

CHAPTER 1

Vertebrate-dispersed plants: why they don't behave the way they should

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Abstract. Recent field studies of the interaction between vertebrate-dispersed plants and their seed vectors have often revealed patterns departing significantly from those predicted by earlier coevolutionary approaches. It is argued here that two families of assumptions implicit in these approaches account, in the case of plants at least, for their frequent predictive failure. These assumptions are that (1) the interaction between a plant and its vertebrate dispersal agents takes place in a world where they virtually are the only inhabitants; and (2) plant attributes relevant to the dispersal process effectively undergo measurable evolutionary change within a reasonable time frame in response to changing ecological conditions. It is shown that these two sets of assumptions are not generally supported by available evidence.

Introduction

A peculiarity of ecological studies on seed dispersal by frugivorous vertebrates is the relative abundance of straightforward, testable predictions which were generated during the earliest stages of recent evolutionary approaches (Snow, 1965, 1971; McKey, 1975; Howe and Estabrook, 1977; Howe, 1979). These predictions mostly related to how plants and their vertebrate seed dispersal agents 'should behave' in relation to each other, both on ecological and evolutionary time scales. They were based on a delicate, and at times weak, combina-

tion of plausible assumptions and observed facts, as necessarily happens with starting theories. Relatively few facts were available when these predictions were made, and assumptions behind these predictions were disproportionately abundant. Some of these assumptions were explicitly recognized, but others remained implicit and have begun to be made explicit only recently. In the last decade, rapidly increasing field studies of tropical and nontropical plant-seed disperser systems have often tested predictions (or, more generally, 'expectations') and, more importantly, have accumulated facts. These facts have often not supported expectations derived from earlier approaches or, at the very least, fit very poorly in the original theoretical framework (see Howe and Smallwood, 1982; Janzen, 1983b; Herrera, 1984c; 1985a; Howe, 1984, in press; and references therein).

These findings, along with some theoretical considerations, have led to the reassessment of earlier models and their coevolutionary postulates (Wheelwright and Orians, 1982; Janzen, 1983a; Howe, 1984; Herrera, 1985a). To date, however, no detailed, critical examination has been made of the set of assumptions that lies behind the central tenet of all recent ecological work on plant-seed disperser evolutionary interactions, viz. that some mutual adaptations (*i.e.*, evolved phenotypical adjustments) are to be expected in interacting plant and disperser species. The objective of this paper is to identify and critically assess some of these central assumptions and to examine in detail the one

that is probably most decisive in accounting for the frequent failure to find clear adaptations of plants to their current dispersers – the actual ability of fleshy-fruited plants to evolve certain adaptations to their current dispersal agents. (I am concerned here with plant adaptations alone; the evolution of seed dispersal agents will not be considered.) Explicit consideration of the main ‘families’ of assumptions may help broaden our ecological and evolutionary perspectives on plant seed dispersal by vertebrates and may also highlight some obvious limitations of prevailing approaches in evolutionary ecology, particularly when long-lived organisms (both as individuals and species) are involved.

The ecological vacuum

Under this heading may be placed all versions of the implicit assumption that the basic interaction between a plant and its vertebrate dispersal agents (production of the fruit by the plant, ingestion by the dispersers) takes place in a world in which they virtually are the only inhabitants. Assumptions belonging to this family have plagued both theoretical and field studies, although less frequently so in recent investigations (*e.g.*, Morden-Moore and Willson, 1982; Herrera, 1982a; Willson, 1983; Howe, 1979; Herrera, 1984d; Manzur and Courtney, 1984; Manasse and Howe, 1983). A variety of coexisting organisms are relevant to the plant-disperser interaction through its being relevant to the plant. These may be classed into two major categories, depending on their potential ability to promote adaptive changes of dispersal-related traits: (1) potential selective agents on plant traits related to the dispersal process and thus to the interaction of plants and dispersers. Prominent among these are nonmutualistic frugivores, *i.e.*, organisms taking advantage of the food resource in fruits and seeds but that do not perform seed dispersal as a consequence of their frugivory. (2) Components of the environment that, in spite of influencing inter-individual differences in dispersal success, could hardly exert significant selective pressures on dispersal-related traits. Coexisting fruiting plants may be included here as part of what may be termed ‘the fruiting environment’.

