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Correlated evolution of fruit and leaf size in bird-dispersed plants: species-level variance in fruit traits explained a bit further?

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The astounding morphological diversity exhibited by the fruits of vertebrate-dispersed plants has been traditionally interpreted as the adaptive outcome of divergent selective pressures exerted on plants by the broad array of frugivorous animals involved in seed dispersal. Although the selective capacity of frugivores provides support to this interpretation, recent studies have challenged it by documenting a strong phylogenetic component associated to interspecific variation in most fruit characteristics. Size-related fruit traits provide a conspicuous exception to this pattern, because they exhibit considerable variation at the between-species level which is largely independent of phylogeny and is correlated with consumption by differently-sized dispersal agents. Substantial species-level variance in size-related traits may reflect genuine disperser-driven diversification, but may also be partly influenced by correlated evolution of fruit size with the size of other plant structures. This latter possibility is tested here for bird-dispersed plants of the Iberian Peninsula using phylogenetically independent contrasts. Results demonstrate the existence of correlated evolution of fruit and leaf size at the species level. As all the plant taxa considered have their fruits eaten, and seeds dispersed, by the same relatively reduced set of frugivorous bird species, results suggest that a significant fraction of the variation in fruit size represented in the species sample may be explained as an indirect consequence of variation in leaf size, rather than being associated with adaptive divergence related to seed dispersal agents.

The fruits of vertebrate-dispersed plants are notorious for the bewildering diversity of sizes, colors, structures, and amount and nutritional characteristics of the pulp reward offered to vertebrate frugivores (van der Pijl 1969). This extraordinary interspecific variance in fleshy fruit features has been traditionally interpreted as the ultimate result of divergent selection by a broad array of frugivorous mutualists that differ in fruit selection patterns, mobility, trophic apparatus, sensory capacities, and fitness consequences to plants of their seed-processing behavior (van der Pijl 1969, McKey 1975, Snow 1981). Frugivorous animals effectively possess the ability to select differentially among plant species and individuals with fruits differing in characteristics such as color, size and nutritional reward (Howe and Vande Kerckhove 1980, McPherson 1988, Willson et al. 1990, Avery et al. 1993, Sallabanks 1993, Rey et al. 1997). This undisputable selective capacity of frugivores, along with the potential influence of their activity on the fitness of fruiting plants (Herrera et al. 1994, Schupp 1995), is consistent with the evolutionary role granted to them by adaptive interpretations of interspecific variance in fruit features. Nevertheless, an increasing number of studies have recently shown that phylogenetic effects may be equally or more important than seed dispersers in explaining patterns of interspecific variation in fruit features (Debussche et al. 1987, Herrera 1987, 1992, Ehrlén and Eriksson 1993, Fischer and Chapman 1993, Jordano 1995, Eriksson and Ehrlén 1998; see Herrera 2002 for review), thus challenging the prevailing role of frugivores in the diversification of fruit characteristics.

Size-related fruit traits represent conspicuous exceptions to the strong phylogenetic component of interspecific variation in morphological and nutritional fruit traits revealed by the "phylogeny-aware" studies mentioned above. Some of these investigations (Herrera 1992, Fischer and Chapman 1993, Jordano 1995; see also Mack 1993) have shown that a substantial fraction of interspecific variation in size-related fruit traits is not accounted for by phylogeny, and is significantly correlated with consumption by different kinds of dispersers with contrasting body size distributions (e.g. birds vs mammals; Jordano 1995). Does this residual interspecific variance in size-related fruit traits (after accounting for phylogenetic correlations at the genus level and above) mainly reflect genuine disperser-driven diversification generated by fruit selection patterns by dispersers differing in body size and/or trophic apparatus?

This question may be addressed by seeking correlative evidence relating interspecific variation in size-related fruit traits with differences in the size distributions of their consumer frugivores. Such relationships have been reported by a number of studies, irrespective of whether they accounted (Mack 1993, Jordano 1995) or not (Herrera 1985, 1989, 1992, Pratt and Stiles 1985, Debussche and Isenmann 1989) for the effects of phylogenetic correlations. Unfortunately, however, such correlative evidence fails critically at discriminating between the adaptive hypothesis that "differently-sized fruits have come into existence because they have evolved in response to selection by the differently-sized animals that feed on them" from the equally plausible non-adaptive one stating that "because of inherent morphological or behavioral restrictions, differently-sized animals tend to feed on different segments of the fruit size spectrum available to them".

