

Original article

Patterns of fruit traits in a tropical rainforest in Xishuangbanna, SW China

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Abstract

As a basis for determining how vertebrate frugivores influence the evolution of tropical fruits, we investigated distribution patterns of different fruit traits that are known to influence frugivore food choice, drawing on data gathered from 626 plant species in a primary tropical rainforest at Xishuangbanna, SW China. Species with fleshy fruits are common (66%) in the forest; the proportion of fleshy fruits differed among different growth forms: canopy trees (63%), subcanopy trees (83%), shrubs (74%), lianas (67%), herbs (65%) and epiphytes (49%). Dry fruits had a higher frequency of small-seeded species (length of seed <2 mm) compared to fleshy fruit (34% vs. 14%, respectively), and a lower proportion of species with few seeds (1–3 seeds per fruit) (52% vs. 77%). In fleshy fruits, small fruits (<20 mm in length) were predominant (69%) while medium-sized fruits (20–50 mm) were produced by 105 species (26%), and 20 species (5%) produced large fruit (>50 mm). As a whole, black fruits were most common (40% of 389 species), followed by fruits with red, brown, yellow and bicolored (19%, 13%, 13% and 8%, respectively); green, white, and blue fruits were relatively rare (4%, 2% and 1%, respectively). Characteristics of small fleshy fruits included thin husks, red, white, or black colors and a few medium-sized seeds (2–10 mm). Many medium-sized fruits had large, well-protected seeds. The distribution of plant species among various fruit and seed categories is non-random in this forest. Nested ANOVA revealed a significant phylogenetic component in the variances of most fruit traits while fruit size and color showed 39.7–48.1% of within-genus variances from non-phylogenetic factors.

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Fruit traits may influence the accessibility and foraging preference of frugivores, consequently different plant seeds are dispersed by different animals (van der Pijl, 1982; Charles-Dominique, 2001). To evolutionary ecologists, a major question is, “To what extent are fruit traits evolutionary adaptations to dispersers?” Many studies have suggested that the relationship between fruiting plants and their fruit consumers/seed dispersers occurs via “diffuse coevolution” (Howe and Vande Kerckhove, 1980; Wheelwright and Orians, 1982; Janzen, 1983, O’Dowd and Gill, 1986; Janson, 1992; Stiles and Rosselli, 1993 and many others; but see Fischer and Chapman, 1993; Herrera, 1998; Levey and Benkman, 1999), which Janzen (1980) defined as “...[it] occurs when either or both populations in the coevolution are represented by an array of populations that generate a selective pressure as a group.” While it is difficult to test this hypothesis directly, attempts are often made to examine diffuse

coevolutionary relationships indirectly, e.g., by studying whether certain associations exist among different fruit traits and particular groups of dispersers, or whether there is a correlation between a fruit display and its frugivores (McKey, 1975; Gautier-Hion et al., 1985; Mack, 1993; Fischer and Chapman, 1993; Fuentes, 1995; Jordano, 1995; Kalko et al., 1996; Herrera 1982, 1985, 1995, 1998). Results of these studies have often disagreed with each other, and the question is still open for discussion (Levey and Benkman, 1999; Fuentes, 2000).

Characteristics that may influence the food choice of frugivores (but see Sallabanks and Courtney, 1993; Ladley and Kelly, 1996) include fruit size (Snow, 1981; Knight and Siegfried, 1983; Wheelwright, 1985), fruit color (Janson, 1983; Wheelwright and Janson, 1985; Willson et al., 1989; Willson and Whelan, 1990), fruit protection (Janzen and Martin, 1982, Gautier-Hion et al., 1985; Charles-Dominique, 1993), fruit phenology (Stiles, 1980; Corlett, 1996), seed size (Gautier-Hion et al., 1985; Fleming et al., 1993; Murray et al., 1993), seed number (Gautier-Hion et al., 1985), and

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nutritional aspects of fruit pulp (Johnson et al., 1985; Herrera 1982, 1984, 1998). Some of these traits are often used as bases for categorizing different dispersal types (van der Pijl, 1982; Howe, 1986; Janson, 1992). By incorporating information on animal aspects, geographic comparisons of the pattern of seed dispersal syndromes, either on a community scale (Jordano, 1993; Fuentes, 1995) or on a regional scale (Fleming et al., 1987; Willson et al., 1989; Fischer and Chapman, 1993; Mack, 1993), have been conducted to explore the ecological and evolutionary implications of interactions between plants and their frugivores. However, these attempts have often been constrained by an imbalance in the existing data on plants and animals, by different standards used for assessment, and by the relatively few areas in which extensive research has been conducted.