Selective agents: nonmutualistic frugivores

Among nonmutualistic frugivores (those damaging seeds and/or fruits), birds and mammals have most frequently received attention, and their importance has often been recognized (*e.g.*, Janzen, 1981; 1982a, b; Howe, 1977; 1980; Bonaccorso *et al.*, 1980; Denslow and Moermond, 1982; de Steven and Putz, 1984). Invertebrates and pathogens, in contrast, have infrequently been considered in seed dispersal studies, yet they most likely have had an important influence on dispersal-related plant traits. I presume they have been important in the past because: (1) they are important in present-day plant communities, as show later; (2) phytophagous insects and pathogens were present in the ecological scenario well before the first frugivorous birds and mammals evolved or, at any rate, their diversification predated that of most present-day frugivorous vertebrate groups (Scott and Taylor, 1983; Strong *et al.*, 1984; Southwood, 1985); and (3) certain features of fruits (*e.g.*, plant defensive compounds in some ripe fruits; Janzen, 1977; Herrera, 1982a) are suggestive of the past influence of organisms other than mutualistic seed dispersers. The *potential* for an interaction between fleshy fruits and damaging invertebrates and pathogens is older than any observed interaction with current legitimate dispersers, since the fleshy fruit habit of gymnosperms and early angiosperms certainly antedates the main radiation events of present-day major dispersal agents (birds and mammals).

Few studies have directly addressed the question of the actual impact of nondisperser frugivores, particularly insects and pathogens, on the reproductive performance of fleshy-fruited species. Available data frequently reveal an important influence, at least if one considers the proportion of damaged fruits (Table 1). In some cases, up to 60% of the fruits in individual crops may be destroyed or badly damaged. In species with appropriate data, extreme inter-individual variation exists, which provides the raw material for selection whenever fruit damage rates depend to some extent on plant heritable attribute(s). The critical point here, however, is that (in addition to the obvious impairment

in reproductive performance) the destruction of fruits by invertebrates is also evolutionarily relevant to the seed dispersal process because fruit selection by frugivorous insects is generally dependent on plant or fruit attributes that also influence disperser preferences or behavior:

(a) The volume of seeds in individual fruits is frequently considered in general discussions on plant-disperser interactions (*e.g.*, Snow, 1971, 1981; McKey, 1975; Herrera, 1981a) and has been shown to affect fruit selection by some avian dispersers (Howe and Vande Kerckhove, 1980, 1981; Herrera, 1981b). In *Berberis hispanica*, a southern Spanish bird-dispersed shrub, fruit selection by ovipositing flies results in differential predation on fruits differing in seed volume (Herrera, 1984a).

(b) Individual fruit size has been often considered a trait relevant to the dispersal process (Snow, 1971; Howe and Estabrook, 1977) and has been found to influence intra- and interspecific fruit selection by seed dispersers (Pratt, 1983; Herrera, 1984c, e; Jordano, 1984; Wheelwright, 1985). The influence of fruit size on female oviposition behavior, on the other hand, is well known for several species of insect frugivores (Prokopy, 1969, 1977; Prokopy and Bush, 1973; Prokopy and Haniotakis, 1976; Nakagawa *et al.*, 1978; Dreyer, 1984).

(c) Chemical composition of fruits, with regard to both nutrients and secondary compounds, has been considered to be a key element in the evolution of plant-disperser interactions (Snow, 1971; McKey, 1975; Howe and Estabrook, 1977; Stiles,

Table 1. Some estimates of the incidence of invertebrate damage (on seeds and/or pulp) on fruits from some bird-dispersed plants. Species for which damage was not recorded are omitted, hence these data can only be taken as an indication of levels of damage when it actually occurs.

	Location	Damaging agent	Percent fruits damaged	Reference
<i>Pistacia lentiscus</i> (Anacardiaceae)	Spain	Cynipid wasp	5.3–9.4 (4470) ^b	Jordano (1984)
<i>Olea europaea</i> var. <i>sylvestris</i> (Oleaceae)	Spain	<i>Dacus oleae</i> (Tephritidae)	0–48.6 (10) ^a	Jordano (1984)
	Spain	<i>Prays oleae</i> (Yponomeutidae)	0.4–36.3 (9) ^a	Jordano (1984)
<i>Osyris quadripartita</i> (Santalaceae)	Spain	Several	4.5 (967) ^b	Herrera (1985b)
<i>Berberis hispanica</i> (Berberidaceae)	Spain	Tephritid fly	45.1 (466) ^b	Herrera (1984a)
<i>Crataegus monogyna</i> (Rosaceae)	England	<i>Blastodacna hellerella</i> (Momphidae)	9.7–62.0 (20) ^a	Manzur & Courtney (1984)
<i>Actaea rubra</i> (Ranunculaceae)	U.S.A.	<i>Eupithecia cimifugata</i> (Geometridae)	20–49 (1053) ^b	Willson (1983)
<i>Prunus serotina</i> (Rosaceae)	U.S.A.	Several	19.1 (2665) ^b	Morden-Moore & Willson (1982)
<i>Lantana</i> spp. (Verbenaceae)	Brazil	<i>Ophiomyia lantanae</i> (Agromyzidae)	1.5 (32411) ^b	Winder (1982)
<i>Gaiadendron punctatum</i> (Loranthaceae)	Costa Rica	Unidentified	31.8 (22) ^b	Herrera & Jordano (unpubl.)
<i>Hesperomeles obovata</i> (Rosaceae)	Costa Rica	Unidentified	20.0 (20) ^b	Herrera & Jordano (unpubl.)
<i>Miconia</i> sp. (Melastomataceae)	Costa Rica	Unidentified	10.0 (20) ^b	Herrera & Jordano (unpubl.)
<i>Hirtella</i> sp. (Rosaceae)	Costa Rica	Unidentified	53.3 (30) ^b	Herrera & Jordano (unpubl.)

