

Pianka, E.R., 1987. The subtlety, complexity and importance

of population interactions when more than two species are involved. *Revista Chilena de Historia Natural*, **60**: 351–362.

Pianka, E.R., 1988. *Evolutionary Ecology*. Fourth Edition. Harper and Row: New York. 468 pp.

Price, M.V. and Wasser, N.M., 1979. Pollen dispersal and optimal outcrossing in *Delphinium nelsoni. Nature*, **277**: 294–297.

Rand, A.S., 1967. Predator-prey interactions and the evolution of aspect diversity. *Atas do Simposio sobre a Biota Amazonica*, **5**: 73–83.

Rathcke, B. and Lacey, E.P., 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology Systematics*, **16**: 179–214.

Rausher, M.D., 1978. Search image for leaf shape in a butterfly. *Science*, **200**: 1071–1073.

Rausher, M.D., 1988. Is coevolution dead? *Ecology*, **69**: 898–901.

Rhoades, D. and Cates, R., 1976. Toward a general theory of plant antiherbivore chemistry. *Recent Advances in Phytochemistry*, **10**: 168–213.

Quinn, J.A., 1987. Complex patterns of genetic differentiation and phenotypic plasticity versus an outmoded ecotype terminology. *Differentiation Patterns in Higher Plants*, Chapter 5, 95–113.

Salisbury, E.J., 1942. *The Reproductive Capacity of Plants*. Bell: London.

Seifert, R.P. and Seifert, F.H., 1976. A community matrix analysis of *Heliconia* insect communities. *American Naturalist*, **110**: 461–483.

Singer, M.C., 1983. Determinants of multiple host use by a phytophagous insect population. *Evolution*, **37**: 389–403.

Smith, C.C., 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecological Monographs*, **40**: 349–371.

Stone, A.R. and Hawksworth, D.L. (eds), 1986. *Patterns in Coevolution*. Clarendon: Oxford.

Stanton, M.L., Snow, A.A. and Handel, S.N., 1986. Floral evolution: attractiveness to pollinators influences male fitness. *Science*, **232**: 1625–1627.

Thompson, J.N., 1982. *Interaction and Coevolution*. John Wiley and Sons: New York.

Thompson, J.N., 1986. Patterns in coevolution. pp. 119–143 in A.R. Stone and D.L. Hawskworth, (eds), *Patterns in Coevolution*. Clarendon: Oxford.

Venable, D.L. and Lawlor, L.R., 1980. Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia*, **46**: 272–282.

Wasser, N.M. and Price, M.V., 1981. Pollinator choice and stabilizing selection for flower color in *Delphinium nelsonii. Evolution*, **35**: 376–390.

Wheelwright, N.T., 1985. Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. *Oikos*, **44**: 465–477.

Wheelwright, N.T. and Orians, G.H., 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *American Naturalist*, **119**: 402–413.

Whittaker, R.H., 1965. Dominance and diversity in land plant communities. *Science*, **147**: 250–260.

Whittaker, R.H., 1976. Gradient analysis of vegetation. *Biological Review*, **42**: 207–264.

Willson, M.F., 1972a. Evolutionary ecology of plants: A review. I. Introduction and energy budgets. *The Biologist*, **54**: 140–147.

Willson, M.F., 1972b. Evolutionary ecology of plants: A review. II. Ecological life histories. *The Biologist*, **54**: 148–162.

Willson, M.F., 1973a. Evolutionary ecology of plants: A review: III. Ecological genetics and life history. *The Biologist*, **55**: 1–12.

Willson, M.F., 1973b. Evolutionary ecology of plants: A review. IV. Niches and competition. *The Biologist*, **55**: 74–82.

Willson, M.F., 1973c. Evolutionary ecology of plants: A review. V. Plant/animal interactions. *The Biologist*, **55**: 89–105.

Willson, M.F., 1979. Sexual selection in plants. *American Naturalist*, **113**, 777–790.

Willson, M.F. and Burley, N., 1983. *Mate Choice in Plants*. Princeton University Press: Princeton, N.J.