One alternative way of addressing the question above would be to evaluate the merits of plausible alternative hypotheses that do not take into consideration the role of dispersers, yet may account for some fraction of interspecific variance in fruit size. For example, an increasing number of studies show that the sizes of different plant structures, including branches, leaves, flowers, inflorescences and seeds, are significantly correlated across species (White 1983, Primack 1987, Bond and Midgley 1988, Midgley and Bond 1989, Andersson 1993, Ackerly and Donoghue 1998, Cornelissen 1999). If fruit size of vertebrate-dispersed plants were significantly correlated with the size of some other plant structure, then interspecific variance in size-related fruit traits might be at least partly explained by that relationship. The possibility that fruit and leaf size may be linked has already been suggested by Primack (1987), who found the prediction supported in three of the six intrageneric correlations tested (including one fleshy-fruited, vertebrate-dispersed genus). To my knowledge, the possible relationship between fruit and leaf size has not been explored to date for vertebrate-dispersed plants in a broad taxonomic context, despite the considerable effort devoted in the last two decades to explore the adaptive basis and ecological correlates of interspecific variation in fruit characteristics (Herrera 1987, Jordano 1995, and references therein). Using an independent comparisons approach (Felsenstein 1975, Burt 1989, Harvey and Pagel 1991), I examine in this paper the relationship between fruit and leaf size among species of Iberian bird-dispersed plants. Results clearly indicate that fruit size and leaf size exhibit correlated evolutionary change at the terminal, between-species level of diversification, and suggest that climate-driven diversification in leaf size may ultimately account for an important fraction of interspecific variance in fruit size in the set of bird-dispersed species considered.

Taxa sample and methods

Information on mean length, width (cross diameter) and fresh mass of bird-dispersed fruits was drawn from a large database containing information on structural and nutritional characteristics of Iberian fleshy-fruited plants. Except for minor additions, the database used was essentially the same analyzed by Herrera (1987) and summarized in Tables A1 and A2 of that publication. The database contains information on the characteristics of the fruits of ~120 species of vertebrate-dispersed plants native to the Iberian Peninsula. This represents about 95% of the families, 87% of genera and an estimated 62% of species with fleshy fruits that occur on the Iberian Peninsula (see Herrera 1987 for sampling methods and geographical locations). I screened the database for sets of congeneric species that would qualify to test for a relationship between fruit and leaf size using phylogenetically independent contrasts for the two traits. Only species known or presumed to be exclusively or predominantly dispersed by a relatively small group of small (mainly *Sylvia* spp.) and medium-sized (mainly *Turdus* spp.) frugivorous passerine birds were considered, based on information in Herrera (1995), and references therein; and unpublished observations). As the focus of this study was on patterns of variation below the level of genus, and infrageneric phylogenies are not available for the plant genera involved, species sets had necessarily to be defined on the basis of their affiliation to genera or, in a few instances, to well-supported infrageneric (subgenus or section) categories. Using taxonomic affiliation instead of resolved phylogenies as the basis for selecting groups of taxa for independent contrasts may lead to biased results if the taxonomic entities chosen are not strictly monophyletic (Burt 1989, Harvey and Pagel 1991). In the present instance, however, it seems reasonable to assume that the generic and infrageneric categories considered represent monophyletic lineages.

