

Fruits of Melastomataceae: phenology in Andean forest and role as a food resource for birds

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Abstract: The fruits of Melastomataceae are consumed by many Neotropical frugivorous birds. Several studies have reported segregated fruiting seasons of melastomes, but this pattern is not widespread. The segregated fruiting phenologies of congeneric sympatric species may be an evolutionary response to reduce competition for seed dispersers. Alternatively, aggregated fruiting phenologies may be favoured if local fruit abundance attracts more frugivores, thus enhancing seed dispersal. We monitored melastome fruiting in transects over a 2-y period at a cloud-forest site in the Colombian Andes. Fruiting periods of nine melastome species were aggregated and fruiting peaks coincided with rainy seasons. In a separate 6-mo study, observations at focal plants revealed that 47 of 61 bird species fed on 10 species of melastome, representing 37.4% of feeding events observed. Melastomes were consumed by birds in a higher proportion than expected from their availability and peak melastome fruit abundance coincided with the breeding season of the frugivore community, when melastomes constituted 54% of feeding records. Melastomes interact with a large number of bird species throughout their annual cycles, and seem to constitute pivotal elements that sustain the frugivore community in montane forests.

Key Words: Andes, Colombia, frugivorous birds, frugivory, fruiting phenology, *Miconia*, *Miconia theizans*

INTRODUCTION

The fruits of typical endozoochorous melastomes (Melastomataceae) are small berries with a sweet and watery pulp that are consumed by many species of frugivorous birds (Charles-Dominique 1993, Snow 1965, Wheelwright *et al.* 1984). Sympatric species of melastome produce fruit at different times, but these species collectively provide a continuous food supply, maintaining bird populations over the entire annual cycle and providing the energy required for reproduction (Galetti & Stotz 1996, Stiles & Rosselli 1993). The fruiting periods of melastomes may be influenced by abiotic and biotic factors. Flowering and fruiting periods of plants may respond to climatic variables, which act as proximate cues that trigger the different phenological events (van Schaik *et al.* 1993).

Fruiting cycles of plants may also be moulded by selection caused by plant–animal interactions (Jordano 2000, Rathcke & Lacey 1985). For example, if plants

compete for seed dispersers, selection will favour staggered fruiting phenologies (competition avoidance hypothesis; Poulin *et al.* 1999, Snow 1965, Wheelwright 1985). Alternatively, simultaneous fruiting in a neighbourhood may enhance the attractiveness of the area for frugivores, thereby increasing fruit removal rates and the movement of frugivores between plants of different species (facilitation hypothesis; Rathcke & Lacey 1985, Saracco *et al.* 2005, Sargent 1990).

The fruiting patterns of plants, in turn, play a central role in the ecology of frugivores (Jordano *et al.* 2003). Fruiting periods strongly influence the reproductive activity and seasonal movements of frugivores that depend on plants (Levey 1988, Loiselle & Blake 1991, Thies & Kalko 2004).

The staggered fruiting seasons exhibited by sympatric bird-dispersed species of melastome in tropical lowland rain forest in Trinidad (Snow 1965), is frequently cited as evidence of segregation in fruiting times as a result of competition for dispersal agents (Potts *et al.* 2009, Sloan *et al.* 2007, Wheelwright 1985). However, Gleeson (1981) reanalysed the data of Snow (1965) and found that the fruiting pattern was statistically

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indistinguishable from a random pattern generated by a null model. Studies in a tropical lowland rain forest in Panama (Poulin *et al.* 1999) and a lower-montane rain forest in Colombia (Hilty 1980) also reported a staggered pattern, but melastome fruit abundance was markedly seasonal. Stiles & Rosselli (1993) also found that the fruiting peaks of the three most common bird-dispersed melastomes overlapped in a mid-elevation tropical forest in Costa Rica. Therefore, segregated fruiting is not necessarily the norm for melastomes.

The factors that affect fruiting times, such as climatic seasonality, the community context with which plants interact, and the outcome of the interactions themselves vary extensively across space (Thompson 1982). Therefore, geographical differences in phenological patterns and in the role that particular resources play in the ecology and annual cycles of frugivores are expected. In particular, in relatively aseasonal environments such as Andean cloud forest, biotic interactions may be more important than physical factors in determining fruiting times. In this study, we document the melastome fruiting pattern and determine the role of melastome fruits for frugivorous birds, in a mid-elevation cloud forest in the Colombian Andes. We contrasted temporal patterns of melastome fruit production with a null model of temporally random fruiting. To establish the role of melastomes for birds, we quantified fruit consumption of melastomes and other species in relation to fruit abundance, under the null hypothesis that birds should consume melastomes in proportion to their abundance.