^a Estimates for individual crops, number of crops in parentheses.

^b Estimates for pooled fruit samples from several individual plants, number of fruits in parentheses.

1980; Herrera, 1982a), and supporting evidence exists (e.g., Kear, 1968; Glander, 1979, 1982; Herrera, 1982a, b; Sorensen, 1983). Although nutritional requirements of insect frugivores are poorly known (Bateman, 1972), some evidence indicates that variation in nutritional composition (Levinson and Levinson, 1984) and secondary compounds (Greany *et al.*, 1983) of fruits may result in differential infestation by insects.

(d) Fruit color and shape, which are important elements in the plant-disperser interaction (Snodderly, 1979; Willson and Thompson, 1982; van der Pijl, 1982; Willson and Melampy, 1983; Janson, 1983), are also strongly influential in host selection by some insect frugivores (Prokopy, 1969; Prokopy and Economopoulos, 1976; Prokopy and Haniotakis, 1976; Morden-Moore and Willson, 1982; Hill and Hooper, 1984; but see Willson, 1983). Bicolored fruit displays, which have been shown experimentally to increase fruit consumption by birds (Morden-Moore and Willson, 1982; Willson and Melampy, 1983), also influence fruit predation rates by invertebrates (Morden-Moore and Willson, 1982).

(e) Crop size, in addition to playing an important role in seed disperser attraction (e.g., Howe and Estabrook, 1977; Howe, 1977), is also probably very important in host selection by some insect frugivores (Roitberg *et al.*, 1982; Dreyer, 1984; Jordano, 1984; Courtney and Manzur, in press). For wild olive trees (*Olea europaea* var. *sylvestris*) in southern Spain, a positive linear relationship exists between log crop size and proportion of fruits infested by *Dacus oleae* (Tephritidae) and *Prays oleae* (Yponomeutidae) (Jordano, unpubl. data).

While information available on factors influencing fruit choice by frugivorous invertebrates in natural conditions is still incomplete, this information shows that exactly the same plant or fruit attributes (seediness, size, and color of fruit; pulp constituents; crop size) may play a role in the interaction between plants and their seed dispersers and fruit-damaging agents. The evolutionary interpretation of plant fruiting features based solely in reference to their dispersal agents is, therefore, unwarranted unless there are reasons to believe that the combined selective pressures exerted on these features

by non-disperser organisms are small relative to those exerted by dispersers alone. A satisfactory assessment of the comparative consequences for plants of the activity of disperser and nondisperser frugivores has not been conducted so far. Some preliminary evidence, however, suggests that the potential selective effects of nonmutualists on dispersal-related attributes is far from negligible, as illustrated by the following example (see also Herrera, 1984d). In some mediterranean habitats of southern Spain, the local fruiting phenology of *Asparagus aphyllus* (Liliaceae) is directly determined by the action of larvae of the moth *Metachrostis dardouini* (Noctuidae), a fruit predator. Plants flower in July, but virtually all the resulting developing fruits are destroyed well before maturation by caterpillars feeding on pulp and seeds. A second flowering episode generally follows in late August-early September, and larvae of the same moth species again destroy the resulting fruit crop. Finally, a third flowering episode, occurring in October, leads to a successful fruit crop in November-December. In habitats where the insect pest is apparently absent, ripe fruits resulting from a single flowering period in early summer are produced in September. Regional variation in fruiting phenology of *A. aphyllus* is therefore associated with variation in pest abundance (or host plant selection) (C.M. Herrera, unpubl. observations between 1978-1984).

Non-selective factors: the fruiting environment

As Howe (1983, p. 219) states, 'to determine likely sources of natural selection, one must evaluate sources of variance in dispersal, including those under the control of the parent and those over which the parent can exert no influence.' In the first category may be placed plant attributes such as phenology, crop size, and fruit composition, that were already in the focus of the earliest evolutionary approaches. The second category includes the influence of other fruiting plants, growing site-specific attributes, and relation to salient topographical features. An implicit assumption of all evolutionary approaches to vertebrate seed dispersal is that dispersal-related factors affecting plant fitness

have an important heritable component or, in other words, that the effect of environmental variance, as opposed to genetically determined variance, is relatively unimportant (see Howe, 1984; Herrera, 1985a).