To qualify for analysis, the leaves of all species in a given set should have the same basic shape and differ only by a scale factor. In this way, one could safely assume that differences in linear measurements (length and width, see below) accurately reflected differences in leaf size (i.e. area or mass). To the same end, taxa with compound leaves (e.g. *Pistacia*, *Rosa*, *Sambucus*, some *Sorbus* species) were excluded from analysis because the size of single leaflets, the information usually reported in floras (see below), may not adequately reflect actual differences in overall leaf size. Eventually a total of 21 sets of congeneric bird-dispersed species were retained for the independent contrasts analysis (Table 1). Two sets were made up of species within distinct subgenera of the same genus (*Prunus*), and four comprised species within distinct sections of two genera (*Lonicera* and *Rhamnus*). Mean fruit size of each species was initially assessed using both linear and mass measurements. As analyses based on the two metrics of fruit size yielded identical results, only the results based on linear dimensions will be presented here for simplicity. For each species, the geometric mean of average fruit length and width will be used as the descriptor of "fruit size". Information on mature leaf size of all the species considered was gathered from regional (Valdés et al. 1987), national (Castroviejo 1986–1999) or continental (Tutin et al. 1964–1980) standard floras, mentioned in decreasing order of search priority. With only one exception (*Atropa* spp.), all leaf dimension data for species in the same set were taken from the same literature source, to avoid possible inconsistencies among monographers in reporting leaf size. For the purposes of the analyses, "leaf size" was defined as the geometric mean of the midpoints for the reported ranges of leaf length and width.Three of the 21 sets of species chosen for analysis were composed of three species, and one was composed of four species (Table 1). In these cases, linear contrasts were computed using Pagel's (1992) method. Species in the set were first divided into two groups according to their values of leaf size. Those with

Table 1. Species sets ("independent contrasts", IC) of Iberian bird-dispersed plants chosen for the analysis of the correlation between fruit and leaf size. Nomenclature follows Tutin et al. (1964–1980).

IC # [a]	Genus (Family)	Species	Fruit size (mm) [b]	Leaf size (mm) [c]
1	*Asparagus*	*acutifolius*	6.8	1.4
	(Liliaceae)	*aphyllus*	6.9	3.7
2 *	*Atropa*	*baetica* (S)	11.0	68.7
	(Solanaceae)	*belladonna* (N)	12.4	86.6
3 *	*Berberis*	*hispanica* (S)	7.2	10.0
	(Berberidaceae)	*vulgaris* (N)	7.6	22.8
4	*Cotoneaster*	*granatensis*	7.2	22.9
	(Rosaceae)	*integerrimus*	6.3	19.8
5	*Crataegus*	*laciniata*	11.8	25.0
	(Rosaceae)	*monogyna*	10.6	20.0
6	*Daphne*	*gnidium*	5.6	11.2
	(Thymelaeaceae)	*laureola*	7.8	41.1
		oleoides	5.4	11.8
7	*Euonymus*	*europaeus*	5.9	41.7
	(Celastraceae)	*latifolius*	6.0	73.9
8	*Juniperus*	*communis*	6.2	3.6
	(Cupressaceae)	*oxycedrus*	9.5	3.8
9	*Lonicera* (sect. *Caprifolium*)	*etrusca*	7.4	34.1
	(Caprifoliaceae)	*implexa*	6.7	28.3
		splendida	9.7	30.7
10 *	*Lonicera* (sect. *Lonicera*)	*arborea* (S)	7.8	24.5
	(Caprifoliaceae)	*xylosteum* (N)	8.5	41.8
11	*Osyris*	*alba*	8.8	7.1
	(Santalaceae)	*quadripartita*	7.4	12.0
12	*Phillyrea*	*angustifolia*	5.2	24.5
	(Oleaceae)	*latifolia*	7.3	33.2
13 *	*Prunus* (subgen. *Cerasus*)	*mahaleb*	8.1	31.0
	(Rosaceae)	*padus* (N)	7.9	56.5
		avium (N)	13.1	76.0
		prostrata (S)	7.1	11.6
14 *	*Prunus* (subgen. *Prunus*)	*ramburii* (S)	8.9	9.5
	(Rosaceae)	*spinosa* (N)	13.3	15.8
15	*Rhamnus* (sect. *Alaternus*)	*alaternus*	5.9	34.5
	(Rhamnaceae)	*myrtifolius*	6.5	10.3
16	*Rhamnus* (sect. *Rhamnus*)	*lycioides*	5.9	17.7
	(Rhamnaceae)	*saxatilis*	5.5	13.2
17	*Ruscus*	*aculeatus*	11.5	25.5
	(Liliaceae)	*hypophyllum*	12.8	49.0
18	*Solanum*	*nigrum*	6.9	39.3
	(Solanaceae)	*dulcamara*	9.2	51.2
19	*Sorbus*	*latifolia*	13.2	87.5
	(Rosaceae)	*aria*	11.0	66.3
		mougeotii	10.2	72.5
20 *	*Viburnum*	*lantana* (N)	7.5	75.0
	(Caprifoliaceae)	*tinus* (S)	6.6	52.6
21 *	*Viscum*	*album* (N)	7.9	40.9
	(Viscaceae)	*cruciatum* (S)	6.0	23.6

[a]: IC's marked with asterisks are considered in the Discussion, and consist of species with vicariant distributions in the Iberian Peninsula, occupying either moist temperate forests in the north (species coded with N) or summer-dry Mediterranean habitats in the south (S).