Reasons that account for patterns of fruit traits are often complex (Herrera, 1987, 2002b; Thompson, 2002). Several studies have demonstrated that when phylogenetic effects are taken into account, diffuse coevolution with frugivores explains little of the variation of fruit traits (Herrera, 1992; Fischer and Chapman, 1993). Jordano (1995), in a thorough investigation, found that dispersal syndromes are only minimally attributable to plant adaptations to dispersers. Instead, they largely reflect the great influence of plant phylogeny on fruit traits. After accounting for phylogenetic effects, he concluded that “correlated evolution (of fruit traits) with type of seed disperser is, at best, only evident for fruit diameter”.

Xishuangbanna is well known for its rich biodiversity and still maintains the most representative and the best conserved tracts of tropical rain forest in China (Zhu, 1997). Floristic analysis indicates that the forest in Xishuangbanna is true tropical rain forest; it has the same profile, physiognomic characteristics, species richness per unit area, numbers of individuals per tree species and diameter classes of trees as classic lowland tropical rain forests (Zhu, 1997). In contrast, to the extensive work conducted by Chinese scientists cataloguing plants in this area (XTBG & DE-KIB, 1996), information in English about these forests is relatively lacking (but see Zhang and Cao, 1995; Zhu, 1997). As a result, many geographic comparisons often exclude this area.

In this study, we describe the pattern of fruit characters of plants and examine whether non-random associations exist for different traits of fruits that are known to influence frugivore food choice. We then examine the extent to which this variation can be attributed to phylogenetic effects. Finally, we discuss the effects of frugivores and the environment on patterns of fruit traits.

1. Materials and methods

1.1. Study area

Xishuangbanna (21°10′–22°40′ N, 99°55′–101°50′ E) is a prefecture of Yunnan province of China with a total area of 19,220 km². Bordered by Myanmar to the southwest and

Laos to the south and southeast, the region is controlled by a typical tropical monsoon climate characterized by a distinct rainy season (May–October), with peak precipitation occurring in July–September, followed by a cool dry season (November–January) and a hot dry season (February–April). Its altitude varies from 420 to 2400 m, and climate changes conspicuously with altitude. In Xishuangbanna, tropical rainforests occurs mainly in valleys and on lower hills below 900 m where annual precipitation is about 1500 mm and annual mean temperature is 21–22.8 °C (Zhu, 1997). For a detailed description of the forest, see Zhu (1997).

1.2. Data collection

Instead of using all the plants in the regional flora, we developed a list of plants for this study based on 19 sample plots with a total area of 7.3 ha from published literature (Wu and Zhu, 1987; Zhu, 1997; Wang et al., 2001; Zhu et al., 2001). We assumed that the 626 plant species in this study are representative of the flora in the tropical rainforest in this area, which contains about 1000 species (Zhu, 1997). All of the plot data were from primary forest; most plants in secondary forest were excluded from this study.

Data on different plant and fruit parameters are based on published literature and floras (Institutum Botanicum Kunmingense Academiae Sinicae Edita, 1975, 1979, 1983, 1986, 1991, 1995, 2000, 2001), as well as the authors' field observations (LZ, HW and JC). Definitions and categories used in the study were fleshy vs. dry fruit, plant growth form (Charles-Dominique, 2001), season of fruit ripening, fruit size, fruit color (Wheelwright and Janson, 1985; Willson 1989), fruit protection (Gautier-Hion et al., 1985), seed protection (Gautier-Hion et al., 1985), seed size and number of seeds per fruit (Table 1). About 2% of the data with questionable determinations were excluded from this study (e.g., 89 exclusions out of 12 characteristics × 412 species = 4944 data points for fleshy fruits). For fruit size, we note that various methods and standards have been used in previous studies, i.e., the cutoff criteria for small fruits/bird fruits were 10 mm (Howe, 1986) and 14 mm (Janson, 1983) in length; 20 mm (Willson et al., 1989) and 25 mm in diameter (Wheelwright and Janson, 1985) or three groups based on cutoff criteria of 5 and 50 g (Gautier-Hion et al., 1985). In this study, we use maximum length to classify fruit size into three groups. We did this because maximum length is significantly positively related to fruit weight based on our unpublished data for 37 species of fleshy fruits in the area ($R^2 = 0.937$, $N = 37$, $P < 0.001$). Furthermore, maximum lengths of 20 and 50 mm are equivalent to fruit weights of 5 and 50 g, respectively. We divided the year into three seasons of four months each; this is somewhat subjective because the rainy season often starts in May. We did this to equalize the length of each season for categorization purposes. Plants ripening their fruit across different seasons were recorded in each season. We also used maximum length for measuring seed size; maximum length is also signifi-

