

Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates

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Patterns contradicting expectations from earlier coevolutionary models, and the observation that optimality and fine scale adjustments are conspicuously absent in many instances, suggest that coevolved, interdependent plant-vertebrate seed dispersal systems are, at best, very rare in nature. Weak selective pressures of dispersers on plants, temporal and spatial unpredictability of favourable germination sites and disperser behaviour, extensive plant gene flow derived from distant seed dispersal and frequent dioecy, and slow evolutionary rates relative to recurrence of environmental perturbations (animal species' extinctions), all combine to render close coevolution between particular plant and disperser species unlikely. Slower species turnover of woody plants over geological time relative to vertebrate dispersers may have favoured a sort of very coarse diffuse coevolution, through long-lived plant species having acted as "carriers" of information through evolutionary time. This may suffice to explain patterns of successful plant-disperser interaction commonly observed not only in natural habitats, but also in artificial systems recently assembled by man and lacking a common historical background to participant organisms. This background is indispensable for non-diffuse, species-to-species coevolution to have actually taken place.

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1. Introduction

In recent years, the concept of coevolution has become tightly coupled to virtually every study of plant-animal interactions, largely as a consequence of the pioneering works by Ehrlich and Raven (1965), Janzen (1966) and several contributors to Gilbert and Raven (1975). After its initial invasion into the habitat of plant-animal studies, rapid radiation took place and coevolution has since been suggested to explain an enormous variety of patterns and situations related to the interaction of plants with herbivores or mutualists. Several authors, including some earlier advocates of the concept, have recently raised objections against its uncritical application or questioned on varied grounds the very existence of the phenomenon (Howe 1980, Janzen 1980, 1981a, b, c, 1983, Heithaus 1982, Howe and Smallwood 1982, Wheelwright and Orians 1982). Reasons adduced

against the notion of coevolution are quite diverse, but most often relate to particular features or special conditions of the system under consideration. My purpose here is to examine in a more general way some ecological and evolutionary constraints that call for care in claiming of occurrence of plant-animal coevolution. Although I will concentrate on the mutualistic system involving plants producing fleshy fruits and vertebrate frugivores which disperse their seeds, the general constraints on coevolution considered below may also apply to other plant-animal systems.

Although the term coevolution conveys an essentially qualitative concept, the kind of process it is intended to account for may acquire a broad range of "quantitative" levels (see e.g. Brooks 1979). The implicit recognition of this principle has led to restricting the use of the term to those instances in which, under the personal judgement of the investigator, the intensity of the putative

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coadaptive process exceeds some tacitly set threshold. This intensity has most often been evaluated a posteriori by the unlikelihood of random occurrence of the mutual adaptations observed. Reliance on personal assessments of quantitative thresholds may cause some confusion regarding what is interpretable in terms of coevolution, hence I will consider coevolution by stressing its qualitative nature, i.e. "an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first" (Janzen 1980; see also Janzen 1966, Baker 1973).

2. Plant-disperser coevolution

Mutualistic congruency between plants and vertebrate frugivores dispersing their seeds initially suggested plant-disperser coevolution, and prompted some coevolutionary models (Snow 1971, McKey 1975, Howe 1977, Howe and Estabrook 1977, Howe 1979). Subsequent field studies have very often falsified predictions derived from these models, and have shown that coarse, or diffuse, rather than fine-tuned, adjustments between plant and disperser species occur in nature (e.g., Howe 1980, 1981, 1983, Frost 1980, Fleming 1981, Herrera and Jordano 1981, Heithaus 1982, Herrera 1982a, Howe and Smallwood 1982, Jordano 1982, Moore and Willson 1982, Morden-Moore and Willson 1982, Herrera 1984c). Also becoming clear is that the existence of plant and animal traits resulting in successful seed dispersal and vertebrate frugivory is a necessary, but not sufficient condition to infer coevolution. This is clearly illustrated by nicely congruent plant-disperser systems which have been recently brought about by human action and thus lack the historical background indispensable to coevolution. Introduced plant or bird species very often interact strongly with native counterparts found in their new habitats, giving rise to successful seed dispersal and frugivory (e.g., Heim de Balsac 1935, Sherburne 1972, Glyphis et al. 1981, Alexandre 1982, Gleadow 1982). That mutualistic congruency is insufficient to infer coevolution is also supported by studies of plant-pollinator (Cortés 1978, Valentine 1978) and plant-guarding ants (Koptur 1979) systems (see also Janzen 1967). In the case of vertebrates, morphological or behavioural preadaptations not evolved in relation to frugivory may enable them to participate successfully in seed dispersal (Janzen 1981d, e, 1982a, Herrera 1984d).