'Non-selective' agents have begun to be considered in field studies quite recently. As shown below, these studies serve to demonstrate the important influence on variation in dispersal success of factors over which the parent plant can exert no or very little influence. I will be concerned here only with the influence of coexisting fruiting plants of the same or different species, which I collectively call 'the fruiting environment.' Its significance for dispersal may be assessed by considering its influence on differential fruit removal rates or seed shadows, or both.

The spatial distribution of conspecifics (*e.g.*, isolated *vs.* clumped plants) often affects the rate of removal of ripe fruits by seed dispersal agents, as shown for the bird-dispersed *Lindera benzoin* and *Prunus serotina* by Moore and Willson (1982) and Morden-Moore and Willson (1982) (see also Thompson and Willson, 1978; Willson and Melampy, 1983). In *Virola surinamensis*, which is also bird-dispersed, conspecific fruit produced within the immediate vicinity of individual trees significantly depressed individual dispersal in two out of three years. In this species, neither crop size, kurtosis of individual fruiting schedules, nor nutritional composition of arils (factors all belonging in the 'parent-controlled' category) influence the proportion of fruits taken from individual trees (Howe, 1983; Manasse and Howe, 1983). The relative position of neighboring conspecifics may also substantially affect seed shadows of individual plants, as found by Herrera and Jordano (1981) in a group of fruiting *Prunus mahaleb* trees. Interference from neighboring plants sets limits to the direction of origin and destination of the avian dispersers visiting a given tree. The directional pattern of the departing seed flow (which may eventually affect the success of dispersed seeds) is therefore strongly affected by purely topographical relations to conspecifics (see also Jordano (1982) for similar results in *Rubus ulmifolius*). Influence of conspecific crop locations on the seed shadows

of plants may also be inferred from studies on the foraging ecology of neotropical frugivorous bats (Heithaus and Fleming, 1978; Morrison, 1978; Fleming and Heithaus, 1981) and primates (Estrada and Coates-Estrada, 1984; Robinson, 1984).

Interference between conspecifics is an obvious consequence of their sharing of dispersal agents. Sets of locally coexisting plant species also share dispersal agents, both in terms of species and individuals. Many frugivorous vertebrates tend to rely on a variety of fruit species for food over periods of weeks or months (*e.g.*, Snow, 1970; Heithaus *et al.*, 1975; Bonaccorso, 1979; Lieberman *et al.*, 1979; Jordano and Herrera, 1981; Wheelwright, 1983), but foraging individuals often also ingest several fruit species over much shorter time periods (*e.g.*, Fleming and Heithaus, 1981; Stocker and Irvine, 1983; Robinson, 1984; Herrera, 1984c; Fleming, this volume). These observations indicate that the spatial location of simultaneously fruiting individuals of different species may effectively be important in determining seed shadows and disperser visitation rates of individual plants. Nevertheless, these effects have been examined so far in some detail only in a single instance (Herrera, 1984d). In some southern Spanish habitats, *Rosa canina* and *Crataegus monogyna* share the same birds for seed dispersal, which preferentially consume *Crataegus* fruits, although regularly ingesting some fruits of *Rosa*. Where the two species coexist locally, the seed shadows of *Rosa* plants are extremely heterogeneous, and a high concentration of seeds accumulates under *Crataegus* bushes owing to the heavy use of these highly preferred food plants by frugivores. *Rosa* plants, furthermore, may grow either as isolated individuals or as climbing bushes associated with *Crataegus*. Individuals growing alone have much higher relative fruit removal rates than those climbing on *Crataegus*. Among populations, the greatest relative removal rates occur where *Rosa* does not coexist with *Crataegus*. These results demonstrate that the spatial relationships of heterospecific fruiting plants may actually influence both seed shadows and fruit removal rates, although much further work along these lines is still needed to evaluate the generality of the phenomenon and its genetic and demographic implications.

The implications of filling the vacuum

Information available on the mechanisms involved in the interaction between fruiting plants and non-mutualistic invertebrate frugivores and the fruiting environment is still remarkably scarce. Virtually nothing is known about their interaction with fruit-damaging pathogens. Furthermore, other components of the interaction between fruits and the nondisperser subset of the environment still remain unexplored; for example, the potential for highly complex evolutionary interactions between fruits and similarly colored, aposematic frugivorous insects (Herrera, 1985c), or between fruits and the parasitoids of insect frugivores (Glas and Vet, 1983). At any rate, however, even the relatively limited information discussed in the preceding sections indicates that 'filling' the conceptual ecological vacuum initially perceived around the basic fruit-disperser interaction has profound implications for our understanding of observed patterns, and particularly the rather generalized departure from coevolutionary expectations. In an evolutionary context, the overwhelming effect of non-disperser organisms will be a significant depression of the net selective capacity of dispersers on dispersal-related plant traits and, therefore, the degree of adaptedness of plants to their vertebrate dispersal agents. The mechanisms involved, however, differ for the two categories of factors considered above. Counteracting pressures of dispersers and non-dispersers on dispersal-related plant traits will tend to favor the evolution of compromise situations as a consequence of the functional conflicts they generate (e.g., defense-attraction; Janzen, 1977; Herrera, 1982a, 1984b). In contrast, factors over which the parent plant can exert no (direct) influence (such as the spatial configuration of the contiguous fruiting environment), by increasing non-genetically determined dispersal variance, will decrease the probability and/or the rate of evolutionary change in dispersal attributes.