Table 1
Definitions and categories of fruit parameters in this study

Parameter	Category and definition
Fleshy vs. dry fruit	Fleshy fruit, dry fruit. Fleshy fruit followed Willson et al. (1989). Otherwise, classified as dry fruit.
Growth form	Canopy tree (CT), subcanopy tree (ST), shrub (SH), liana (LI), herb (HE), epiphyte (EP). Canopy trees occur in the top layer of forest or are emergent; otherwise we classified them as subcanopy trees. Other growth forms follow Charles-Dominique (2001).
Season of fruit ripening	Hot and dry season (February–May), rainy season (June–September), cool and dry season (October–January). See text for more information.
Fruit size	Maximum fruit length: small: <20 mm; medium: 20–50 mm; large: >50 mm. See text for more explanation.
Fruit color	Black, blue, red, orange, yellow, white, green, brown, or bicolor. Classification of color based on definitions of Wheelwright and Janson (1985) except bicolor for which we follow Willson et al. (1989).
Fruit protection	(1) Dehiscent; (2) indehiscent, thin husk; (3) indehiscent, thick husk. Definitions follow Gautier-Hion et al. (1985).
Seed protection	(1) No protection; (2) thin seed coat; (3) thick seed coat. Definitions follow Gautier-Hion et al. (1985).
Seed size	Maximum seed length: small: <2 mm; medium: 2–10 mm; large: >10 mm. See text for more explanation.
No. of seeds per fruit	Few: 1–3; some: 4–10; many: >10.

cantly positively related to seed weight ($R^2 = 0.919$, $N = 36$ species, $P < 0.001$).

A variety of methods have been described in recent years to assess the influence of phylogeny on interspecific patterns (e.g., Felsenstein, 1985; Pagel and Harvey, 1988; Bell, 1989). Some of them require a detailed knowledge of the phylogeny of the species involved (Freckleton et al., 2002). Methods that infer phylogeny from the taxonomic hierarchy and that are based on the use of nested analysis of variance and covariance are more appropriate in this study. Using nested ANOVA (BIOMstat 3.2 software, Sokal and Rohlf, 1995), we tested the degree to which taxonomic level contributed to differences in fruit traits. Fruit characters that we tested included fruit size, fruit color, fruit protection, seed size and seed number. Five taxonomic levels (genus, family, order, subclass, class) were incorporated in a nested ANOVA for the traits. An analysis was run for each of the classification schemes of Hutchinson (1934) and Cronquist (1981).

2. Results

2.1. General flora

This study included a total of 626 species belonging to 109 families and 333 genera; the number of species per family and per genus averaged 5.7 and 1.9, respectively. Growth forms included 339 species of trees (including 194 canopy trees and 145 subcanopy trees (54%)), 119 lianas (19%), 69 herbs (11%), 62 shrubs (10%), and 37 epiphytes (6%).

2.2. Fleshy vs. dry fruits

A total of 412 species (66%) produces fleshy fruits. Of these, 195 species (47%) produce drupes followed by 131 species (32%) of berries, 59 species (14%) of syncarps, 21 species (5%) of capsules, two species of pomes, and four undetermined species. For dry fruits, capsules were produced by 110 species (54%), followed by 42 species of nut and winged fruits (or seeds), 23 species of pods, 10 achenes, 19 follicles, one utricle, and nine undetermined species.