Introductions of plants and animals most commonly provide an unquestionable proof of the absence of a common history for the interacting counterparts, but hidden situations of this kind are probably much more common than suspected in "natural", undisturbed habitats. Many small-fruited, Tertiary subtropical relict plants in the Mediterranean Basin are currently very successfully dispersed by a few small-sized bird species of recent Palaearctic origin which really are relative

newcomers to the local scene of seed dispersal. In contrast, other similarly ancient, but large-fruited taxa have failed to overlap with dispersers of appropriate size since the appearance of mediterranean conditions in the Pliocene, and seed dispersal is quite unsuccessful among these species (Herrera 1984c). There has been a trend in the literature to search for the reasons of the absence of coadaptation upon contemplation of conspicuously disadjusted plant-vertebrate seed dispersal interactions (e.g., Howe and Vande Kerckhove 1979, Janzen and Martin 1982). Nevertheless, questions of this kind have been posed more rarely when the system seems to be efficiently tuned or fit the expectations from coevolutionary models (but see, e.g., Janzen 1981c, Herrera 1981, 1984c, Janzen and Martin 1982). This unrigorous behaviour has sometimes led to uncritical acceptance of plant-disperser coevolution. We should ask not only, Why did this conspicuously disadjusted system not coevolve?, but also, Is there any realistic chance that this particularly well-adjusted system has come about through coevolution? It is the second class of questions I wish to address, specifically Is it likely that coevolution between species of plants and vertebrates which disperse their seeds becomes widespread in nature? A third question, namely, Does coevolution necessarily lead to congruency?, will not be considered here, and I assume that it does in most cases of mutualism.

3. General constraints: evolutionary rates

The more similar are the potential rates of evolutionary change in relevant traits, *measured in relation to absolute time units*, the more likely will be coevolution between two organisms once some elemental interaction exists (e.g., based on preadaptation). I do not mean that congruency of evolutionary rates is an essential requisite to coevolution, but only that it greatly increases its probability of occurrence, as discussed later. Increasing asymmetry in the rates of change will lead to more pronounced adaptive changes of the faster-evolving participant in response to the selective pressures exerted by the slower-evolving one, hence rendering difficult (although not definitely precluding it, see later) stepwise, reciprocal coadaptation. A heritable phenotypical trait subject to natural selection will change more rapidly (expressed in respect to absolute time units) the greater the intensity of selection and the shorter the average generation time of the organism (Fisher 1958, Crow and Nagylaki 1976) (and the fewer other parts of the organism have to change as the change selected for changes, but these structural constraints will not be considered here). Assuming for simplicity that intensities of selection exerted by the two organisms are roughly similar (this assumption will be relaxed later), congruence in generation length alone should favor coevolution.