Evolutionary plasticity of dispersal-related traits

An additional central assumption of evolutionary

formulations of seed dispersal by vertebrates is that plant attributes relevant to the dispersal process effectively undergo measurable evolutionary change within a reasonable temporal frame in response to changing ecological conditions. In fact, this idea is deeply rooted in the very foundations of contemporary evolutionary ecology, as discussed later. Rather strikingly, no study has critically evaluated any direct evidence bearing on this assumption, perhaps because of its broad acceptance in other fields of evolutionary ecology that initially sparked the interest on coevolution (e.g., plant-herbivore interactions; Ehrlich and Raven, 1965). The actual ability of dispersal traits to experience substantial evolutionary modification in response to dispersal agents has been questioned recently, mostly on the basis of indirect evidence or inductive reasoning (Howe, 1984; Herrera, 1985a). I attempt here to assess the validity of the assumption by examining directly relevant evidence. My treatment will be far from exhaustive because I have had to rely on anecdotal or incomplete information originally collected for other purposes and which was gathered from a variety of heterogeneous literature sources. Nevertheless, the following information will serve to illustrate that the fruit or fruiting traits of some plants (of the type generally considered to experience evolutionary change in response to selection by dispersers) often seem to have remained virtually unaltered during extremely long periods, even though these plants have most likely faced contrasting ecological, and hence dispersal conditions, in that time.

The fossil record

Information available on fossil fruits of vertebrate-dispersed plants is relatively scarce and, because of its rather coarse nature, is of limited value for comparisons with extant forms. Even these imperfect data indicate, however, that gross fruit features may experience negligible changes over very long periods. The fruits of living *Taxus* species, for example, seem essentially identical to those of *Palaeotaxus*, an Upper Triassic close relative living about 175 Myr B.P. (Emberger, 1968). The best comparative studies published to date have been

those concerned with the fruits and seeds of Magnoliaceae, Vitaceae, and Nyssaceae from the Oligocene Brandon Lignite of west-central Vermont, USA (Eyde, 1963; Eyde and Barghoorn, 1963; Tiffney and Barghoorn, 1976; Tiffney, 1977). These studies clearly reveal that, although fossil and modern forms differ in some detailed aspects (e.g., thickness of seed wall), the basic morphological characteristics of the fruits of modern species were present at their initial appearance; the fossils do not suggest any particular evolutionary trends.

Geographical disjunction and constancy in dispersal traits

A comparison of the fruiting traits of closely related species currently living in contrasting ecologi-

Table 2. Characteristics of the ripe fruits of *Laurus azorica* (an endemic from Azores and Canary Islands) and *Laurus nobilis* (from the Mediterranean Basin).

	<i>azorica</i>	<i>nobilis</i>
Fruit ^a		
Length (mm)	15.1 ± 0.6	14.7 ± 0.5
Diameter (mm)	11.7 ± 1.1	12.2 ± 0.5
Fresh weight (g)	1.27 ± 0.23	1.26 ± 0.12
Seed dry weight (g)	0.608 ± 0.083	0.698 ± 0.100
Pulp dry weight (g)	0.166 ± 0.056	0.283 ± 0.029
Gross pulp composition (percent dry weight)		
Ash	2.37	2.61
Lipids	59.37	54.34
Protein	5.38	6.22
Fiber	11.29	8.85
Nonstructural carbohydrates	21.59	27.98
Mineral fraction of the pulp		
Macroelements (mg/g)		
K	8.5	10.0
Na	0.15	0.20
Ca	0.85	0.35
Mg	0.15	0.15
P	0.56	0.46
Trace elements (ppm)		
Fe	42	30
Mn	0.6	0.6
Zn	7	2
Cu	2	1

^a Mean ± s.d.; N = 20 fruits per species.

cal settings and for which there are reasons to expect that they diverged very long ago may provide insights into the evolutionary plasticity of these traits. Constancy in space of fruiting attributes will warn us against uncritical acceptance of the assumption of broad evolutionary plasticity. This constancy would warrant the consideration of these traits as phylogenetically constrained characters. Appropriate information is scarce and of variable quality, but the examples below point to constancy rather than to plasticity.

