

Fleshy fruits – origins, niche shifts, and diversification

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We examined shifts in fruit type, fleshy vs non-fleshy, in relation to habitat-related niche shifts, species richness, and historical distribution, in 50 phylogenetically independent plant lineages. Each lineage consisted of a sister-group pair of fleshy vs non-fleshy taxa and their outgroup. Niche shifts were assessed based on plant community characteristics. Two niche dimensions assumed to reflect community dynamics were derived: spatial predictability of disturbances and canopy closure. Phylogenetically independent origins of fleshy fruit types (1) were correlated with changes to habitats characterized by more shaded and spatially more unpredictable disturbances, (2) had an opposite effect on species richness in woody and herbaceous clades, enhancing species richness in woody clades, and (3) were continuously distributed over a period covering the last 70 million years. These results support the hypothesis that fleshy fruit evolution is driven by vegetation dynamics, and suggest that the strength of frugivore mediated selection on fleshy fruits increases when recruitment sites are spatially unpredictable and/or characterized by low light conditions.

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Dispersal is a crucial process for plants at several scales (Davis 1981, Ehrlén and Eriksson 2000, Harms et al. 2000) and angiosperms feature a wide range of dispersal mechanisms (Ridley 1930, van der Pijl 1972, Spjut 1994). The large variation in seed and fruit types found today did not evolve along with the first phases of angiosperm diversification during the Cretaceous. Instead, there was a conspicuous increase in seed and fruit sizes in the early Tertiary, reaching the levels of present day floras (Tiffney 1984, Wing and Boucher 1998, Eriksson et al. 2000a, b). This increase also encompassed fleshy fruit types adapted for animal dispersal, and the proportion of fleshy fruited taxa reached 70% in some early Tertiary floras (Eriksson et al. 2000a). Thus, important changes in the adaptive landscape for angiosperm fruits seems to have taken place during the early Tertiary.

Two different, though not mutually exclusive, hypotheses have been proposed for the early Tertiary increase of fleshy fruited plants. In both hypotheses, the adaptive radiation of mammals and birds, the development of

dense, shady, multistratal forests, and the evolution of larger seeds are interactive parts. Tiffney (1984) suggested that radiation of frugivores, i.e. mammals and birds (Ericson et al. 2003, Springer et al. 2003), was the primary reason for the evolution of larger fruits and seeds. By acting as seed dispersing agents, the radiating frugivores allowed for the development of larger seeds, and the larger frugivores thereby paved the way for angiosperms from open habitats to more closed and tree-dominated habitats. As an alternative, Eriksson et al. (2000a) suggested that a major climatic change in the early Tertiary (Zachos et al. 2001, Janis 2003) initiated a change of vegetation where recruitment became limited by light. Under these conditions selection favoured the development of larger seeds, and selection to maintain dispersibility promoted evolution of fleshy pulp mediated by an existing frugivorous fauna.

The present study investigates correlations between shifts in fruit type and shifts in habitat type, using a sample of phylogenetically independent changes of fruit

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type where fleshiness has either evolved or been lost. Adding data from the time-calibrated phylogeny of angiosperms (Wikström et al. 2001) and extant species richness (basically Mabberley 1997), our data set also allows for a description of the historical distribution of origins and losses of fleshy fruit types and tests of correlations between fruit type and species richness. Sampling phylogenetically independent units strengthens the generality of the results from comparative studies, as evolutionary independent events are replicated (Felsenstein 1985, Harvey and Pagel 1991). The attractiveness of the statistical argument (i.e. phylogenetic independence) is somewhat reduced as phylogenetically independent contrasts require change in at least one of the characteristics analyzed, and thereby adaptive processes, such as phylogenetic niche conservatism (Lord et al. 1995), tend to be underestimated in independent contrasts studies (Westoby et al. 1995). In the present study we also consider the direction of fruit type change further strengthening conclusions on causation (Wanntorp 1983). Out of the numerous studies using phylogenetic comparative methods that have been done, some are particularly pertinent to this study. The evolution of fleshy fruits have been analyzed in relation to habitat (Patterson and Givnish 2002), frugivores (Mack 1993, Jordano 1995a), and allometry (Herrera 2002a). Marvaldi et al. (2002), Hodges and Arnold (1995), and Bolmgren et al. (2003) analyzed correlations between niche shifts and species richness, and several studies have looked for an effect of animal dispersal on species richness (Eriksson and Bremer 1992, Ricklefs and Renner 1994, Tiffney and Mazer 1995, Dodd et al. 1999, Smith 2001, de Queiroz 2002).

Fleshy animal-dispersed fruits are mainly associated with tree- and shrub-dominated habitats (Herrera 2002b, Patterson and Givnish 2002). However, it is less clear whether there is a consistent positive correlation between increasing vertical vegetation structure and the proportion of endozoochorous plants, as both shrublands, forest margins, and mature forests have been found to harbour the comparatively highest proportions of fleshy fruited plants in different studies (Willson et al. 1990, Guitian and Sanchez 1992, Jakobsson and Eriksson 2002). Two studies of temperate floras also found an association between seed size and endozoochorous dispersal (Hughes et al. 1994, Leishman et al. 1995), and Leishman et al. (2000) concluded that the relationship between large seeds and shaded habitats is "the strongest pattern of seed mass variation in relation to environmental factors" (Salisbury 1942, Hodgson and Mackey 1986, Mazer 1989, 1990, Hewitt 1998, but see Metcalfe and Grubb 1997). The advantageous mechanism of larger seeds in shady habitats seems to be confined to the early cotyledon-phase of the seedling (Leishman et al. 2000), where larger seeds develop into seedlings capable of dealing with different hazards

associated with tree-dominated vegetation types (e.g. litter, falling debris, shade). However, there is also a potential trade-off of being large as, everything else being equal, larger seeds disperse shorter distances. This negative effect of large seed size on dispersal has been used to explain why larger seed size is associated with endozoochory (Tiffney and Mazer 1995).

The anticipated advantage of effective seed dispersal by frugivorous animals boosted research in plant–frugivore interactions in the 1970s (Snow 1971, McKey 1975, Howe and Estabrook 1977), but the presumed diffuse interactions (Howe 1984, Herrera 1985, 1998) have not revealed significant coevolutionary patterns nor strong correlations between fleshy-fruited plant and frugivore characteristics (Jordano 2000, Herrera 2002b), except for fruit size (Wheelwright 1985, Mack 1993, Sallabanks 1993, Jordano 1995a, b, Rey et al. 1997, Lord et al. 2002). Furthermore, despite the diversity of adaptations for animal seed dispersal, the numerous independent origins of fleshy fruit types, the connection between speciation mechanisms and spatial dispersal (allopatric speciation), and the biotic interaction with seed dispersing frugivores, no consistent correlation have been found between biotic dispersal and extant species richness (Tiffney 1984, Herrera 1989, Eriksson and Bremer 1991, 1992, Ricklefs and Renner 1994, Tiffney and Mazer 1995, Dodd et al. 1999, but see Smith 2001, de Queiroz 2002).