METHODS

Study area

Our study site was the Santuario de Fauna y Flora Otún Quimbaya (SFFOQ; 4°43'N, 75°34'W), on the western slope of the Central Cordillera of the Andes, Municipality of Pereira, Risaralda Department, Colombia. SFFOQ is a montane forest at 1800–2100 m asl. The rainfall regime is bimodal, with a mean annual precipitation of 2700 mm. Peaks of precipitation occur in April–May and October–November. A mild dry season occurs in December–January, and a more pronounced one in July–August, when monthly rainfall is < 100 mm. Mean annual temperature is 15 °C. The SFFOQ encompasses 459 ha and is adjacent to Ucumari Regional Park, with 4000 ha of continuous forest. Vegetation cover in SFFOQ includes successional stages from early second-growth to mature forest, and non-commercial tree plantations of native and exotic species.

Data collection

Most studies that have evaluated melastome phenologies have included only species in the genus *Miconia* (Hilty 1980, Poulin *et al.* 1999, Snow 1965). In the areas studied by Snow (1965) and Hilty (1980), this genus included most of the bird-dispersed melastomes, but in those studied by Stiles & Roselli (1993) and Poulin *et al.* (1999) other genera were also well represented. In this study we included all bird-dispersed melastome genera that were represented in transects: *Miconia*, *Ossaea*, *Leandra* and *Henriettella*. All these genera are closely related (Michelangeli *et al.* 2004) and their fruits are consumed by birds (MKR, pers. obs.).

Field work was carried out in two phases. Phase one (6 mo) was conducted between November 2001 and April 2002, when we simultaneously evaluated fruit abundance and consumption by birds. Phase two (2 y) was conducted between October 2002 and September 2004, during which we evaluated monthly melastome fruit abundance.

To estimate fruit abundance and consumption, in phase one we established 18 transects (30 × 4 m) separated by at least 100 m. Transects were scattered throughout the SFFOQ to cover habitat heterogeneity and were located in 5–15-y-old second-growth (six transects) and in old-growth forest (six on hillsides and six on ridges). In each transect we marked and monitored all individual plants (melastomes and non-melastomes) with fleshy fruits that might be consumed by frugivorous birds. We only included individuals rooted within the transect. Fruits were considered as potentially consumed by birds based on our observations over 4 y and reports in the literature (Snow 1981, Wheelwright *et al.* 1984). We made monthly counts of fruit abundance in all trees and shrubs of all species bearing fruit (low understorey to canopy). For each individual plant we made direct counts of fruits but for individuals with large numbers of fruits (> 1000) we counted a subsample of fruits (dividing the crown in four equal parts and estimating the number of fruits in one of the parts) and extrapolated to the entire plant. Counts were carried out by a single observer and count calibrations, in which counts of the actual numbers of fruits in a tree were compared to extrapolated values, were carried out before and during the study.

For analyses of fruit abundance we included both ripe and unripe fruits. For each month we counted the number of species and individuals in fruit and total fruit abundance per individual, per species, and per transect. Monthly biomass of fruits was calculated by multiplying a species' mean dry pericarp mass by its fruit crop, then summing across species and dividing by sampled area. To estimate fruit biomass we separated the pericarp and dried it until constant mass. For melastome species with the smallest fruits (< 6 mm), pericarp and seeds were weighed

together due to the difficulty in separating the tiny seeds from the pulp. We calculated monthly fruit biomass for melastomes and for the entire plant community (overall fruit abundance). We tried to estimate fruit abundance from a 'bird's perspective'. Nevertheless, we recognize this may involve some degree of error due to the inclusion of potential resources actually not consumed by birds, the underestimation of fruit abundance because of ripe fruits falling to the ground or plants having ephemeral fruit crops, and the inherent error in the estimation of large crops, particularly of canopy species (Blake *et al.* 1990).

For each melastome species we determined the length of the fruiting period by assessing the presence of mature fruits every month. For species represented by few individuals in transects, additional focal individuals were observed to confirm the pattern at the species level. Only for one species in phase one (*Leandra melanodesma*) and another in phase two (*Miconia* sp. 2), less than five individuals were monitored for phenological records. The fruiting peak for each species was defined as the period when more than 50% of the individuals were recorded producing large quantities of fruits (Frankie *et al.* 1974).

We documented frugivore diets using two methods: direct observations of birds visiting fruiting plants in transects, and collecting faecal samples. We chose focal species of fruiting plants and did 231 h of observations on melastomes and 297 h on non-melastome species in the 18 transects. Observations were made in three sessions, 06h00–09h00, 11h00–13h00 and 15h00–18h00, alternating sessions in transects in different months. The duration of observation periods differed among focal plants, so we used the rate of individual feeding visits to a plant as a measure of consumption for each bird and plant species. An individual visit was defined as the first time a bird was observed in the focal tree feeding on fruits, independently of the time the bird remained in the plant. Faecal samples were obtained from birds captured in mist nets and held in cloth bags for 5–10 min. We captured birds using six mist nets (9 × 2.6 m, 38-mm mesh) for 4 d each month. Each month nets were randomly set in different sectors of the study area. Nets were opened between 05h30 and 12h00 and checked hourly. Faecal material was preserved in alcohol and seeds were later identified using a reference collection (Rios *et al.* 2004). The frequency of melastome seeds in faecal samples was established based on the percentage of samples containing melastome seeds. We counted the presence of seeds of each species in a faecal sample as a consumption event.