Two species are recognized in the genus *Laurus* (Lauraceae), *L. azorica* from the Azores and Canary Islands, and *L. nobilis* from the Mediterranean Basin. They differ in morphological features and chromosome numbers, and presumably were derived from a common ancestor, the extinct *Laurus abchasica*, which was widespread in Tertiary floras from southern and central Europe throughout west-central Asia (Ferguson, 1974). *L. azorica* apparently has closer affinities with the ancestral form than *L. nobilis*. The information available on the phytogeography of the Canary Islands (Ciferri, 1962; Bramwell, 1972, 1976) indicates that the divergence between the two extant species most likely started around the Pliocene or before (≥ 7 Myr B.P.). They currently inhabit contrasting environments characterized by different climatic regimes (laureaceous-dominated cloud forest for *azorica*; summer-drought mediterranean-climate forest for *nobilis*; Boyko, 1947; Bramwell and Bramwell, 1983), and their fruits are eaten by very different arrays of frugivorous birds which presumably apply different selective pressures on fruit traits (Barquín and de la Torre, 1975; Herrera, unpubl. data). The fruits of the two species, however, are virtually identical in mensural characters (Table 2), color, and smell (to the human nose). Furthermore, the chemical composition of the pulp is also remarkably similar, even in the finest details of the mineral fraction (Table 2).

The genus *Pistacia* (Anacardiaceae) comprises 11 species of shrubs or small trees. It has a broadly disjunct world-wide distribution, with five more-or-less isolated centers in Asia, north-central America, and the Mediterranean Basin (Zohary, 1952; the following account is also based on this

source, unless otherwise stated). Four distinct sections are recognized in the genus on the basis of morphological characters. The taxa in each section are closely linked with one another and abrupt discontinuity exists between sections. Fossil evidence indicates that the genus probably originated during the Cretaceous, and that some sectional differentiation was already apparent in the Oligocene. The divergence of species in different sections thus took place about 35 Myr ago. Consideration of the closely allied sections *Lentiscella* and *Eulentiscus*, those containing the most geographically distant extant species, is particularly illustrative. The former comprises *P. mexicana* and *P. texana*, which are confined to Mexico and Texas. *P. mexicana*, the most widespread, inhabits tropical dry deciduous forests characterized by species of *Alvaradoa*, *Ceiba*, *Cochlospermum*, *Bursera* and *Pithecellobium* (Rzedowski, 1966, 1978). Section *Eulentiscus* contains *P. lentiscus* (Canary Islands and Mediterranean Basin) and *P. weinmannifolia* (China, Burma, Tibet, Malaya), two species whose divergence started as far back as the early Tertiary. *P. lentiscus* inhabits mediterranean scrublands and forests at low to middle elevations. *P. weinmannifolia* occupies temperate to subtropical rain forests at high elevations (1000–3000 m). The ripe fruits of *mexicana*, *lentiscus*, and *weinmannifolia* are identical in every descriptive fruit attribute for which I was able to find comparative information: shape (globular compressed, slightly broader than long), bilateral symmetry (obliquely apiculate), size (4–8 mm wide in every species), color (black), pulp texture (fleshy-juicy), and the characteristically thin coat of the single, lenticular seed. Furthermore, unripe fruits are red, turning black at maturity, thus presumably producing a bicolored display in all species of the type I am familiar with in *P. lentiscus*.

The genus *Ilex* (Aquifoliaceae) provides further examples of strong interspecific constancy in some fruiting attributes. According to Hu (1949, p. 255), 'the fruiting branches of *Ilex tsoii* from east, central and south China, resemble so closely those of *Ilex montana* of eastern North America that only a specialist could distinguish them. The same is true of *Ilex aculeolata* of China and *Ilex decidua* of

eastern North America; *Ilex asprella* of south China, Taiwan and Luzon, and *Ilex longipes* of eastern North America; *Ilex yunnanensis* of China and *Ilex glabra*; and *Ilex serrata* var. *sieboldi* of China and Japan and *Ilex verticillata* of eastern North America. In general, however, there is a vast difference between the Chinese and the American *Ilex*. In China more than ninety per cent of the species are evergreen, with comparatively few deciduous species, while in eastern North America most of the species are deciduous'.

Constancy is also revealed by the characteristic sequence of colors (green-red-black) exhibited by the fruits of numerous species of *Smilax* vines (Smilacaceae), regardless of whether they inhabit Mediterranean Basin scrublands, Central American lowland rainforest, or southeastern Asian monsoon rainforest (Koyama, 1975, Croat, 1978; C.M. Herrera unpubl. data).

Many further examples could be addressed similarly illustrating conspicuous similarity in fruit attributes of closely allied species living in (geographically and ecologically) distant conditions (e.g., in the genera *Ocotea*, *Ficus*, *Paeonia*, *Prunus*), but space limitations preclude a more detailed treatment. Conversely, there are also examples of dissimilarity in some fruit traits (e.g., color) between allied species (e.g., in the genera *Cornus*, *Rosa*, *Crataegus*) (See Charles-Dominique, this volume). These counterexamples illustrate that substantial heterogeneity exists among taxa in the degree and nature of fruit variation following species radiation. We know next to nothing about the proportion of 'plastic' and 'non-plastic' groups, but the very existence of a gradient of evolutionary 'responsiveness' in fruit traits indicates that the assumption of evolutionary plasticity does not apply universally.