The highest proportion of fleshy fruits occurred in subcanopy trees (83%), followed by shrubs (74%), lianas (67%), herbs (65%), canopy trees (63%), and epiphytes (49%). As a group, 71% of all trees bear fleshy fruits ($N = 339$).

Proportions of different seed sizes differed significantly between fleshy and dry fruits. Dry fruits had a relatively higher frequency of small-seeded species (length of seed <2 mm) compared to fleshy fruit (34% vs. 14%, respectively) (Table 2). Fleshy and dry fruits also differed in seed number per fruit. Fleshy fruits tended to have a higher proportion of species with few seeds (1–3 seeds per fruit) than dry fruits (77% vs. 52%). Distribution of growth form, season of fruit ripening, and seed protection did not differ between species producing fleshy or dry fruits (Table 2).

2.3. Size of fleshy fruit

Most fleshy fruits (69%, $N = 277$) were small (<20 mm in length). Medium-sized fruits (20–50 mm) were produced by 105 species (26%), and 20 species (5%) produced large fruit (>50 mm).

2.3.1. Fruit size and life form

The distribution of fruit sizes differed significantly among plant growth forms ($\chi^2 = 59.224$, $df = 10$, $P < 0.0001$). Most plants bearing large fruit (65%) were canopy trees. Canopy trees (39%), subcanopy trees (35%), and lianas (20%) produced medium-sized fruits. Small fruits occurred in all growth forms (Fig. 1A).

2.3.2. Fruit size and season of ripening

The distribution of different-sized fruits also differed significantly by fruiting season ($\chi^2 = 14.560$, $df = 4$, $P = 0.0057$). This difference resulted from the difference between large fruits and both medium- and small-sized fruit (two-sample test, $\chi^2_{1-s} = 10.98$, $df = 2$, $P = 0.004$, $\chi^2_{1-m} = 10.660$, $df = 2$, $P = 0.005$). Plants with large fruit had a high proportion of species (65%) with ripe fruits in the cool and dry season whereas small- and medium-sized fruits were produced in the rainy season (65% and 74%, respectively).

Table 2
Comparison of frequencies of species number of fleshy fruits and dry fruits for different parameters. See Table 1 for definitions of each category of the parameters

Parameters	Fleshy fruit	Dry fruit
<i>Growth form</i>		
$\chi^2 = 8.915$, df = 5, $P = 0.113$		
<i>N</i>	412	214
Canopy tree	29.6	33.6
Subcanopy tree	29.1	11.7
Shrub	11.1	7.5
Liana	19.4	18.2
Herb	6.3	6.5
Epiphytes	4.4	8.9
<i>Season of fruit ripening</i>		
$\chi^2 = 4.013$, df = 2, $P = 0.135$		
<i>N</i>	412	214
Hot and dry	16.3	19
Rainy	64.6	47.7
Cool and dry	42.5	53.8
<i>Seed protection</i>		
$\chi^2 = 1.124$, df = 2, $P = 0.570$		
<i>N</i>	398	207
No protection	19.8	25.1
With thin protection	34.2	28.5
Well protected	46	46.4
<i>Seed size</i>		
$\chi^2 = 11.196$, df = 2, $P = 0.0037$		
<i>N</i>	397	206
Small	13.9	34
Medium	57.7	45.1
Large	28.5	20.9
<i>Number of seeds per fruit</i>		
$\chi^2 = 13.125$, df = 2, $P = 0.0014$		
<i>N</i>	399	205
Few	76.7	52.2
Some	9	21.5
Many	14.5	26.3

2.3.3. Fruit size and color

Fruit size appeared to be strongly associated with fruit color ($\chi^2 = 69.358$, df = 12, $P < 0.0001$, data for blue color were excluded from this analysis to avoid bias due to small sample size). Black and red were the predominant colors in small fruits (43% and 26%, respectively). Black was also common (35%) in medium-sized fruit while red fruit were much less common (6%) in this size category. Yellow (30%) and brown (25%) occurred much more frequently in large than in smaller fruits. Orange and blue colors were rare across all fruit sizes (Fig. 1B).

2.3.4. Fruit size and protection

Different-sized fruit differed significantly in fruit protection (Fig. 1C, $\chi^2 = 53.748$, df = 4, $P < 0.0001$). Most small fruits (83%) were indehiscent with a thin husk. Both types of indehiscent fruits with thin husk (43%) and thick husk (42%) occurred in medium-sized fruits. The three types of fruit protection occurred more even in large-sized fruits (tested by 1:1:1, $\chi^2 = 3.054$, df = 2, $P = 0.217$).