Generation times of most vertebrate frugivores and

vertebrate-dispersed plants are notoriously dissimilar. These plants are mostly long-lived shrubs and trees with life spans in the order of five to hundreds of years (Harper and White 1974). The vast majority of vertebrate dispersers, in contrast, have much shorter lives (see e.g. Haukioja 1969, Botkin and Miller 1974, Souza Lopes et al. 1980, for birds). In plant populations having overlapping generations, particularly those of earlier successional perennials, actual "generation length" (Caughley 1977) may be substantially shorter than suggested by life span data, but in mid- and late-successional species it is probably of the same order of magnitude, and roughly similar to the turnover rate of forests (Auclair and Cottam 1971, Harper and White 1974, Van Valen 1975, Hartshorn 1978, Bullock 1980, Brokaw 1982). Turnover of individuals is thus substantially faster among frugivores than among plants; most individual plants whose fruits are currently being fed upon by vertebrates come from seeds which were dispersed by individual frugivores dating back 20-100 generations. Short life-cycles of frugivores relative to plants give frugivore populations a capacity to quickly adapt to fruit resources, often giving rise to conspicuous examples of adaptation to frugivory and seed dispersal (e.g., Morrison 1980, Milton 1981, Herrera 1984d). In order for plant-disperser coevolution to proceed in a reasonably symmetrical sequence, selection intensity on plants should be strong enough to compensate for their long generation times, but a constellation of factors render this difficult as discussed later.

Estimated speciation rates indicate that shrubs and trees, with which most vertebrate dispersers interact, actually evolve more slowly than vertebrates (Stebbins 1949, Brodtkorb 1960, 1971, Levin and Wilson 1976, Bush et al. 1977). Evolutionary rates of vertebrate-dispersed plants most likely are still lower than for tree and shrub growth forms in general (Levin and Wilson 1976). Long-distance seed dispersal resulting from endozoochory, very often associated with obligate outcrossing derived from dioecy (Bawa 1980), combine to increase gene flow and thus, presumably, to retard the rate of genetic differentiation among vertebrate-dispersed plants. Speciation rates are indicative of the evolutionary rates of dispersal-related traits to the extent that these traits constitute differential attributes of plant species. The persistence of dispersal-related plant structural traits over long geological periods without noticeable change suggests, however, that their evolutionary rates may often be even slower than speciation rates. The fruits of living *Taxus* species, for instance, seem essentially identical to those of *Palaeotaxus*, an Upper Triassic close relative living about 175 Myr ago (Emberger 1968). Remarkable within-genus constancy in fruit attributes (shape, colour, size, nutritional value of pulp), commonly observed in genera having broadly disjunct world distribution (e.g. *Ilex*, *Ocotea*, *Olea*, *Osyris*; Herrera unpubl.), similarly indicates that evolutionary rates of

structural dispersal-related traits have often been much slower than speciation rates (see Raven and Axelrod 1974).

In response to selective pressures from vertebrate seed dispersers, plants may evolve non-structural adaptations (e.g., phenology) whose evolutionary rates are difficult to assess by consideration of speciation rates alone. Assuming that these adaptations require smaller selection intensities than structural ones, they should indeed be expected in view of the generally low selective pressures exerted by individual disperser species (see later). No information on (dispersal-related) functional features of fruiting plants is available to evaluate potential evolutionary rates of these traits, but some evidence suggests that they may be extremely low in some instances. The congeneric *Osyris quadripartita* and *O. compressa* (Santalaceae), native to the western Mediterranean Basin and South Africa, respectively, exhibit the same unusual phenology and fruit-ripening patterns in the two regions (Herrera 1984c), despite very long isolation (see Pons 1981), occupying contrasting habitat types, and having quite different dispersal agents in the two regions. In contrast, functional adaptations to frugivory have evolved among recent vertebrate disperser taxa (Berthold 1976, Milton 1981, Herrera 1984d).