Here, we will change the focus from the frugivores to the plant community, asking whether variation in the plant community gives momentum to the evolution of fleshy fruit types. First, we examine phylogenetically independent fruit type shifts in relation to two habitat features: light conditions and spatial predictability of disturbances. In deteriorating light conditions, one fitness advantage would be to have larger seeds. But larger seeds have a reduced dispersibility and would thus benefit from evolving a dispersal attribute, like fleshiness, to uphold a sufficient (escape and/or colonize) dispersal. By sufficient dispersal we mean avoiding disproportionate mortality close to the mother plant (Janzen 1970, Connell 1971, Harms et al. 2000) or encountering randomly distributed recruitment sites. As an alternative hypothesis, fleshiness might evolve to avoid the deteriorating light conditions. By using animals for dispersal, plants may disperse their seeds in a non-random fashion to forest margins, gaps and clearings where the 'ancestral' light conditions are preserved. In communities characterized by recurring large-scale disturbances, safe sites are highly predictable in space. The selective regime in such communities may not favour costly dispersal traits, such as fleshy fruits. On the other hand, in communities structured by small scale disturbances (gap dynamics), the advantage of directed dispersal is much greater. As seeds themselves are unable to target their dispersal, the evolution of biotic dispersal

has been interpreted as the acquisition of this ability (Howe and Smallwood 1982, but see Wheelwright and Orians 1982). Empirical evidence for directed dispersal is scarce (Hoppe 1988, Wenny and Levey 1998), but spatially unpredictable sites, like canopy gaps, seem to be easily located by the frugivore guild (Levey 1988, Debussche and Isenmann 1994), and frugivores are often attracted to canopy gaps, as they are likely to provide abundant food (Jordano 2000).

Taking growth form and ancestral fruit type into account we examine associations between present day species richness and fruit type. The hypothesis of enhanced diversification through biotic interactions is based on the idea of specialized frugivores, similar to the idea of faithful pollinators (Crepet 1984). Such animal behaviour could generate reproductive isolation and subsequent allopatric speciation through microevolutionary change. An alternative hypothesis for present day species richness is that the improved dispersibility in fleshy fruited plants reduced extinction rates (Tiffney and Mazer 1995). Still, previous analyses have not found any effect of biotic dispersal on species richness (Tiffney 1984, Herrera 1989, Eriksson and Bremer 1991, 1992, Ricklefs and Renner 1994, Tiffney and Mazer 1995, Dodd et al. 1999), unless they have controlled for growth form (Smith 2001, de Queiroz 2002). The principal reason for taking growth form into account is that there is a cost of producing dispersal attributes such as fleshiness. Such a cost may reduce seed output which has a proportionally more negative effect on smaller plants (de Queiroz 2002).

We also examine the historical distribution of fruit type changes, challenging the idea that evolutions of fleshy fruits are, in general, confined to the early Tertiary (Tiffney 1984, Eriksson et al. 2000a, Knapp 2002). Climate changes are generally viewed as the main driver behind global vegetation change during the Tertiary (Zachos et al. 2001). After the Eocene climatic maximum followed a period of decreased temperature and a drastic drop at the Eocene–Oligocene boundary (Prothero 1994). The temperature fluctuated from late Oligocene to mid Miocene, after which global temperature has declined towards the present (Zachos et al. 2001). The distribution of closed, semi-open, and open vegetation has basically mirrored these climatic changes, with recurring shifts in openness of vegetation from the Eocene and onwards (Janis 1993, Prothero 1994, Graham 1999, Jacobs et al. 1999). According to paleoecological data, there seems to be certain periods during evolution that have been particularly important for fleshy fruit radiation, e.g. during Paleocene and Eocene in the early Tertiary (Tiffney 1984, Eriksson et al. 2000a). Both species richness and abundance of plants with larger seeds and fruits adapted to endozoochorous dispersal rose during these periods. But it is still not resolved whether the evolutionary importance of frugiv-

ory was restricted to these periods (Tiffney 1984, Jordano 1987, Eriksson and Bremer 1992, Herrera 1992, Jordano 1995a, Eriksson et al. 2000a, Knapp 2002). Particularly, no analysis has yet been performed to examine the frequency distribution of phylogenetically independent origins of fleshy fruits during the periods following the Eocene.

Thus, in the present study, fleshy fruit evolution is examined in relation to the plant community context, and not in the usually applied frugivore perspective. Based on a set of phylogenetically independent contrasts, including origins and losses of fleshy fruit types, four predictions will be examined: (1) shifts to a fleshy fruit type are correlated with shifts to more shaded habitats; (2) shifts to fleshy fruit type are correlated with shifts to spatially more unpredictable safe sites; (3) fleshy fruits are associated with a higher species richness in woody plants; and (4) fleshy fruits are continuously originating and lost in evolutionary time from the Eocene and up to the present.

Methods

Data set

Flora Europaea (Tutin et al. 1964–1980) was scanned for families including both fleshy and non-fleshy fruit types. Thereafter, the literature was searched for phylogenetic hypotheses with high enough resolution to let us locate the node of fruit type change (gain or loss of fleshy fruits). The same phylogenies were then used to derive the contrasted sister clades (fleshy vs non-fleshy) and an outgroup, i.e. the most closely related clade to the sister clades, and to derive the direction of fruit type change. Thus, as the phylogenies, and not Flora Europaea, defined which taxa/clades that should be contrasted, the data set consisted of taxa from all over the world. Table 1 includes the full list of contrasted taxa, including references to the reconstructed phylogenies used, and trait values used for all phylogenetically independent contrasts (PICs). Our data set included 50 phylogenetically independent replicates of fruit type change representing 18 families. At 36 phylogeny nodes fleshy fruits evolved, and at the other 14 fleshiness was lost. Even though the analyses only considered fleshy vs non-fleshy fruit types, we treated fleshy fruits as animal dispersed fruits in the discussion. This classification introduces two simplifications. First, plants dispersed by small frugivores (e.g. many birds, bats) and large frugivores (e.g. many mammals) are pooled despite the different dispersal patterns they may create (Howe 1989). Still, most plant–frugivore interactions are diffuse, comprising different kinds of dispersal, and both large and small frugivores generate the kind of dispersal that forms the basis for the hypothesis on vegetation driven evolution of fleshy fruit types. Second, the non-fleshy

Table 1. A compilation of the phylogenetically independent nodes and data used in the different analyses. In the sister clades columns, * indicates subsets used in the habitat contrasts. Columns headed with (out), (F), and (N-F) contain data for outgroup, fleshy fruited and non-fleshy fruited clades respectively, while columns headed with NPRS and Fossil include clade age data (million years before present) based on non-parametric rate smoothing and fossil records respectively. The 'Closedness index' gives a semi-quantitative value of the light conditions in plant communities, and the 'Predictability index' gives a semi-quantitative value of the spatial predictability of disturbances in plant communities (see Methods, Fig. 1). References to cladograms used to identify sister clades and outgroups, and to floras used to derive habitat conditions:

Cladograms: PIC no. 1–2 (Loconte and Estes 1989), no. 3 (Gustafsson and Bremer 1997), no. 4 (Bogler and Simpson 1995), no. 5 (Conti et al. 1993), no. 6–9 (Olmstead and Palmer 1992), no. 10–11 (Rodman et al. 1998), no. 12–14 (Anderberg 1993), no. 15–17 (Wallander and Albert 2000), no. 18 (Gadek and Quinn 1993), no. 19–20 (Wiegrefe et al. 1998), no. 21–26 (Sennblad 1997), no. 27–31 (Wagstaff and Olmstead 1997), no. 32 (Johansson 1995), no. 33 (Sheahan and Chase 1996), no. 34 (La Duke and Doebley 1995), no. 35–37 (Rova 1999), no. 38–43 (Andersson and Rova 1999), no. 44–46 (Morgan et al. 1994), and no. 47–50 (Eriksson et al. 1998).