2.3.5. Fruit size and seed characters

Seed size also differed significantly by fruit size (Fig. 1D, $\chi^2 = 82.908$, df = 4, $P < 0.0001$). Most small fruits (70%) had medium-sized seeds (2–10 mm in length), in contrast to medium-sized fruits in which most species (72%) had large seeds (>10 mm in length). Large fruit had both medium seeds (55%) and large seeds (35%). Small seeds occurred in relatively low proportion across all three fruit types (3–18%). The distribution of seed protection also differed significantly among different fruit sizes (Fig. 1E, $\chi^2 = 42.357$, df = 4, $P < 0.0001$). Medium and large fruits had relatively high proportions of well-protected seeds (Fig. 1E). For both small- and medium-sized fruits, most species bear fruits with few seeds per fruit (1–3 seeds per fruit) (83% and 71% of these plants, respectively); large fruits had more species with many seeds per fruit (Fig. 1F).

2.4. Color of fleshy fruits

As a whole, black fruits were most common and represented 40% of total species ($N = 389$). The next most common colors were red, brown, yellow and bicolored (19%, 13%, 13% and 8%, respectively). Green, white, and blue fruits were relatively rare (4%, 2% and 1%, respectively).

2.4.1. Fruit color and growth form

Fruit colors were distributed non-randomly across growth forms. Black and brown fruits were produced mostly by trees (77% and 73% of plants producing these fruits, respectively). Lianas had a higher proportion of yellow fruit (39%) than other growth forms. Red and green fruits occurred in all growth forms.

2.4.2. Fruit color and fruit characters

Red, white and black colors were often associated with small fruits. Most red and black fruits (92% and 78%, respectively) had thin husks. Brown and green fruits were more evenly distributed among the three categories of fruit protection.

2.4.3. Fruit color and seed characters

White and green fruits occurred in high proportions (78% and 75%, respectively) in species with medium-sized seeds. Most other fruits had few seeds per fruit except yellow fruits, which had a more even distribution among the three categories of seed number.

2.5. Phylogenetic analysis

Nested ANOVA showed that taxonomic position above the ordinal level explained little variation in the fruit and seed characters we examined. At the ordinal level, based on the Cronquist (1981) scheme, phylogeny accounted for a significant amount of variation in seed size ($P = 0.002$), fruit color ($P = 0.011$), seed number ($P = 0.016$) and seed protection ($P = 0.032$). For Hutchinson's (1934) orders, seed number