These observations indicate that, in general, vertebrate-dispersed plants and their dispersal agent substantially differ in evolutionary rates, as expected from considerations above on differential generation length. Even in these conditions, however, coevolution may conceivably occur, but slow evolutionary "responsiveness" of plant counterparts will set a "bottleneck" to the process and, consequently, it could only proceed at a slow rate (unless only a small change is required for the plant and a large one for the vertebrate, in which case they can go at about the same rate). The slower this coadaptive rate, the higher the probability of being irreversibly disrupted by recurrent perturbations, the most obvious of which is the extinction of one of the participants. Mean species duration times of shrubs and angiosperm trees, which include the vast majority of vertebrate-dispersed plants, are 27 and 38 Myr, respectively (Levin and Wilson 1976; see also Stebbins 1982). In contrast, mean species duration of mammals and birds are 0.5-4.0 (depending on the group) and about 0.5 Myr, respectively (Brodtkorb 1960, 1971, Bush et al. 1977) Any vertebrate-dispersed plant species has thus almost certainly faced in the course of its existence an uninterrupted sequence of extinctions and successive replacements of its vertebrate counterparts. Situations analogous to the one described by Janzen and Martin (1982) for central American trees dispersed by large mammals have most likely happened many times over geological time, and not necessarily in connection with mass extinction of vertebrate species. In this sense, most vertebrate-dispersed species actually are "anachronisms", insofar as they have largely evolved in ad-

vance of their current dispersers (Janzen 1981a, c), but I further submit that this is an *inherent* property to these very long-duration plant taxa. Some of the plants which today constitute anachronisms in central American dry forests after extinction of the Gomphotheres and allied forms (yet the plants still exist there), were already anachronistic in some respects when Gomphotheres first contacted them and fed on their fruits, since they probably antedated (as species) these animals on the geological scene (Janzen and Martin 1982, Janzen 1983). The same situation would apply to some Cotingid and Lauraceous species, which have been suggested to constitute a coevolved seed dispersal system but in which plants probably antedated birds with at least several million years (Chesters et al. 1967, Cronquist 1981, Snow 1981, C. G. Sibley pers. comm.).

Consideration of differential evolutionary rates and species duration times of vertebrate-dispersed plants and their dispersal agents leads to the conclusion that coevolution (in the sense defined earlier) is unlikely to become common. Slow evolutionary responsiveness of plants coupled with very short duration of vertebrate taxa over geological time in relation to plant taxa, represent two important constraints to coevolution. I examine in the next section some factors generally precluding high selection intensities on plants by dispersers, hence hindering a rapid evolutionary response of plants which could compensate for their long generation times.

4. Specific constraints: low selection intensity of dispersers on plants

Several features inherent to plant-vertebrate seed dispersal systems combine to produce generally low selection of individual disperser species on plants. These include, among others, (1) limited ability of plants to restrict the range of disperser species feeding on their fruits and dispersing their seeds, which gives rise to "guild effects"; (2) very high environmental (as opposed to genetical) variance commonly associated with the seed dispersal process; and (3) low selective pressures of dispersers relative to nondisperser organisms.

4.1. Guild effects

As used here, "guild effects" refer to the (mostly indirect) influence that biological diversity per se has on the intensity of selection by disperser species on dispersal-related plant traits. Guild effects originate from dispersal agent and fruiting plant species assemblages.

4.1.1. Diversity of dispersal agents

There are relatively few proximate options available to plants to restrict the range of vertebrate species which feed on their fruits *beyond a certain threshold*. Infructescence structure and diameter of the supporting stem, fruit size and colour, and palatability of the pulp, all