Floras: PIC no. 1–2 (Shishkin 1937, Hitchcock et al. 1964, Webb 1964, Ohwi 1965), no. 3 (Allan 1961, Harden 1992), no. 4 (Correll and Johnston 1970, McVaugh 1989), no. 5 (Shishkin and Bobrov 1974, Wiggins 1980, Webb et al. 1988), no. 6–9 (Wiggins and Porter 1971, Robertson et al. 1982, Harden 1992, Gentry 1993, Shishkin and Bobrov 1994, Liogier 1995), no. 10–11 (Bush 1970, Correll and Johnston 1970), no. 12–14 (Ridley 1923, Shishkin and Bobrov 1967, Tutin et al. 1972), no. 15–17 (Cooke 1908, Gamble 1921, La Bathie 1952, Tutin et al. 1972, Polunin and Stainton 1984, Green 1988), no. 18 (Il'in 1968, Hitchcock et al. 1969, McVaugh 1989), no. 19–20 (Sargent 1917, Li et al. 1976, Gentry 1993, Ying et al. 1993), no. 21–26 (Ridley 1923, Shishkin and Bobrov 1967, Henderson 1974, Wiggins 1980, Van Balgooy 1984, Liogier 1995, Berry et al. 1995), no. 27–31 (Ridley 1923, Backer and Bakhuizen van den Brink 1965, Polunin 1969, Tutin et al. 1972, Henderson 1974, Shishkin and Yuzepchuk 1976, Cronquist et al. 1984, Polunin and Stainton 1984, Jessop and Toelken 1986), no. 32 (Shishkin 1937, Ohwi 1965), no. 33 (Codd 1968, Hedberg and Edwards 1992), no. 34 (Corell and Corell 1982, Edwards et al. 1995, Liogier 1995), no. 35–37 (Ridley 1923, Backer and Bakhuizen van den Brink 1965, Henderson 1974, Rogers 1984, Burkhil 1997), no. 38–43 (Backer and Bakhuizen van den Brink 1965, Adams 1972, Henderson 1974, Polunin and Stainton 1984, van Roosmalen 1985, Harden 1992, Gentry 1993, Press and Short 1994, Stannard 1995), no. 44–46 (Valentine and Chater 1968, Yuzepchuk 1971, Wiggins 1980, Polunin and Stainton 1984, Hitchcock and Cronquist 1996), and no. 47–50 (Valentine and Chater 1968, Yuzepchuk 1971, Grierson and Long 1987, Krok and Almqvist 1994).

PIC no.	Outgroup	Ancestral fruit type	Family	Sister clades		Age (Myr BP)		Growth form		Species richness		Closedness index			Predictability index		
				F	N-F	NPRS	Fossil	F	N-F	F	N-F	out	F	N-F	out	F	N-F
1	<i>Nandina</i>	fleshy	Berberidaceae	<i>Caulophyllum</i>	<i>Gymnospermium</i> , <i>Leontice</i>	<55–44	46	H	H	3	11	0	0.75	0.25	1	0.5	0.5
2	<i>Ranzania</i>	fleshy	Berberidaceae	<i>Diphylleia</i> *, <i>Dysosma</i> , <i>Podophyllum</i> (incl. <i>Sinopodophyllum</i>)	<i>Achlys</i> *, <i>Bongardia</i> , <i>Epimedium</i> , <i>Vancouveria</i> , <i>Jeffersonia</i> (incl. <i>Plagiorhegma</i>)	<55–44	46	H	H	15	53	1	1	0.75	1	1	1
3	<i>Carpodetus</i>	fleshy	Carpodetaceae	<i>Abrophyllum</i>	<i>Cuttisia</i>	–	–	W	W	1	1	0.75	0.5	0.75	0.5	0.5	0.5
4	<i>Agave</i>	dry	Agavaceae	<i>Yucca treculeana</i>	<i>Y. elata</i>	58–35	–	W	W	1	1	0.5	0.5	0	0.5	0.5	0
5	<i>Lopezia</i>	dry	Onagraceae	<i>Fuchsia</i>	<i>Circaea</i>	67–20	46	W	H	105	7	0.25	0.25	0.75	1	0.5	0.5
6	<i>Lycium</i>	fleshy	Solanaceae	<i>Atropa</i>	<i>Hyoscyamus</i>	<13–11	13	H	H	4	15	0.5	0	0	0	1	1
7	<i>Atropa</i>	fleshy	Solanaceae	<i>Grabowskia</i> , <i>Lycium</i> *	<i>Nolana</i>	<13–11	13	W	M	106	31	0	0.5	0	1	0	1
8	<i>Grammosolen</i>	dry	Solanaceae	<i>Duboisia</i>	<i>Cyphanthera</i>	<14–11	13	W	W	3	9	0.25	0.5	0.5	0.5	0.5	0.5
9	<i>Sapiglossis</i>	dry	Solanaceae	<i>Cestrum</i>	<i>Vestia</i>	<25–11	13	W	W	175	1	–	–	–	–	–	–
10	<i>Reseda</i>	dry	Capparaceae- Brassicaceae	<i>Capparis</i> *	<i>Cleome</i> *	31–24	38	–	–	–	–	0.25	0.5	0	0.5	0	1
11	<i>Tropaeolum</i>	dry	Caricaceae- Moringaceae	<i>Caricaceae</i>	<i>Moringaceae</i>	61–58	–	W	W	33	12	–	–	–	–	–	–
12	<i>Daboecia</i>	dry	Ericaceae	<i>Corema</i> *, <i>Ceratiola</i> , <i>Empetrum</i>	<i>Loiseleuria</i> *, <i>Phyllodoce</i> , <i>Rhodoreae</i> , <i>Bejaria</i> , <i>Kalmia</i> , <i>Epigaea</i> , <i>Cladothamneae</i> , <i>Diplarche</i>	<67–59	65	W	W	5	735	0.25	0	0	0.5	1	1
13	<i>Vaccinium</i>	fleshy	Ericaceae	<i>Gaultheria</i>	<i>Andromeda</i>	<67–59	65	W	W	134	1	0.5	0.75	0.5	0.5	0.5	0.5

Table 1 (Continued)