Phylogenetic correlates of interspecific variation

The assumption of evolutionary plasticity in fruiting traits in response to selection by dispersers would be seriously challenged in those instances where interspecific variation in relevant fruit characteristics bears a closer relationship to phylogeny than to ecology. I will disregard those fea-

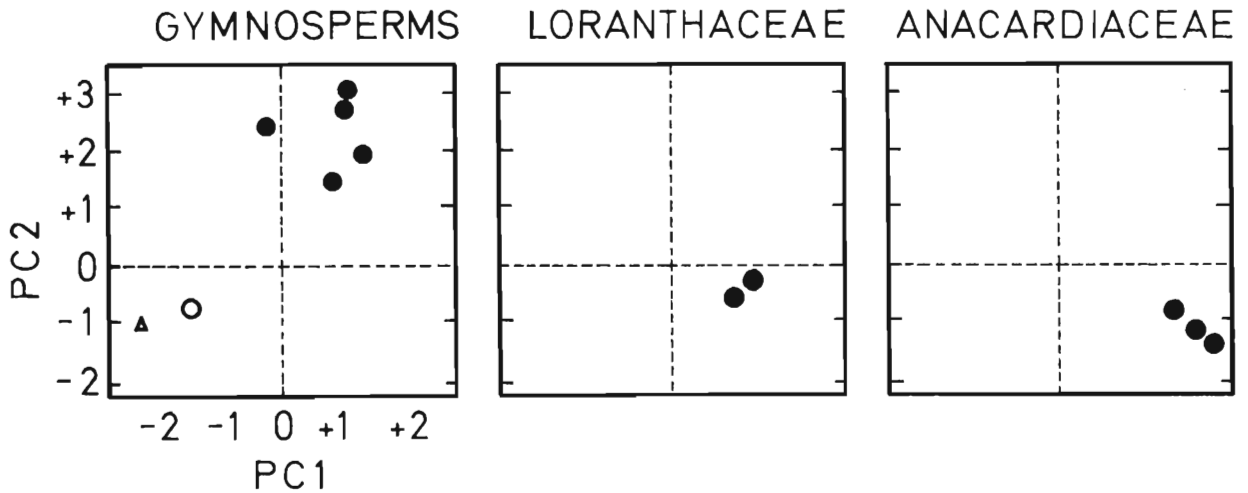


Fig. 1. Position on a principal components plane of Iberian species of fleshy-fruit-producing gymnosperms, Loranthaceae and Anacardiaceae. PC1 and PC2 are the first two principal components resulting from the correlation matrix for water and organic constituents of fruit pulp in a 111-species sample of vertebrate-dispersed plants from the Iberian Peninsula (Herrera, unpubl. data; see text for further details). Gymnosperms: filled dots, *Juniperus* spp. (*communis*, *oxycedrus*, *phoenicea*, *sabina*, *thurifera*); open dot, *Taxus baccata*; triangle, *Ephedra fragilis*. Loranthaceae, *Viscum album* and *V. cruciatum*. Anacardiaceae, *Pistacia lentiscus*, *P. terebinthus* and *Rhus coriaria*.

tures which are obviously dependent on tightly integrated developmental programs and which should be expected to be relatively resistant to evolutionary modification (e.g., endocarp texture; number of seeds in fruits from single- or few-ovule flowers). Instead, I will consider a set of traits presumably responsive to selection by dispersers, namely chemical composition of fruit pulp.

In a study of the characteristics of 111 vertebrate-dispersed species from the Iberian Peninsula (C.M. Herrera, unpubl. data), I was able to identify the main trends of interspecific variation in the gross chemical composition of fruit pulp by means of principal components analysis. The position of individual species may then be plotted in the plane defined by the two first components (accounting for 72% of the total variance). To illustrate the case of ecologically-independent, strongly phylogenetically-determined nutritional configuration of fruit pulp, I will consider here the position in this plane of gymnosperms, Anacardiaceae, and Loranthaceae (Fig. 1). These groups include the most extreme species in terms of pulp composition.