may play a proximate role in restricting the assemblage of frugivores interacting with any given plant species (Turcek 1963, Diamond 1973, Katak 1979, Snodderly 1979, Denslow and Moermond 1982, Herrera 1982b, Howe 1983, Sorensen 1983). In spite of these mechanisms, it is impractical to plants to restrict access to their fruits beyond a certain threshold (Wheelwright and Orians 1982, Janson 1983), and it is a common observation that the fruits of single plant species, both tropical and nontropical, are locally fed upon by a variety of vertebrate species, not all of which actually disperse seeds (e.g., Howe 1977, 1981, McDiarmid et al. 1977, Herrera and Jordano 1981, Bonaccorso et al. 1980, Jordano 1982, 1983). There also may be variation over relatively short distances in the identity of vertebrates dispersing a plant species (Howe and Vande Kerckhove 1979, Cant 1979), further contributing to increase the diversity of a species' dispersal agents. Individual plant species will respond evolutionarily to the integrated selective pressures of the combined set of counterparts with which it interacts, rather than to pressures from any single species. The latter will ordinarily be heavily diluted into the overall selection pressure, or even cancelled out by opposed pressures exerted by other species. Importantly, intense selection in a defined direction may only result from the summation of analogous pressures from several species, which could originate "diffuse coevolution" (Janzen 1980, Herrera 1982a). The greater the species diversity of disperser assemblages, the lower the probability of simple, stepwise coevolution as defined above, and the higher the probability of diffuse coevolution, as has been suggested for plant-herbivore and competitive systems (Connell 1980, Fox 1981).

The depressing effect of high diversity on coevolution applies only if most or all species involved actually interact, as is usually the case in plant-vertebrate seed dispersal systems as discussed above. The inability of fruiting plants to restrict substantially the range of mutualistic organisms which have access to the reward offered (fruit pulp) is inherent to the type of reward itself. This inability is important in promoting guild effects and diffuse coevolution as illustrated by other plant-animal mutualistic coevolved systems where morphological features of plant structures (e.g., flowers) set efficient filters to visitors (Janzen 1966, 1979, Ramírez 1974, 1978).

4.1.2. Diversity of fruiting plants

Guild effects are not limited to a simple dilution of selective pressures of individual disperser species and its amalgamation into a combined multi-species pressure favouring diffuse coevolution. More important, *the nature and intensity of selective pressures from dispersers experienced by a plant depend not just on dispersers, but also on the characteristics of coexisting plant species*. Individual species of frugivorous vertebrates feed on many fruit species and are dispersers for a variety of plants (e.g., Snow 1962a, b, Snow and Snow 1971,

Heithaus et al. 1975, Bonaccorso 1979, Lieberman et al. 1979, Jordano and Herrera 1981, Wheelwright 1983). This diversity usually has an important seasonal component, but most seed dispersers feed on a variety of fruits at any one time. This implies not only that locally or regionally coexisting plant species ordinarily share to some extent the same dispersal agents, but also that they will often be functionally interdependent for dispersal (Herrera 1984c). Coexisting plant species usually differ greatly in the nutritional configuration of fruit pulp (relative proportion of lipids, protein, carbohydrates, minerals and vitamins) and the identity and concentration of secondary compounds present (Herrera 1984c, in press), hence mixed fruit diets most likely derive from the need of optimizing food composition with regard to nutrients and secondary compounds (Westoby 1974, 1978, Herrera 1982b). One or a few highly nutritious and preferred species in a habitat may facilitate the dispersal of other less nutritious, somewhat toxic ones; these latter may be used just as a minor (in volume), yet regular dietary complement by frugivores and actually experience very weak selective pressures while still accomplishing their dispersal very successfully (Herrera 1984c, in press). On the other hand, variations naturally occurring in plant communities in composition and relative abundance of species may give rise to locality-specific selection regimes on fruiting plants (Herrera in press). Extensive gene flow (endozoochory plus dioecy, see above) coupled with the temporal dynamics of vegetation (and resulting locality-specific selection) would most likely promote genetic mixing and slow down evolutionary change in the species as a whole, rather than favouring local genetic differentiation.

Although the many complications introduced by guild effects in the evolution of plant-disperser interactions have just begun to be explored (see Herrera 1982b, 1984c, in press, Howe 1984), I expect that their general effect will be a depression of selective pressures of individual species, as examples above suggest. It is also important to recognize that "complex interacting *assemblages* have special properties that cannot be derived just by summing up all of the simple interactions that occur" (Fox 1981, italics added), a fact largely ignored in most earlier coevolutionary approaches.