PIC no.	Outgroup	Ancestral fruit type	Family	Sister clades		Age (Myr BP)		Growth form		Species richness		Closedness index			Predictability index		
				F	N-F	NPRS	Fossil	F	N-F	F	N-F	out	F	N-F	out	F	N-F
14	<i>Pyrola</i>	dry	Ericaceae	<i>Cheilotheca*</i> , <i>Pityopus</i> , <i>Pleuricospora</i> , <i>Hemitomes</i>	Monotropa	<67–59	65	H	H	8	2	0.5	1	1	0.5	1	1
15	<i>Forsythia</i>	dry	Oleaceae	<i>Myxopyrum</i>	<i>Nyctanthes*</i> , <i>Dimetra</i>	<48–39	51	W	W	4	3	0	1	1	1	0	0
16	<i>Comoranthus</i> , <i>Schrebera</i>	dry	Oleaceae	<i>Ligustrum</i>	<i>Syringa</i>	<48–39	51	W	W	40	23	0.75	0.5	0.5	0.5	0	0
17	<i>Comoranthus</i> , <i>Schrebera</i>	dry	Oleaceae	<i>Chionanthus</i> , <i>Foresteria</i> , <i>Haenianthus</i> , <i>Hesperelaea</i> , <i>Noronhia</i> , <i>Olea</i> , <i>Priogymnanthus</i> , <i>Nestegis</i> , <i>Notelaea</i> , <i>Osmanthus</i>	Fraxinus	<48–39	51	W	W	219	65	0.75	0.75	0.75	0	0	0.5
18	<i>Calocedrus</i>	dry	Cupressaceae	<i>Juniperus</i>	<i>Cupressus</i>	–	–	W	W	50	13	1	0.5	0.5	1	0.5	1
19	<i>Aphananthe</i>	fleshy	Ulmaceae	<i>Celtis</i>	<i>Pteroceltis</i>	<34–25	73	W	W	100	1	1	0.5	0.75	0.5	0.5	0.5
20	<i>Hemiptelea</i>	dry	Ulmaceae	<i>Ampelocera</i>	<i>Holoptelea</i>	<57–55	55	W	W	10	2	0	1	1	1	1	0
21	<i>Ochrosia</i>	fleshy	Apocynaceae	<i>Rawolfia</i>	<i>Vinca*</i> , <i>Catharanthus</i>	53–18	55	W	M	60	13	0.5	0.5	0.5	0.5	0.5	0.5
22	<i>Alstonia</i>	dry	Apocynaceae	<i>Vallesia</i>	<i>Aspidosperma</i>	53–18	55	W	W	8	80	0.5	0.5	0.5	1	0.5	0.5
23	<i>Diplorhynchus</i>	dry	Apocynaceae	<i>Melodinus</i>	<i>Craspidospermum</i>	53–18	55	W	W	75	1	0.5	1	1	0.5	0.5	0
24	<i>Crasidiospermum</i>	dry	Apocynaceae	<i>Picralima</i> , <i>Pleiocarpa</i>	<i>Diplorhynchus</i>	53–18	55	W	W	4	1	1	0.75	0.5	0	0	0.5
25	<i>Allemanda</i> , <i>Plumeria</i>	dry	Apocynaceae	<i>Cerbera*</i> , <i>Thevetia</i> , <i>Anechites</i>	<i>Cameraria</i>	53–18	55	W	W	12	6	0.75	0.5	0.5	0	0.5	0
26	<i>Chilocarpus</i>	fleshy	Apocynaceae	<i>Alyxia</i>	<i>Lepinia</i>	53–18	55	W	W	120	3	0.75	0.5	1	0.5	0.5	0
27	<i>Teucrium</i>	dry	Lamiaceae	<i>Clerodendrum</i>	<i>Ajuga*</i> , <i>Caryopteris</i> , <i>Trichostema</i>	<28–17	38	W	M	400	72	0.25	0.5	0.25	0.5	0.5	0.5
28	<i>Pogostemon</i>	dry	Lamiaceae	<i>Holmskioldia</i>	<i>Scutellaria*</i> , <i>Timnea</i>	<28–17	38	H	H	1	369	0.75	0.5	0.5	0.5	0	0.5
29	<i>Pogostemon</i>	dry	Lamiaceae	<i>Prasium</i>	<i>Physostegia*</i> , <i>Lamium</i> , <i>Marrubium</i>	<28–17	38	W	H	1	82	0.75	0	0.25	0.5	1	0.5
30	<i>Teucrium</i>	dry	Lamiaceae	<i>Gmelina</i>	<i>Prostanthera</i>	<28–17	38	W	W	40	100	0.25	0.75	0.5	0.5	0	0.5
31	<i>Tectona</i>	dry	Lamiaceae	<i>Congea</i>	<i>Salvia*</i> , <i>Mentha</i> , <i>Glechoma</i> , <i>Elsholtzia</i> , <i>Plectranthus</i>	<33–23	38	H	M	7	1170	1	0.5	0.5	0	0	0.5
32	<i>Anemonopsis</i>	dry	Ranunculaceae	<i>Actaea</i>	<i>Cimicifuga</i>	<66–51	38	H	H	8	12	1	0.75	0.5	1	0.5	0.5
33	<i>Neoluederitzia</i>	dry	Zygophyllaceae	<i>Balanites</i>	<i>Sisyndite</i>	<70–64	–	W	W	25	1	0	0.5	0	1	0	1
34	<i>Abelmoschus</i>	dry	Malvaceae	<i>Malvaviscus</i>	<i>Pavonia</i>	<31–28	42	W	W	3	150	0.25	0.5	0.5	0.5	0.5	0.5
35	<i>Retiniphyllum</i>	fleshy	Rubiaceae	<i>Mussaenda</i>	<i>Pseudomussaenda</i>	<56–55	55	W	W	100	4	0.25	0.75	0.25	0.5	0.5	0.5
36	<i>Greenea</i>	dry	Rubiaceae	<i>Ixora</i>	<i>Aleisanthiposis</i> , <i>Aleisanthia*</i>	<56–55	55	W	W	300	4	0	0.5	0.5	1	0.5	1
37	<i>Glaesonia</i>	dry	Rubiaceae	<i>Posoqueria</i>	<i>Molopanthera</i>	<56–55	55	W	W	12	1	0.5	0.75	1	0.5	0	0
38	<i>Coussarea</i> , <i>Farama</i>	fleshy	Rubiaceae	<i>Coccocypselum</i>	<i>Hindsia</i> , <i>Declieuxia</i>	<56–55	55	H	W	20	35	1	0.25	0.5	0	0.5	0.5
39	<i>Heterophyllaea</i>	dry	Rubiaceae	<i>Lasianthus</i>	<i>Perama</i>	<56–55	55	W	W	170	9	0.5	0.5	0.5	0	0	1

Table 1 (Continued)

PIC no.	Outgroup	Ancestral fruit type	Family	Sister clades		Age (Myr BP)		Growth form		Species richness		Closedness index			Predictability index		
				F	N-F	NPRS	Fossil	F	N-F	F	N-F	out	F	N-F	out	F	N-F
40	<i>Opercularia</i>	dry	Rubiaceae	<i>Coprosma*</i> , <i>Nertera</i>	<i>Galopina</i> , <i>Nenax</i> , <i>Phyllis*</i>	<29–28	55	W	W	105	15	0.5	0.5	0	0.5	0.5	1
41	<i>Opercularia</i>	dry	Rubiaceae	<i>Mycetia</i>	<i>Argostemma</i>	<29–28	55	W	H	25	100	0.5	1	0.5	0	0	0.5
42	<i>Paederia</i>	fleshy	Rubiaceae	<i>Serissa</i>	<i>Leptodermis</i>	<29–28	55	W	W	2	30	0.5	1	0.5	0.5	0	0.5
43	<i>Rubia</i>	fleshy	Rubiaceae	<i>Didymaea</i>	<i>Valantia</i> , <i>Galium*</i> , <i>Crucianella</i> , <i>Asperula</i> , <i>Sherardia</i>	<29–28	55	H	H	5	424	0.5	1	0.25	0.5	0.5	0.5
44	<i>Lindleya</i>	dry	Rosaceae	<i>Sorbus</i> , <i>Amelanchier</i> , <i>Eriobotrya</i> , <i>Crataegus</i> , <i>Photinia</i>	<i>Vauquelinia</i>	<35–29	60	W	W	503	3	–	0.5	0	–	0.5	1
45	<i>Prinsepia</i>	fleshy	Rosaceae	<i>Osmaronia</i> (= <i>Oemleria</i>)	<i>Exochorda</i>	<47–46	60	W	W	1	4	0.75	0.75	0	0.5	0.5	1
46	<i>Spiraea</i>	dry	Rosaceae	<i>Rhodotypos</i>	<i>Nevusia</i>	<47–46	60	W	W	1	1	–	–	–	–	–	–
47	<i>Filipendula</i>	dry	Rosaceae	<i>Rosa</i>	<i>Sanguisorba*</i> , <i>Potentilla</i> (- <i>P. indica</i>), <i>Horkelia</i> , <i>Ivesia</i> , <i>Alchemilla</i> , <i>Aphanes</i> , <i>Sibbaldia</i> , <i>Chamaerhodos</i> , <i>Agrimonia</i> , <i>Aremonia</i> , <i>Hagenia</i> (- <i>Fragaria</i>)	<76	60	W	M	100	851	0.5	0.5	0.5	0.5	0.5	0.5
48	<i>Potentilla nivea</i>	dry	Rosaceae	<i>P. indica</i>	<i>P. reptans</i> , <i>P. erecta</i>	<76	60	H	H	1	2	0	0.25	0.25	0.5	0.5	0.5
49	<i>Potentilla fruticosa</i>	dry	Rosaceae	<i>Fragaria</i>	<i>Potentilla anserina</i> , <i>Agrimonia</i> , <i>Aremonia</i> , <i>Hagenia</i>	<76	60	H	H	12	18	0.25	0.5	0.5	0.5	0.5	0.5
50	<i>Filipendula</i>	dry	Rosaceae	<i>Rubus</i>	<i>Fallugia</i> , <i>Geum</i> , <i>Waldsteinia</i>	<76	60	W	H	250	47	0.5	0.5	0.25	0.5	0.5	1