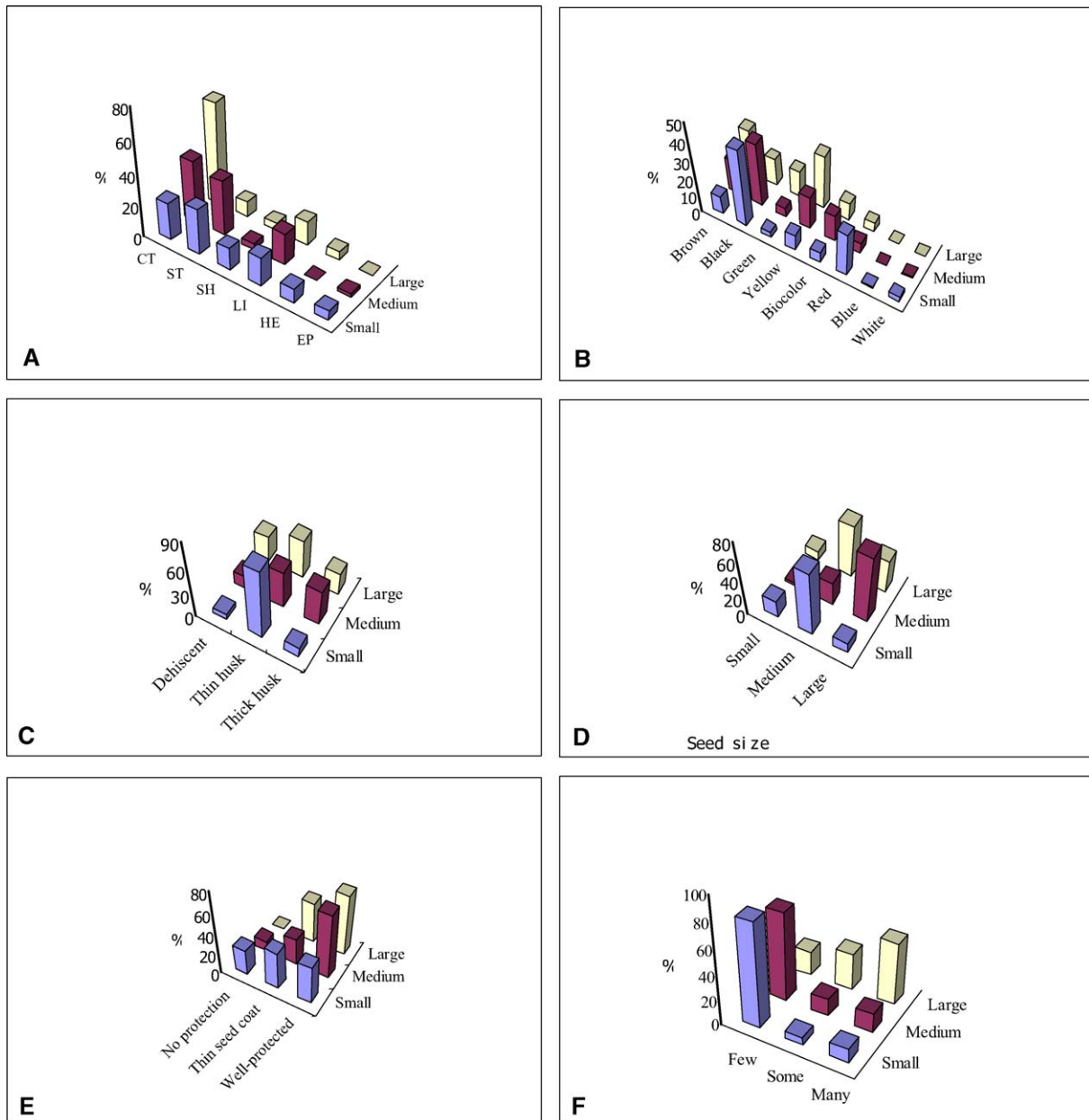


Fig. 1. Comparison of distribution pattern (frequencies of species number) in different parameters by fruit size. See Table 1 for definitions of each category and for abbreviations of the parameters. A: Life form; B: fruit color; C: fruit protection; D: seed size; E: seed protection; F: seed number.

($P < 0.001$), seed size ($P = 0.002$) and pulp protection ($P = 0.046$) varied significantly. All the traits tested at the family and genus level accounted for a significant amount of variation (Table 3). Phylogeny accounted for a high percentage of variation in seed number, seed protection and fruit protection (Table 3).

3. Discussion

The distribution of plant species among various fruit and seed categories is non-random in this forest. Small fleshy fruits were generally associated with thin husks, red, white,

or black colors and few and medium-sized seeds (2–10 mm). Many medium-sized fruits had large, well-protected seeds.

Nested analyses of variance revealed a considerable phylogenetic component in the variation of these traits, especially for seed number, type of seed protection and type of fruit protection (Table 3). The importance of consideration of phylogenetic effects has been acknowledged by other studies (Herrera, 1995; Jordano, 1995; but see Björklund, 1997). Freckleton et al. (2002) examined 103 traits from 26 published ecological studies and found that 60% showed significant evidence of phylogenetic association.

For some fruit traits a relatively high proportion of the total variance remained as error variance within genera, for

Table 3
Results of nested ANOVAs testing for phylogenetic effects in variation of different fruit traits