4.2. Environmental variance

The dispersal process consists of two successive stages, namely (1) removal of fruits from the parent plant effected by dispersal agents, and (2) final deposition of seeds somewhere. Dispersal will be either successful or unsuccessful depending on the postdispersal fate of seeds. The vast majority of field studies have considered stage (1), and evaluated comparative levels (intra or interspecifically) of "dispersal success" on this basis alone (e.g., Howe and Vande Kerckhove 1979, Howe and de Steven 1979, Morden-Moore and Willson 1982, Fleming

1981, Moore and Willson 1982). It is important to recognize that what these studies actually examine are conservative estimates of dispersal *failure rates* (if step 1 fails, there is no longer room for step 2) and, if used to evaluate dispersal *success rates* they will most often produce gross overestimates. Keeping this in mind, these studies serve at least to illustrate that intraspecific differences in fruit removal rates often are more related to non-heritable (or having extremely low heritability) plant characters, such as degree of aggregation of conspecifics, age, and position in relation to topographical features or to fruiting individuals of other species, than to potentially heritable traits under the genetic control of the parent plant (Thompson and Willson 1978, Morden-Moore and Willson 1982, Jordano 1982, Howe 1983, Willson and Melampy 1983, Manasse and Howe 1983, Herrera unpubl.). The few studies which have examined postdispersal seed distribution patterns have revealed that seed shadows of individual plants are often extremely irregular and unpredictable in space, depending to a large extent on distance and position of neighbouring fruiting plants, local topography, or singular features of surrounding vegetation (McAtee 1947, Howe and Primack 1975, Janzen et al. 1976, Janzen 1977a, 1978, Lieberman et al. 1979, Fleming and Heithaus 1981, Herrera and Jordano 1981, Herrera in press). This suggests that a plant's surroundings may be as important in determining its seed shadow as its set of dispersal-related heritable attributes.

Even thorough studies of seed shadows would often fail to provide satisfactory information on the prospects of dispersed seeds of surviving up to a reproductive age, except for some extreme cases of evident dispersal failure (e.g., Snow 1962c, Vázquez-Yanes et al. 1975, Bonaccorso et al. 1980). Favourable germination (and growth) microsites are largely unpredictable in time and space, and seeds often occupy them before their creation (see e.g. Cheke et al. 1979, Holthuijzen and Boerboom 1982). In other words, germination sites frequently do not exist when seeds are dispersed, thus neither the parent plant nor the investigator can "know" in advance where and when will they appear. Most fruiting plants therefore do not have a definite "target" for their seeds (Wheelwright and Orians 1982), hence it is difficult to envisage selective mechanisms enhancing actual dispersal success of genotypes through improvements in the quality of germination microsites reached by their seeds. Some target does exist in a few cases, and it is interesting to note that this spatial predictability of germination microsites has actually made possible the evolution of mechanisms enhancing seed deposition on appropriate places (e.g., Loranaceae, Docters van Leeuwen 1954; see also Janzen in press). (A mechanism available to plants to deal with unpredictability through selection would be the evolution of traits favouring widespread seed dispersal. It remains an open question, however, if this "careless blind-seeding" strategy is conceptually different from a purely random, "null hypo-

thesis-type" pattern of seed distribution independent of natural selection.)

A large environmental variance seems therefore to be invariably associated with the seed dispersal process, and the predictability of success of a given genotype is generally low (Hubbell 1980, Wheelwright and Orians 1982, Herrera 1982c, in press, Howe 1983). This inherent feature most likely sets consistently low upper limits to the selective pressures that dispersers are able to exert on plants (see Herrera in press).