fruited plants were assumed not to have animal mediated dispersal. The non-fleshy fruit types included capsules, follicles, achenes, nutlets, mericarps, samaras, nuts, dry arils, and cones (Table 1). Among the achenes, nuts and mericarps (PIC no. 5, 43, 47, 49, 50), some fruits were equipped with hooked hairs and thus animal dispersed. As adhesive dispersal may result in the same kind of dispersal hypothesized here for the evolution of fleshy fruits, these plants may make it more difficult to reject the null hypotheses. On the other hand adhesive dispersal has not been considered suitable for large seeds and tall-statured plants (Sorensen 1986, Hughes et al. 1994), and the evolution of larger seeds is one of the hypothesized mechanisms behind the evolution of fleshy fruits tested here.

Two habitat indices were derived for each clade: light conditions (closedness index) and spatial predictability of disturbances (predictability index). The indices were based on habitat descriptions taken from floras (see Table 1 for references to floras), and the habitat descriptions were classified and given a semi-quantitative value (Appendix 1) according to Fig. 1. The light conditions were basically classified according to the canopy closure of the community. In communities characterized by large scale disturbances (fire, storm, seasonal flooding, and seasonal drought), spatial predictability of disturbances was considered high, while in communities characterized by small scale disturbances (gap dynamics: tree fall, trampling) spatial predictability of disturbances was considered low. For each clade an unweighted mean was calculated based on the classes that were represented in the clade (Møller and Birkhead 1992, Wickman 1992). For many of the PICs only subsets were used, as the complete clades were unmanageably large. In those cases, the lower-most branch of the phylogenetic clade formed each subset (marked in Table 1). As the habitat descriptions were taken from floras, they give indices of the community where adults live rather than of the species' complete regeneration niche. Several cases are known where seedlings establish under low light conditions but do not develop into reproductive individuals until a canopy gap opens. However, we have no information about how general and important such shifts between juvenile and adult

requirements are in relation to community dynamics, and, most importantly, we have no reason to believe that such shifts depend on fruit type. Thus, despite the fact that the present data set may be biased towards adult requirements, the habitat-related tests will not be confounded.

Both global species richness and growth form were recorded from Mabberley (1997), or from monographies for specific taxa when needed. Growth forms were classified as woody or herbaceous, where trees, shrubs, scrubs, and vines were all referred to as woody. As previous studies have found an interaction effect (fruit type \times growth form) on species richness (Eriksson and Bremer 1991, Tiffney and Mazer 1995, Dodd et al. 1999, Smith 2001, de Queiroz 2002), we performed separate tests for PICs with different growth forms and ancestral fruit types (test 5–7, below).

Clade ages were derived for each PIC from the time-calibrated angiosperm phylogeny by Wikström et al. (2001). They used the method of non-parametric rate smoothing (NPRS) with a singular calibration point (Sanderson 1997). These PIC ages are significantly correlated (Pearson P-M correlation test; $N=20$, $p=0.004$, $r=0.62$) to minimum angiosperm family ages based on fossil records (Collinson et al. 1993). The advantage of the Wikström et al. (2001) paper compared to Collinson et al. (1993) is that it is not restricted to fossil findings, but gives us values of each phylogenetic node.

Analysis

Correlation tests between fruit type change and habitat change (test 1–4) and between fruit type change and species richness (test 5–7), were performed as one-tailed sign tests on phylogenetically independent contrasts, and we calculated cumulative p-values (Sokal and Rohlf 1995).

The effect of fruit type on species richness was also analyzed with a randomization test of key innovations proposed by Goudet (1999). We refer to Goudet (1999) and Slowinski and Guyer (1993) for detailed descriptions of the randomization test of key innovations. We

Fig. 1. The semi-quantitative classification of habitat variables, with examples of classified habitat descriptions. See Appendix 1 for the full list of classified habitat descriptions.

		Closed	Semi-open	Open
	index	1	0.5	0
Spatially predictable disturbances	1	e.g. coniferous forest	e.g. stream bank	e.g. deserts, dunes, ruderal, arable, stony
Spatially unpredictable disturbances	0	e.g. deciduous forest	e.g. shrub- & scrublands	e.g. grasslands

followed Slowinski and Guyer (1993) and calculated p_i for each independent contrast as $p_i = (n-r)/(n-1)$, where r is the number of species in the clade with the suggested key innovation and $(n-r)$ the number of species within the sister clade. Then p_i is the cumulative probability of the clade with the suggested key innovation to have r or more species ($r < n$), based on the assumption of a random speciation and extinction process. In our implementation of the Goudet (1999) randomization procedure, arithmetic means of p_i -values were chosen as the suitable statistic as it allows clades to have only one species. Each test of the null hypotheses that the key innovation had no effect on extant species richness was based on 5000 simulated p_i -values, and the results ($p(G)$ -values in Table 3) are means based on 30 runs. As the effect of fleshy fruits on present species richness has been referred to both enhanced diversification and reduced extinction rates (Tiffney and Mazer 1995), both tests are warranted.

When testing both habitat and species richness related hypotheses, sample sizes differ from the original number of PICs due to missing data (Table 1: PIC no. 9, 10, 11, 44, and 46), and as sign tests do not gain from zero (0) contrasts, sample sizes were further reduced.

The historic distribution of evolutionary gains and losses of fleshy fruit type, was not analyzed statistically, but judged from the graphical pattern presented (Fig. 3). Several of the evolutionary age values in this data set refer to the same phylogenetic node in Wikström et al. (2001) and the same fossil record in Collinson et al. (1993). This pseudoreplication, which is due to the lower resolution in Wikström et al. (2001) and Collinson et al. (1993) compared to the cladograms used in the present study, made a statistical analysis of the distribution unjustified.

Results

The phylogenetically independent origins of fleshy fruit types were generally correlated to habitat-related niche shifts. In ten out of 13 cases plants evolving fleshy fruits occupied more closed vegetation types than their non-

fleshy fruited sister-taxa (Table 2, test 1; Fig. 2A). Colonization of more closed habitats did not precede the evolution of fleshiness. Only in 15 out of 32

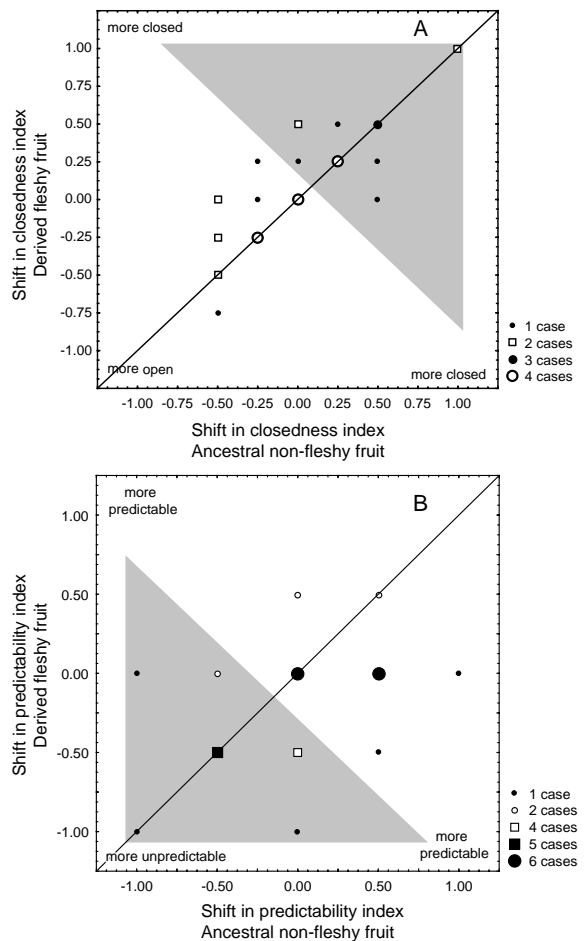


Fig. 2. Changes of habitat indices in clades evolving fleshy fruit type vs clades with conserved non-fleshy fruit type. All cases in this frequency plot represent a phylogenetically independent contrast where fleshiness evolved in one of the contrasted sister clades, while the ancestral, non-fleshy fruit type was conserved in the other. (A) Changes in habitat light conditions (Test 1, Table 2). (B) Changes in spatial predictability of recruitment sites (Test 2, Table 2).