The three anacardiaceous species (*Pistacia lentiscus*, *P. terebinthus*, *Rhus coriaria*) occupy contrasting habitats (lowland mediterranean scrub,

montane mediterranean forest, and disturbed places and early successional patches, respectively) and differ greatly in habit (evergreen shrub, deciduous tree, and deciduous shrub) and seed dispersal agents (C.M. Herrera, unpubl. data). Despite these differences, they form a dense cluster in the principal components plane, revealing close similarities in the chemical composition of fruit pulp. Similarly, despite the very broad variation in ecological settings (from coastal forests to high elevation dwarf scrub) and dispersal agents (mammals, various-sized birds) of *Juniperus* species, their fruits are very similar in nutritional configuration. *Taxus* and *Ephedra* (also gymnosperms as *Juniperus*), which live in mesophytic forests and arid open habitats, respectively, and have contrasting seed disperser assemblages (C.M. Herrera, unpubl. data), are more similar to each other than to any other species of the Iberian fruit-producing flora. The two mistletoe species (*Viscum album*, *V. cruciatum*) have nonoverlapping distributions and ecological requirements. In southern Spain, *album* occurs only in montane pine forests at high elevations, and their seeds are mostly dispersed by the 100 g *Turdus viscivorus*. *V. cruciatum*, in contrast, is a species of lowland evergreen mediterranean

forest, where its seeds are dispersed by the l8g *Sylvia atricapilla*. Despite these ecological differences, fruits of these species are nutritionally nearly identical (Fig. 1).

Further examples could be drawn from other fruit-producing floras similarly suggesting close phylogenetic correlates of fruit nutritional configuration. Compare, *e.g.*, species of Lauraceae in the Neotropics, Australasia and the Holarctic Region (Crome, 1975, pers. comm.; Stiles and White, 1982; Wheelwright *et al.*, 1984; and Table 2), or *Ficus* in the Neotropics, Africa and Australasia (Crome, 1975; Jordano, 1983; Thomas, 1984).

Evolutionary ecology and coevolutionary approaches

The development of coevolutionary approaches has been perhaps one of the most elaborate intellectual constructs generated by the application of evolutionary thinking to ecological problems, *i.e.*, the discipline we usually know as 'evolutionary ecology' (Orians, 1962; Lack, 1965; Harper, 1967; Futuyma and Slatkin, 1983). Research in this field has generally been characterized by the acceptance by ecologists of the evolutionary views (and dogmas) prevailing at the time. For this reason, I believe that coevolutionary models have usually been predicated on the assumption that adaptations of species closely track environmental changes and that evolutionary changes are gradual. (Rather ironically, however, the seminal paper by Ehrlich and Raven, 1965, was not based on these assumptions, as emphasized by Stanley, 1979). Although this view of evolution has been recently challenged (*e.g.*, Stanley, 1979, 1982; Gould and Lewontin, 1979; Gould, 1980, 1982; Stebbins and Ayala, 1981; Eldredge, 1982), this shift in evolutionary views has not yet had much influence on ecological studies. Without entering the contemporary 'macroevolutionary battleground,' I wish to argue here that, on the basis of the evidence presented above (also see Howe, 1984; Herrera, 1985a) and insofar as plant adaptations are concerned, there exists little or no basis for assuming generally gradualistic change and environmental tracking in evolutionary for-

mulations of plant-vertebrate seed disperser interactions. The evolutionary stability that seems to characterize many fruiting traits in many taxa clearly supports this view. This sustained phenotypic stability is not a peculiarity of dispersal adaptations, as it has been long known for a variety of characters in many plant taxa (Stebbins, 1947, 1949, 1982; Zohary, 1952; Stebbins and Day, 1967; Prager *et al.*, 1976; Levin and Wilson, 1976; Goldblatt, 1980). The data reported above indicate that evolutionary rates of some important (in relation to dispersers) traits have often been even slower than speciation rates (see also Herrera, 1985a, where this is discussed in relation to evolutionary rates of dispersal agents). The causes may be the absence of strong and/or consistent selective pressures, the absence of genetical variability, developmental constraints, or some combination of these, as I have discussed in greater detail elsewhere (Herrera, 1985a; also see Howe, 1984). Little is known about the genetic variability available to natural selection in wild fruiting plants, but if one judges from what is known for cultivated species, substantial amounts are to be expected. On the other hand, the process of 'filling' the conceptual ecological vacuum around the plant-disperser interaction has made apparent serious reasons to expect low or inconsistent selective pressures, as noted earlier.

In conclusion, therefore, vertebrate-dispersed plants do not generally behave in the way evolutionary ecologists had initially predicted because 'conventional' evolutionary assumptions underlying coevolutionary models (gradualism, environmental tracking) do not seem to apply universally to dispersal-related traits. Low or inconsistent selection pressures probably contribute decisively to lowering evolutionary rates. But in addition, the peculiar genetic constitution of plants (in comparison to animals), particularly the genetic basis of character divergence (which includes the prevalence of discontinuous character states governed by a single or few genes; Hilu, 1983; Gottlieb, 1984), may also play an important role. If this is true, it follows that coevolutionary formulations of plant-disperser interactions are not unique in requiring profound revision to account for the substantial differences between plants and animals in the ge-

netic basis of phenotypical constitution and also, presumably, evolutionary patterns (Gottlieb, 1984; Herrera, 1985a).

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