4.3. Selective pressures from nondisperser organisms

Higher-order interactions are essential to understand many aspects of plant-disperser interactions (e.g., Janzen 1977b, 1982b, Howe 1979, Herrera 1982b, 1984a, 1984c, in press, Manzur and Courtney 1984). The notion of plant-disperser coevolution implicitly assumes that the combined selective pressures exerted on dispersal-related plant traits by nondisperser coexisting organisms are small relative to those exerted by dispersers alone (a further example of attribution to a single cause of an ecological relation subjected to a multiplicity of factors; Hilborn and Stearns 1982). Nevertheless, selective pressures on plant dispersal-related traits exerted by dispersers could hardly result in observable adaptations if they are offset or reversed by stronger pressures from nondisperser organisms influencing plant fitness. Proper tests of this critical assumption have been not conducted, but some evidence suggests that it may often be unwarranted. Seemingly anomalous patterns, unexpected from plant-disperser coevolution alone (e.g., toxic fruits) are explainable by considering the influence of coexisting fruit-bearing plants or pests attacking ripe fruits (Janzen 1977b, Herrera 1982b, 1984c). Nondisperser organisms may be decisive in selecting for some plant traits intimately associated with the seed dispersal process (e.g., seed size, fruit seediness; Janzen 1969, Herrera 1984b). Browsing ungulates and granivorous rodents are more important than avian seed dispersers themselves in determining the strength and nature of selective pressures exerted by dispersers on plants of *Rosa canina* in southern Spain (Herrera in press).

Counteracting selective pressures of dispersers and nondispersers on dispersal-related plant traits will ultimately result in a reduction of the net selective capacity of dispersers on plants, favouring the evolution of compromise situations and generating functional conflicts for plants (e.g., defence-attraction; Janzen 1977b, Herrera 1982b, 1984a). Except in cases where plants have solved them through conspicuous developmental adaptations (e.g., erect bird-dispersed fruits originating from pendulous hummingbird-pollinated flowers, as in *Macleannia glabra* (Ericaceae); Herrera pers. observ.), most functional conflicts will remain unnoticed, resulting in low adaptedness to each individual counteracting selective pressure.

5. Coevolutionary levels

Important constraints on plant-disperser coevolution have been mentioned earlier, yet both field studies and casual observations unequivocally suggest that fruit-producing plants actually manage to successfully disperse their seeds through the services of vertebrates, and many vertebrates are able to subsist on fruit food. The system therefore works, and some evolutionary explanation should be advanced to account for these observations.

"Coevolution" sensu stricto as used here, where species are the interacting units, is a particular case of "coevolution" sensu lato, where evolutionary interactions may be envisaged between taxonomic units of variable rank. The extremely varied usages of the concept in recent literature all may be conceptually unified into a broader coevolutionary framework just by considering the taxonomic rank of interacting units (species, families, orders, classes). Coevolutionary patterns affect plant and animal groups differing in taxonomic rank (e.g., *Ficus* and Agaonidae, Gramineae and ungulates; Ramírez 1974, 1978, Wiebes 1979, Stebbins 1981) as well as units of similar level (*Yucca* and *Tegeticula*, Pieridae and Cruciferae; Proctor and Yeo 1973, Feeny 1977). Assuming a reasonable degree of phylogenetic congruency in taxonomic hierarchies, I would expect the rank of coevolving units to tend to be higher the slower the progression of the elemental species-to-species coevolutionary process (i.e., the smaller the selective pressures involved in the interaction and/or the longer the generation times of counterparts, as argued earlier). Implications of this expanded notion of coevolution are beyond the scope of this contribution and will be discussed in detail elsewhere. My view of the situation of plants and vertebrate seed dispersers is presented below.

When average species duration of counterparts are markedly unequal and the system is an intrinsically slow-evolving one, the longer-duration taxa will face in the course of its existence a succession of counterpart species. Genotypes of long-duration, evolutionarily slowly-responsive taxa will thus be shaped by selective pressures exerted over extended time periods by many interacting species. Observed adaptations of a given plant for vertebrate dispersal will most likely be the ones consistently selected for by dominant, coincident pressures persistently exerted by the sequence of disperser species with which it has interacted in the past. Differential, species-specific pressures exerted by individual disperser species will often be offset by other species-specific disperser pressures of opposite sign. Expected adaptations for successful dispersal (at least in ancient woody taxa) should therefore be of a generalized, coarse nature, matching broad taxonomic groups of dispersers (whose species are and have been similar enough in some respects so as to make their pressures persistent and additive), rather than particular species.