Table 2. Results of one-tailed sign tests of the correlation between change of fruit type and habitat type (test 1 and 2), and the correlations between conserved fruit type and habitat type (test 3 and 4), using n phylogenetically independent contrasts. N is the number of PICs including draws, which are uninformative in sign tests, m is the number of contrasts supporting the prediction, and p is the cumulative p -value (Sokal and Rohlf 1995).

Test prediction	n (N)	m	p
Fleshy fruits evolve			
1 Fleshy fruited clade was associated with more closed habitats than non-fleshy clades	13 (32)	10	0.046
2 Fleshy fruited clade was associated with plant communities characterized by spatially more unpredictable disturbances than non-fleshy clades	18 (32)	13	0.048
Non-fleshy fruits evolve			
3 Fleshy fruited clade associated with more closed habitats than non-fleshy clades	12 (14)	8	0.19
4 Fleshy fruited clade was associated with plant communities characterized by spatially more unpredictable disturbances than non-fleshy clades	4 (14)	3	0.31

phylogenetically independent origins of fleshy fruit types did the ingroup as a whole (i.e. the means of both sister clades) occupy more closed habitats than the outgroup (Fig. 2A, shaded area).

Plants evolving fleshiness also occupied habitats with spatially more unpredictable disturbances than their non-fleshy fruited sister-taxa in (Table 2, test 2; Fig. 2B). The colonization of habitats characterized by spatially more unpredictable disturbances did not precede the evolution of fleshiness, as the ingroup occupied habitats characterized by spatially more unpredictable disturbances in 13 out of 32 cases (Fig. 2B, shaded area).

Evolutionary changes to non-fleshy fruit types from a fleshy fruited ancestor were not associated with a habitat-related niche shift, neither in relation to light conditions nor to spatial predictability of regeneration sites (Table 2, test 3–4).

There was no general effect of fruit type on species richness (Table 3, test 5a and 5b). Separating the data according to growth form and ancestral fruit type, the sign tests revealed an association between the evolution of fleshy fruits and higher species richness in woody clades (Table 3, test 6a and 6b). However, fleshiness may not be interpreted as a key innovation for woody plants based on the present study, as the key innovation tests did not find a difference between the contrasted clades (Table 3, test 6a and 6b). For herbaceous clades, there was a trend in the opposite direction even if sample sizes were small and p-values were marginal. In both the sign tests and the key innovation tests, non-fleshy fruit types were associated with higher species richness (Table 3, test 7a and 7b).

The graphical presentation of the phylogenetically independent fruit type changes did not reveal an aggregation in evolutionary time, neither regarding direction of fruit type change nor regarding the correlation between fruit type and species richness (Fig. 3). The dating of the nodes used in this study (Wikström et al. 2001), generates a time range when the fruit type change occurred (Table 1). These ranges were represented by their oldest endpoints in Fig. 3, thus giving a conservative picture of the origins and losses of fleshy fruits.

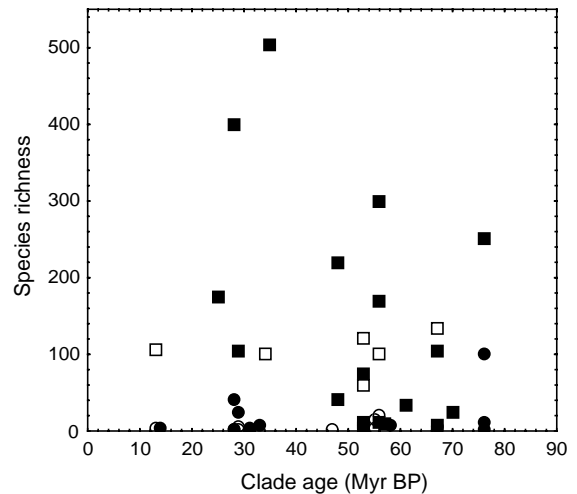


Fig. 3. Extant species richness in fleshy fruited clades in relation to age of clade. Clade age is the oldest inferred age based on non-parametric rate smoothing from Wikström et al. (2001). Filled symbols (■, ●) represent nodes where fleshy fruit evolved and open symbols (□, ○) where fleshiness was lost. Quadrats (■, □) represent clades where the fleshy fruited clade was more speciose than the non-fleshy fruited clade, while circles (●, ○) represent clades where the fleshy fruited clade was less speciose than the non-fleshy fruited clade.

Discussion

Our results suggest that shifts from non-fleshy to fleshy fruit types are correlated with shifts in growth habitat. Fleshy fruited taxa occupied habitats characterized by lower light conditions and spatially more unpredictable disturbances. Furthermore, fleshiness did not evolve as one of two fruit type options to these changing habitat conditions as these habitat shifts did not precede shifts in fruit type. We agree with Miles and Dunham (1993, p. 594) that “given a phylogenetic hypothesis a change in character state or shift in function coincident with a change in the environment would constitute evidence of adaptation”. Thus, we interpret fleshiness as an adaptation to habitats characterized by lower light conditions and spatially more unpredictable disturbances. In relation to the discussion on ‘disperser’ vs ‘vegetation’ driven evolution of fleshy fruits (Tiffney 1984, Eriksson et al.

Table 3. Results of one-tailed sign tests (p (sign)) and key innovation tests (p (G)) of the correlation between extant species richness and fruit type, using *n* phylogenetically independent contrasts. *N* is the number of PICs including draws, which are uninformative in sign tests, and *p* (sign) is the cumulative *p*-value (Sokal and Rohlf 1995).

Test	Growth form	Ancestral fruit state	Prediction	<i>N</i>	<i>n</i>	<i>m</i>	<i>p</i> (sign)	<i>p</i> (G)
5a	mixed	mixed	fleshy > non-fleshy	49	46	26	0.23	0.46
5b	mixed	dry	fleshy > non-fleshy	35	33	20	0.15	0.36
6a	woody	mixed	fleshy > non-fleshy	30	27	20	0.01	0.11
6b	woody	dry	fleshy > non-fleshy	23	21	16	0.01	0.10
7a	herbaceous	mixed	non-fleshy > fleshy	9	9	8	0.02	0.05
7b	herbaceous	fleshy	non-fleshy > fleshy	4	4	4	0.06	0.06

2000a), our results support the 'vegetation' hypothesis. Even if major radiations of frugivores did occur approximately at the same time as the conspicuous increase of fleshy fruited plants in the early Tertiary, the correlated shifts between fruit type and habitat conditions found in the present study suggest that the evolution of fleshiness is related to changing vegetation, which in turn is primarily driven by changing climate (Janis 1993, Graham 1999, Zachos et al. 2001). A compilation of seed sizes was out of scope in the present study, and therefore we only suggest that the association between fleshy fruits and lower light habitats indicate that evolution of larger seed size mediates evolution of fleshiness. Larger seeds are assumed to do better in shady conditions (Leishman et al. 2000), but the 'vegetation' hypothesis does not have to include seed size change. An alternative evolutionary pathway for vegetation driven evolution of fleshy fruits could be that biotic, non-random dispersal (via fleshiness) was acquired to accomplish seed dispersal to high-light habitats (e.g. forest margins, forest clearings, tree fall gaps) when the vegetation in general became more closed. Thereby, any fitness advantages of larger seed size would be reduced. As the evolution of fleshiness was correlated with shifts both to less light and to spatially more unpredictable disturbances, the present study could not discriminate between the alternative mechanisms behind vegetation driven evolution of fleshy fruits.