Variance source	Fruit size			Fruit color			Fruit protection			Seed protection			Seed size		Seed number			
	df	P	VA ^a	df	P	VA	df	P	VA	df	P	VA	df	P	VA	df	P	VA
<i>Based on Hutchinson (1934)</i>																		
Family	69	<0.001	25.5	66	<0.001	23.7	67	<0.001	47.3	67	<0.001	29.9	67	<0.001	44.8	67	<0.001	53.7
Genus	120	<0.001	34.8	121	<0.001	29.7	121	<0.001	49.3	120	<0.001	65.8	118	<0.001	37.6	119	<0.001	41.9
Error	211		39.7	200		46.6	211		3.4	211		4.3	212		17.6	212		4.4
<i>Based on Cronquist (1981)</i>																		
Family	58	<0.001	28	56	<0.001	30.1	57	<0.001	54.2	57	<0.001	39	67	<0.001	44.8	56	<0.001	51.7
Genus	106	<0.001	30	107	0.007	21.8	106	<0.001	42.1	106	<0.001	56.3	118	<0.001	37.6	106	<0.001	45.6
Error	192		42	181		48.1	192		3.7	192		4.7	212		17.6	192		2.7

^a VA, variance accounted for (% of total).

example 39.7% and 48.1%, respectively, for fruit size and color, and 17% for seed size (Table 3). These are traits, therefore, that may have been influenced by natural selection exercised by dispersers or other non-phylogenetic factors.

Fruit size stands out as a trait with considerable within-genus variance. This result agrees with Jordano (1995) study and suggests that fruit size may reflect adaptation to dispersers more often than other fruit traits. After a complete literature study Mack (1993) demonstrated that in all families examined the mean and range of fruit sizes were greater in the Old World than in the New World representatives and he explained that the evolution of large fruits might be more tightly constrained in the Neotropics owing to the relative scarcity of large frugivores there. However, Herrera (2002a) has recently shown that fruit and leaf size may show correlated evolution and that variations in fruit size may just reflect concomitant variation in leaf size.

The role of color as an attractant is far from clear (McPherson, 1988; Willson and Whelan, 1990; Murray et al., 1993). Compared with data summarized in Wheelwright and Janson (1985), the frequency of fruit color among species with thin husks or dehiscent small fleshy fruits in our study area was significantly different from what was found in Peru ($\chi^2 = 35.863$, $df = 7$, $P < 0.0001$), Costa Rica ($\chi^2 = 25.037$, $df = 7$, $P = 0.0007$), and Europe ($\chi^2 = 16.709$, $df = 7$, $P = 0.019$) but not from subtropical Florida ($\chi^2 = 10.177$, $df = 7$, $P = 0.1788$). European bird-dispersed fruit are more likely to be red than black whereas black fruits dominate all tropical and subtropical regions (also see Willson et al., 1989). Plants in Peru and Costa Rica more often bear orange fruits while those in Europe, Florida and tropical China have more brown/yellow fruits. Reason for that pattern is still unknown. One possibility is that the different frequencies of particular colors, or the lack of orange and blue fruits in the studied area may be due to the absence of genera or families that have blue or orange fruits. However, this is unlikely to be the correct explanation. *Symplocos* species (Symplocaceae family) in the Costa Rican lower montane forest bear predominantly blue fruits (Wheelwright et al., 1984) while in Xishuangbanna only one species this genus bears blue fruits

(*Symplocos ramosissima* G. Don) while the other four species bear black fruits. Similarly, two species of *Persea* (Lauraceae family) both bear blue fruits in Costa Rican forest (Wheelwright et al., 1984) while *Persea* species (formally named as *Machilus*, recently changed into *Persea*, <http://mobot.mobot.org/W3T/Search/vast.html>) in our study forest bear predominantly black fruits. These results could suggest that the frequency distributions of fruit color in different areas have a significant environmental component. Florida and Xishuangbanna, for example, have monsoon tropical or subtropical climates with similar annual precipitation (about 1500 mm) and temperature.

Some of the patterns we have identified may also result from environmental influences. For example, few plants bear ripe fruits in the hot, dry season (February–May) simply because many of the plants flower in this period. Plants with large fruits had a high proportion of species with ripe fruits in the dry and cool season whereas many small- and medium-sized fruits were produced in the rainy season, perhaps because of different lengths of fruit development (also see Corlett, 1996).

Determining the factors responsible for patterns of different fruit characters in this (or any other) highly diverse tropical flora is an immense task. The distribution of plant species among various fruit and seed categories is indeed non-random. Phylogenetic effects appeared to have made significant contributions to this variation. Some trait associations may also be ascribable to environmental conditions. Whether the non-random association of different fruit traits is also partly due to the evolutionary adaptation to frugivores in this area requires further study.

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