[b]: Geometric mean of fruit length and width (cross diameter).

[c]: Geometric mean of leaf length and width.

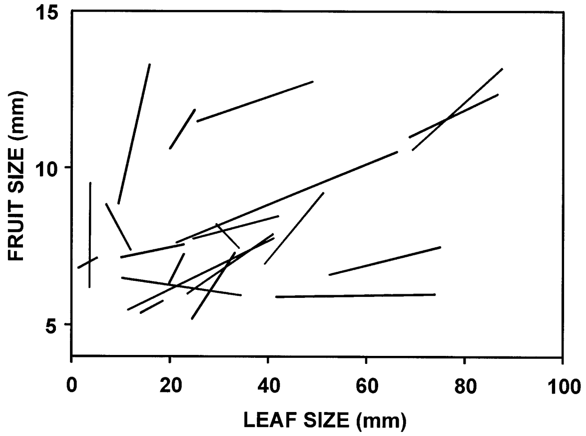

Fig. 1. Relationship between fruit and leaf size in a sample of bird-dispersed, fleshy-fruited Iberian plants. The two values corresponding to each phylogenetically independent contrast (Table 1) are connected by a line. For sets comprising more than two species, contrasts were computed as detailed in the text.

leaf size above the mean for the set were put into one group, while the rest were put into other group. Linear contrast coefficients were then obtained as the reciprocal of the number of species in each group, with those in the second group being given a negative sign. Raw contrasts for leaf size and fruit size were then obtained as the difference of the corresponding group means for these two variables (Harvey and Pagel 1991). Standardized contrasts were obtained using Pagel's (1992) method as implemented in the CAIC program (Purvis and Rambaut 1995).

Results

The sign and magnitude of the raw (nonstandardized) independent contrasts (IC's hereafter) for fruit and leaf size are depicted in Fig. 1. Out of a total of 21 IC's, there were 18 positive relationships between the two variables, i.e. simultaneous increases in both leaf and fruit size. This high proportion of positive associations in the direction of change (85.7%) is significantly greater than that expected by chance alone, i.e. if the two variables covaried independently ($P = 0.0015$, two-sided binomial test). This qualitative finding thus suggests that fruit and leaf size are correlated in the set of species considered.

This is corroborated by the quantitative analysis of the relationship between the standardized contrasts for leaf and fruit size shown in Fig. 2. In this graph, the contrasts in leaf size (horizontal axis) are all made positive by convention, and those for fruit size (vertical axis) are positive or negative depending on whether the changes in the two traits covary positively or negatively, respectively. Correlation or regression analysis of these data must take into consideration the symmetry arising from the arbitrary direction of contrasts, and thus regressions or correlations must be fitted through the origin (Garland et al. 1992). The significance of the relationship between the standardized contrasts for fruit and leaf size was tested by means of the correlation coefficient through the origin (computed using the formula in Martins and Garland 1991), as there were no a priori reasons to assign the roles of dependent and independent variables to these variables in a linear regression. The correlation coefficient was positive and significantly different from zero ($r \pm \mathrm{SE} = 0.613 \pm 0.120$, $N = 21$ contrasts, 95% confidence interval = 0.328–0.802; SE and CI determined using accelerated bias-corrected bootstrap resampling of the standardized contrasts data). Results remained unchanged after excluding from the computations the extreme data point in the top right corner of Fig. 2, corresponding to IC # 13 ($r \pm \mathrm{SE} = 0.523 \pm 0.125$, CI = 0.256–0.747).