It is tempting, considering the conspicuous increase of fleshy fruited taxa in the early Tertiary (Tiffney 1984, Eriksson et al. 2000a), to interpret fleshiness as a key innovation in angiosperm history, but previous studies have not found such an effect among angiosperms in general (Eriksson and Bremer 1992, Ricklefs and Renner 1994, Dodd et al. 1999, Davies et al. 2004). de Queiroz (2002) pointed out that key innovations are context dependent, meaning that analyses may fail to find key innovations when they are performed at too a general level. Adding context parameters into the analyses would then enhance the possibility of finding key innovations. Both Tiffney and Mazer (1995) and Smith (2001) included context parameters in their analyses and found positive associations between fleshy fruit types and species richness. In the present study we considered growth form and ancestral fruit type when analyzing associations between fruit type and species richness among phylogenetically independent fruit type changes in seed plants. Among woody plants, a significant number of phylogenetically independent contrasts with derived fleshy fruits had higher extant species richness than the non-fleshy fruited sister clade. However, the quantitative differences in species numbers were not large enough to suggest that fleshiness is a key innovation among woody angiosperms. The different outcomes from the key innovation and sign tests support Tiffney's and Mazer's (1995) idea that biotic dispersal may reduce

extinction rates rather than increase diversification rates. As predicted, non-fleshy fruits were associated with higher species richness in herbaceous clades. Evolution of non-fleshiness may even be interpreted as a key innovation for herbaceous angiosperms, even if the small sample and marginal p-values call for more extensive studies.

The principal reason for examining effects of fleshiness on extant species richness has been the conception that biotic dispersal may enhance spatial isolation of populations and differentiated reproductive success among isolated genotypes due to variation in fruit preferences among frugivores (cf. Crepet 1984), or that biotic dispersal may reduce extinction rates and thereby generate higher extant species numbers (Tiffney and Mazer 1995). Previous studies have failed to find a positive effect of fleshy fruit types on species richness among angiosperms in general (Eriksson and Bremer 1992, Ricklefs and Renner 1994) unless they have accounted for growth form (Eriksson and Bremer 1991, Smith 2001, de Queiroz 2002). A similar trend, that fleshiness is associated with higher species richness in woody clades and with lower species richness in herbaceous clades, was also found by Dodd et al. (1999) even though their analyses rejected any associations. One reason, why growth form is important for fleshy fruit evolution, is probably that the relative cost of fleshiness is higher for smaller (= herbaceous) plants. Small plants have smaller seeds (Thompson and Rabinowitz 1989, Niklas 1994) which disperse easily even if unassisted. Such higher dispersibility of smaller seeds reduces the payoff of fleshiness for smaller plants. Woody angiosperms, on the other hand, often grow and recruit in habitats where selection favour larger seeds, and larger seeds need assistance to be sufficiently dispersed and thereby the payoff of fleshiness increases. There may also be an ultimate limit for the number of seeds produced per individual to accomplish sufficient dispersal, and this limit may be reached faster by smaller plants due to the cost of fleshiness.

Previous studies have discussed whether the origins of fleshy fruits have been restricted to certain periods, e.g. the early Tertiary (Herrera 1989, Eriksson et al. 2000a). Jordano (1995a) interpreted the lack of close (multi-character) correlations between fleshy fruited plants and their frugivores as if frugivores had been important once upon a time "in shaping the major lines of angiosperm families and genera". There is little doubt that the proportion of larger seeds and fleshy fruits was higher during certain periods (Tiffney 1984, Eriksson et al. 2000a), but considering the present data set where not only gains and losses but also speciose clades are distributed throughout the last 70 million years, we conclude that fleshy fruit evolution is a continuously important and recurring phenomenon in plant evolution (Fig. 3). The pattern of origins and losses of fleshy fruits

during the last 70 million years fits with the idea that climate-driven vegetation change, causing shifts in openness of vegetation (Janis 1993, Graham 1999, Zachos et al. 2001), is a mechanism behind evolution of animal-mediated seed dispersal. The finding by Eriksson et al. (2000a) suggesting a comparatively drastic increase in the fraction of lineages with fleshy fruits during the climatic maximum in the Eocene, may reflect the exceptional climatic conditions during that time whereas later climatic fluctuations have been less pronounced (Zachos et al. 2001).

The scarcity of correlations between fleshy fruit and frugivore characteristics reported in the literature has been interpreted as if the interaction is diffuse and that the evolution of fleshy fruits is phylogenetically constrained (Jordano 2000, Herrera 2002b). However, it may also be due to our inability to follow the fate, and thereby the demographic effects, of dispersed seeds. If we initially focus on recruitment conditions, instead of frugivores, and analyze variation in seed and fruit characteristics in relation to demographic effects, frugivores may well be found to have a stronger impact on fleshy fruit evolution than has previously been found. For example, if seed size, fruit size, and dispersal efficiency (i.e. positive population growth due to specific dispersal) are correlated in relation to variation in plant community characteristics (e.g. succession, light gradient), a reduced number of frugivores may turn up to be comparatively more important for fleshy fruit evolution (Wenny and Levey 1998, Jordano and Schupp 2000). The correlation between frugivore size and fleshy fruit size (Mack 1993, Jordano 1995a) and that frugivores discriminate between fruits of different size (Wheelwright 1985, Sallabanks 1993, Jordano 1995b, Rey et al. 1997) may have important implications when we focus on recruitment conditions. As recruitment in low light habitats may be less affected by density-dependent competition for space and light, seeds capable of developing into self-supporting plants in low light habitats may have a comparatively more positive effect on population growth. Larger seeds have been found to cope with hazards typical of such shady habitats better than smaller seeds (Leishman et al. 2000), but larger seeds are also correlated with larger fruits (Jordano 1995a, Bolmgren 2004). So, to the extent that recruitment in low light habitats is important for population growth, frugivores may exert a strong selection pressure on fleshy fruit size evolution. However, we also found support for fleshy fruit evolution being associated with habitats characterized by spatially more unpredictable disturbances, e.g. gap dynamics. Such a correlation supports a hypothesis where frugivores act as 'homing' dispersers, locating gaps in closed vegetation. The ability to direct dispersal to safe sites was questioned by Wheelwright and Orians (1982), but non-random movement and a significantly enhanced abundance of fleshy-

fruited species and frugivores in gaps have gained support since (Levey 1988, Debussche and Isenmann 1994, Jordano 2000, Willson and Traveset 2000). By dropping seeds non-randomly in spatially unpredictable gaps, frugivores reduce the advantages of larger seeds. In such a scenario the evolution of fleshy fruits is the result primarily of adaptations to the 'homing' frugivores, and can not be considered a device evolved to relieve the negative effects on dispersal of larger seeds. Thereby, the habitat correlated evolution of fleshy fruit types does not indicate whether the frugivores' role in fleshy fruit evolution have been to uphold dispersibility for larger seeds or to locate higher light recruitment sites. However, irrespective of which mechanism is dominating, both habitat shifts support the idea that fleshy fruit evolution is primarily driven by vegetation change.