This is consistent with the observed convergence of most animal-dispersed plants into a few generalized dispersal syndromes regardless of phylogenetic origin (van der Pijl 1972, Janson 1983, Knight and Siegfried 1983). The general lack of specificity in seed dispersal is also consistent with the notion that coevolution reflects adaptation to arrays of similar organisms rather than particular species (Howe and Smallwood 1982). On the other hand, long-duration plant taxa have most likely witnessed adaptive radiation events in their faster-evolving vertebrate counterparts. These plants must have represented a pre-existing, relatively invariant (with respect to faster-evolving organisms) environmental component for radiating frugivores. Accordingly, to the extent that traits (relevant to frugivory) of a rapidly-speciating vertebrate frugivorous group are determined by traits (relevant to seed dispersal) of their fruiting food plants, and these plant traits had in turn been selected for by the combined, additive pressures from evolutionary predecessors of the speciating frugivorous taxa, loose diffuse coevolution on a broad time scale between plant and vertebrate species groups can be adduced to explain plant-disperser mutualistic congruency often observed in nature. As noted earlier this congruency applies even to plant-vertebrate systems artificially assembled as a result of human action.

6. Concluding remarks

As in other fields of evolution and evolutionary ecology, studies of coevolution have been generally impregnated by the neo-darwinian views of evolutionary gradualism and concomitant concepts of fine-scale, permanent adaptation of organisms to their current environment (Stanley 1979). Most earlier formulations of plant-disperser coevolution, and subsequent field studies, have hypothesized patterns presumably derived from fine-tuned reciprocal adaptations, and those results consistent with coevolutionary interpretations have been emphasized. Nevertheless, fine adjustments are insufficient proof for coevolution between species and may simply be a fortuitous consequence of short-term adjustments by behaviourally very flexible vertebrates, or may be explained by alternative hypotheses. Without denying the existence in some cases of gradualistic coevolution (e.g., among fast-evolving annual plants and insect herbivores; Feeny 1977, Berenbaum 1983), there is evidence that plant-disperser mutualistic systems most often reflect situations of weak adaptation to current conditions or, at least, phenotypic stability of plants for long time periods over which it certainly has interacted with a very varied array of vertebrate seed dispersers. Some of the proximate causes of slow changes may be slow evolutionary rates of long-lived plants relative to their animal counterparts, weak selective pressures from dispersal agents, unpredictability in time and space of germination sites, extensive gene flow derived from obligate outcrossing (dioecy), and

slow rate of change compared to the recurrence of environmental perturbations (extinctions). All these factors have caused the adaptation of plants to current dispersers to be of a very coarse nature. I submit that the low species turnover of woody plant species has especially favored, however, a kind of diffuse coevolution in which high-turnover vertebrate species have become involved in a very long process in which the more persistent plants have acted as carriers of information through evolutionary time. Some recent bird families having many seed dispersers (e.g., Tyrannidae, Muscicapidae) radiated into an environment which already contained fruiting plants with traits evolved in response to predecessors of these birds, in turn selecting strongly for adaptations to frugivory in these groups (Herrera 1984d). This coarse coevolution, in which reciprocal selective pressures have operated between blocks of species (temporally non-overlapping in the case of vertebrates), may suffice to explain observed patterns of successful plant-disperser interaction in both natural and man-made habitats.

As stated by Howe and Smallwood (1982), "coevolution, where it occurs, reflects long-term interactions between taxonomic categories far wider than the species or genus". Their statement stems from an inductive approach based on the consideration of observed seed dispersal patterns. I have attempted here a deductive explanation based on the identification of some causes.

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