Discussion

Results of this study provide strong support for the existence of correlated evolution of fruit and leaf size at the species level among Iberian bird-dispersed plants. This conclusion is further strengthened by the fact that the two analytical methods used here, a sign test and correlation based on contrasts computed exclusively at the between-species level, possess low statistical power, thus providing highly conservative tests of trait associations (Ackerly 2000). Current availability of seed plant phylogenies would have made possible the application of independent contrasts at deeper nodes. Nevertheless, the decision of restricting the analysis to the terminal

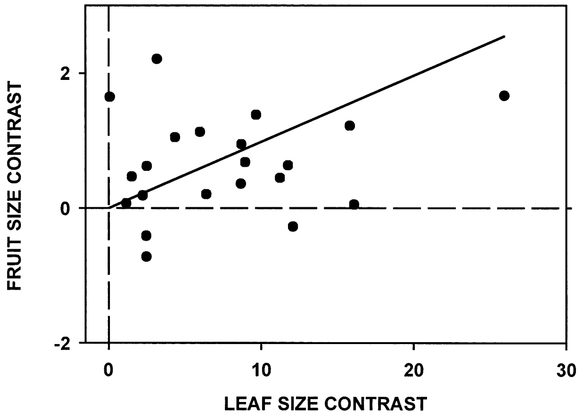

Fig. 2. Scatterplot of standardized independent contrasts of fruit size vs leaf size computed for the congeneric species sets listed in Table 1. Each contrast represents the difference in the corresponding trait values between two sister taxa. The line shown is the reduced major axis regression fitted through the origin ($y = 0.0981x$).

divergences and studying correlated evolution of leaf and fruit traits at the between-species level was dictated by the ultimate goal of this investigation. As noted in the Introduction, my purpose here was to evaluate the possibility that the large residual (i.e. after accounting for pervasive phylogenetic correlations above the species level) interspecific variances in size-related fruit traits documented by some recent investigations may be unrelated to variation in dispersers.

Given the relatively small sample of taxa examined in this study, results of independent contrasts analysis may be influenced by taxon sampling effects (Ackerly 2000). There are reasons, however, to suggest that the correlation between fruit and leaf size found here probably reflects a general relationship occurring in a wider phylogenetic context, and is not the spurious consequence of a phylogenetically biased or otherwise idiosyncratic species set. First, the dataset analyzed includes species from 12 different plant families widely distributed over the seed plant phylogeny (Soltis et al. 2000). Both gymnosperms and angiosperms are represented in the sample and, among the latter, there are both dicot and monocot genera. Results thus suggest that correlated variation between leaf and fruit size occurs repeatedly and consistently in different phylogenetic lines. Secondly, the sample includes species from a variety of habitat types, from Mediterranean-climate woodlands and shrublands through temperate conifer and broadleaved forests (Herrera 1987: Fig. 1). The whole spectrum of growth forms is also represented in the sample, which includes perennial herbs, shrubs, trees and woody climbers. This reduces the likelihood that the character correlation found stems from a biased selection of species from plant communities or growth forms where the association between the characters is stronger than average.

Considerable attention has been paid to the ecological significance of variation in leaf attributes, both across and within habitats, and previous comparative studies have found a variety of relationships of leaf traits among themselves and with other plant traits. In some cases, such relationships presumably reflect the coordinated response to selection of the traits involved. This most likely applies, for example, to correlations predicted by leaf biophysical models based on optimality principles (Parkhurst and Loucks 1972, Givnish and Vermeij 1976, Givnish 1979). The recurrent combination of functional leaf traits in distantly related taxa across biomes (Reich et al. 1999) and the correlated evolution of some of them (Ackerly and Reich 1999) strongly suggest that, in these instances, the correlations themselves possess adaptive value. In other cases, however, the adaptive value of the correlated variation between leaf traits and other plant traits is much less straightforward. This applies to associations frequently reported between leaf size and plant height, stem diameter, inflorescence size, or seed size (White 1983, Bond and Midgley 1988, Midgley and Bond 1989, Andersson 1993, Ackerly and Donoghue 1998, Cornelissen 1999). Correlations between leaf size and any of these characters may reflect parallel, independent adaptive responses to some abiotic or biotic factor, or be the consequence of some allometric relationship mediated by a general “size factor” (e.g. pleiotropic effects of genes controlling size) affecting all plant parts (Primack 1987, Thompson and Rabinowitz 1989, Shipley and Dion 1992). The relationship documented here between fruit and leaf size for Iberian bird-dispersed plants probably belongs to one of these two latter categories. Irrespective of its ultimate adaptive value, an hypothesis of functional correlation may be advanced which could account for the observed correlation between leaf size and fruit size. Both leaves and fruits must be supported biomechanically by the same branches. If there are a limited number of branches there will be parallel size/number tradeoffs for vegetative and reproductive structures at the whole plant level and, if resources for fruit development are supplied by subtending leaves, then larger fruits will be associated with larger leaves (Ackerly and Donoghue 1998, D. Ackerly, pers. comm.). As this hypothesis applies particularly to whole infructescences rather than to individual fruits (Midgley and Bond 1989, Cornelissen 1999), assessing its explanatory value would require simultaneous consideration of the relationships between leaf, fruit, and infructescence size.