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Appendix 1. All habitat descriptions taken from floras and classified according to canopy closure (0 = open, 0.5 = semi-open, 1 = shaded) and spatial predictability of disturbances (0 = spatially unpredictable, 1 = spatially predictable). Excluded habitat descriptions gave no information on plant community types.

Habitat description in floras	Closedness index	Predictability index
Among shrubs and trees in deciduous forests	1	0
Among undergrowth of deciduous and mixed woods	1	0
Broadleaf forest	1	0
Broad-leaved forests	1	0
Brushwood	1	0
Coastal forests	1	0
Coastal to montane forests	1	0
Damp forests	1	0
Deciduous forest	1	0
Early secondary vegetation	1	0
Epiphytic	1	0
Evergreen forests	1	0
Evergreen forests in mountains	1	0
Forests	1	0
Forests in damp spots	1	0
In dry or wet sclerophyll forest in sandstone derived soil	1	0
In laurisilva	1	0
In primary forest at low altitude	1	0
In thin deciduous forests	1	0
Jungles	1	0
Light forests	1	0
Mixed woods	1	0
Moist Eucalypt forest	1	0
Oak forest	1	0
Primary forest	1	0
Shady woods of the maritime zone	1	0
Shady, wet and mossy woods, often on moss-covered logs	1	0
Sublittoral swamp forest	1	0
Tropical moist forests	1	0
Tropical rainforest	1	0
Village groves	1	0
Younger forests	1	0
Bosques rocosos	1	1
Coastal to montane forests	1	1
Coniferous forest	1	1
Dark coniferous pine woods	1	1
Deep woods	1	1
Dense forest	1	1
Dominant in the woodland zone	1	1
Dry forests	1	1
Dry pine woods	1	1
Dry woods	1	1
Forests	1	1
Forming stands	1	1
Forming woods	1	1
In cerrado	1	1
Mangrove	1	1
Mixed coniferous forest	1	1
Mixed woods	1	1
Montane forest	1	1
Secondary forest	1	1

Appendix 1 (*Continued*)

Habitat description in floras	Closedness index	Predictability index
Shady coniferous and mixed woods	1	1
Woods by mountain streams	1	1
Woods in mountains	1	1
Among shrubs	0.5	0
Among trees and shrubs on drier mountain slopes	0.5	0
Bottomland woods and shrub thickets	0.5	0
Brushwood	0.5	0
Bushland	0.5	0
Chaparral	0.5	0
Clearing in primary forests	0.5	0
Coppices on soil rich in humus	0.5	0
Cupresses woodland	0.5	0
Evergreen scrub	0.5	0
Forest glades	0.5	0
Forest margins	0.5	0
Forest's edge	0.5	0
Wooded savanna	0.5	0
Grassy opening in open oak forest	0.5	0
Heaths	0.5	0
In disturbed mallee-spinifex associations	0.5	0
In mallee and woodland communities	0.5	0
In thickets on rocks	0.5	0
In thin deciduous forests	0.5	0
Light forests	0.5	0
Lowland forest, especially in clearings, around margins, in remnant stands and by streams	0.5	0
Margins	0.5	0
Moorland	0.5	0
More open parts of primary forest	0.5	0
Near boarders of woods	0.5	0
On the margins of rainforests alternatively in rainforest regrowth and clearings	0.5	0
Open woods	0.5	0
Riparian forests	0.5	0
Scrub	0.5	0
Scrub-heath on sand plains	0.5	0
Scrubsavannas	0.5	0
Shrublands on tepui summits or upper slopes	0.5	0
Softwood scrub	0.5	0
Sparse stunted forest	0.5	0
Subtropical and warm temperate rain forest, especially along margins and in regrowth	0.5	0
Sunlit places in coniferous and deciduous woods	0.5	0
Thickets	0.5	0
Willow thickets	0.5	0
Virgin or partly cut coniferous forest	0.5	0
Wood margins	0.5	0
Along creeks	0.5	1
Along irrigation ditches	0.5	1
Along smaller water courses	0.5	1
Along stream banks	0.5	1
Along valley streams	0.5	1
Arroyo	0.5	1

Appendix 1 (*Continued*)

Habitat description in floras	Closedness index	Predictability index
Banks	0.5	1
Banks of streams	0.5	1
Cliff edges in mixed tropical forest	0.5	1
Grassy banks	0.5	1
Lowland forest, especially in clearings, around margins, in remnant stands and by streams	0.5	1
Occasionally banks of streams in mountain woods	0.5	1
Open areas, especially along streams	0.5	1
Open places such as villages, riverbanks, sea shores and in secondary growth	0.5	1
Riparian forests	0.5	1
Riverbanks	0.5	1
Rivers	0.5	1
Streamsides	0.5	1
Widespread in a variety of habitats. In rocky gullies in dry, sclerophyll forest, on exposed rocky spurs in scrubland, common after fire, in scrubland on exposed sites.	0.5	1
Alpine meadows and pastures	0	0
Damp meadows	0	0
Dry savannah	0	0
Dry steppes	0	0
Fallow fields	0	0
Grassland	0	0
Grassy slopes	0	0
In damp grassy savannas in wet areas	0	0
Indulated meadows	0	0
Marshes	0	0
Meadows	0	0
Mossy bogs	0	0
Plains	0	0
Steppes	0	0
Along irrigation ditches	0	1
Along mountain paths	0	1
Along pathside banks	0	1
Among crops	0	1
Arid hills	0	1
As weeds in crops	0	1
Bare mountain peaks	0	1
Barrancas	0	1
Beaches	0	1
Chalky outcrops	0	1
Coastal dunes	0	1
Damp or shady places, mainly in the mountains, rocks and scree	0	1
Deserts	0	1
Disturbed sites	0	1
Dry barren slopes	0	1
Dry hills	0	1
Dry moss- and lichen tundra	0	1
Dry or windblown mountain slopes	0	1
Dry washes	0	1
Edges of fields	0	1
Exposed places	0	1
Feldmark in open sites above snowline	0	1

Appendix 1 (Continued)

Habitat description in floras	Closedness index	Predictability index
Fencerows	0	1
Field margins	0	1
Gorges	0	1
Gravelly slopes	0	1
Gravelly soils and rocks	0	1
Grows by dwellings, deserts, thickets	0	1
Gullies	0	1
Hedges	0	1
In arid areas on sand or limestone rocks	0	1
In banks of soil and debries	0	1
In earth banks	0	1
In hills and on serpentine rocks	0	1
In loess banks	0	1
Levada walls	0	1
Maritime sands	0	1
On sandstone rocks, in clefts	0	1
On seashores at tidal creeks	0	1
On sloping desert hills	0	1
On steep, rocky, exposed coastal sites	0	1
Open areas, especially along streams	0	1
Open stony slopes	0	1
Periodically dry localities	0	1
Periodically indulated riverbank or swamp	0	1
Ploughed fields	0	1
Ravines	0	1
Roadsides	0	1
Rocky ground	0	1
Rocky outcrops	0	1
Rocky peaks	0	1
Ruderal	0	1
Sand plains and low dunes	0	1
Sandy or rocky areas. On well drained soil from sea level to 4000m	0	1
Sandy or rocky places	0	1
Sandy, gravelly or rocky places just above high-tide mark	0	1
Semideserts	0	1
Steep mountainsides	0	1
Stony bush tundra and balds, on grassless ground	0	1
Stony hills	0	1
Stony slopes	0	1
Taluses	0	1
Waste ground	0	1
Waste places	0	1
Weed infested places	0	1
Coastal headlands	excl.	excl.
Hummocks	excl.	excl.
In damp areas	excl.	excl.
Loma formations	excl.	excl.
Valleys	excl.	excl.
Slopes	excl.	excl.