Part of the interspecific variance in leaf size occurring in my species sample is attributable to the broad range of ecological conditions sampled. As noted earlier, the sample of bird-dispersed taxa considered includes species inhabiting diverse habitat types from contrasting climatic regions in the Iberian Peninsula, ranging from moist temperate forests in the north to summer-dry, Mediterranean scrublands in the south. A relationship between climate and leaf size has been known for a long time (Parkhurst and Loucks 1972, and references therein), and Mediterranean-climate regions of the World are no exception to the pattern of decreasing leaf size with increasing aridity and insolation (Parsons and Moldenke 1975, Parsons 1976, Ackerly et al. 2002). A similar trend exists in the Iberian Peninsula for decreasing leaf size as one moves from northern moist temperate forests to southern dry Mediterranean shrublands. This pattern is illustrated in the species sample examined here by seven sets of vicariant congeners having disjunct geographical distributions, with species occuring in either northern (moist temperate) or southern (dry Mediterranean) habitats (Table 1). In all the seven instances, southern taxa had smaller leaves than their sister northern taxa, which departs significantly from random expectation ($P = 0.016$, two-sided binomial test). This finding, along with the observation that six of the seven southern, smaller-leaved vicariants are endemic to Mediterranean-climate regions of southern

Spain and northwestern Africa, provide compelling evidence that part of the variation in leaf size represented in my species sample most likely originated as an adaptive response to variation in abiotic conditions. In this scenario, and keeping in mind that all the plant taxa considered here largely share the same species of seed dispersers, the correlated evolution of fruit and leaf size found in this study would reflect either (1) changes in fruit size were subsequent to, and a mere allometric consequence of, adaptive changes in leaf size occurring in response to the biotic environment; or (2) changes in fruit size reflect parallel adaptive modification in response to the abiotic environment. Developing fleshy fruits are photosynthesizing structures themselves, and thus perhaps also susceptible to the same abiotic factors that are generally accepted to select for evolutionary modifications of leaf traits. Decreased moisture levels in Mediterranean-climate regions could thus not only select for a reduction in leaf size, but also for a parallel reduction in fruit size. The information available does not allow for discriminating between these two explanations.

Regardless of its ultimate cause and proximate mechanisms involved, the correlation between leaf and fruit size documented here for a set of bird-dispersed plants serves to suggest plausible alternative scenarios and hypotheses for the evolution of interspecific variance in size-related fruit traits that are independent of the selective action of dispersal agents. Results also highlight the importance of considering allometric relationships in studies of plant reproduction, because of both its inherent explanatory potential and its value as suitable "null models" in comparative studies (Bond and Midgley 1988, Thompson and Rabinowitz 1989, Shipley and Dion 1992). Among other consequences, recognition of these possibilities calls for a reassessment of the presumed adaptive basis in relation to dispersers of some geographic or elevational trends in fruit size reported previously (e.g. Herrera 1985). In the light of the results reported here, these patterns in fruit size might merely ensue from geographical variations in abiotic factors, either directly or indirectly through their effects on leaf size. Concomitant changes in disperser composition and size distribution could be a secondary ecological consequence brought about by the operation of "ecological fitting" processes (sensu Janzen 1985), rather than its ultimate evolutionary cause. Further studies are needed to evaluate these possibilities.

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