Phase two was conducted as part of a phenological study of fruit production in the SFFOQ. We established 15 transects (50 × 4 m) in forest interior (old- and second-growth). These transects were placed in different places than those of phase one. Along each transect we marked all individual melastomes with dbh > 2.5 cm and counted

fruit abundance each month. The method used during phase one was also used to estimate fruit abundance during this phase.

To determine whether melastome species differed in their ecological attributes, we characterized each species according to the habitat where individuals were most frequently found, their abundance and morphological characteristics of plants and fruits. To calculate species density we counted all the individuals of melastomes found in transects. To describe fruit characteristics, we collected 5–10 fruits from each of 2–10 trees of every species. We recorded fruit colour and measured the diameter of the whole fruit.

Data analysis

We used a null model analysis to test the hypothesis that the fruits of Melastomataceae species mature independently in time. The hypothesis was tested for the entire fruiting period and fruiting peaks during phase two. The observed fruiting period for each species was randomly placed along the time axis by randomizing the mid-point while preserving its length. Five thousand randomizations were performed for each data set with algorithms written in MatLab v.6.0 (Math Works Inc., Natick, MA, USA). We calculated the number of overlapping fruiting species for each month in each simulation (resulting in 5000 simulated fruiting curves), and for the observed fruiting data. We obtained the expected number of fruiting species per month as the mean of the 5000 iterations and calculated a displacement value (D) as the absolute difference between the expected value and the number of species per month in each simulation. Then we obtained a mean D_{null} value for each iteration by averaging D_{null} . The D_{obs} value for the observed fruiting curve was calculated as the absolute difference between the expected value and the number of species per month in the observed fruiting period. D_{obs} was compared with the distribution of D_{null} values. With a two-tailed test, the D_{obs} value is significantly different from the expected if 97.5% or 2.5% of D_{null} values are greater than the D_{obs} value. P -values > 0.975 indicate staggered fruiting and P < 0.025 indicate aggregated fruiting.

To test for temporal variation in melastome fruit abundance, we evaluated monthly differences in number of fruiting individuals, number of fruits and fruit biomass by using repeated-measures ANOVA or the equivalent non-parametric Friedman test. To assess the role of melastome fruits for frugivorous birds we compared melastome fruiting and consumption patterns with those at the community level (all non-melastome fruiting species).

Spearman correlations were used to evaluate the association between melastome fruit abundance (number

Table 1. Ecological characteristics of endozoochorous melastome species (species of *Miconia*, *Ossaea*, *Leandra* and *Henriettella*; nomenclature according to Tropicos. Missouri Botanical Garden <http://www.tropicos.org>) at the Santuario de Fauna y Flora Otún Quimbaya, Central Andes of Colombia. Data are mean \pm SE. Habitat: R = ridge, H = hillside, E = early second growth, open areas and forest edges, G = forest gaps, F = forest-interior. Habit: ST = small tree, MT = medium-sized tree, LT = large tree, S = shrub, L = liana. Colour: P = purple, W = white, L = lilac, O = orange.

Species	Habitat	Habit	Density (ind. ha ⁻¹)	Fruits		
				Crop size	Diameter (mm)	Colour
<i>Miconia</i>						
<i>acuminifera</i>	F	ST-MT	220 \pm 206	462 \pm 86	8.2 \pm 0.1	P
<i>M. notabilis</i>	E, G	MT	5.1 \pm 20.2	1500 \pm 300	11.5 \pm 0.1	P
<i>M. theizans</i>	E, G	ST-MT	80.3 \pm 181	117,700 \pm 3569	5.0 \pm 0.1	W
<i>M. aeruginosa</i>	E	MT	20.2 \pm 72.2	887 \pm 356	5.8	P
<i>M. wurdackii</i>	F, R	MT-LT	47.0 \pm 138	6895 \pm 1789	5.5 \pm 0.1	L
<i>M. smaragdina</i>	F, H	MT	32.3 \pm 73.1	158 \pm 71	6.4 \pm 0.1	P
<i>M. aff. resima</i>	F, H, G	MT	13.6 \pm 54.9	1646 \pm 1026	7.7 \pm 0.3	W-L
<i>M. caudata</i>	E, G	MT	6.0 \pm 16.6	649 \pm 46	8.1 \pm 0.1	P
<i>Miconia</i> sp. 1	F, H, G	MT	41.4 \pm 73.6	904 \pm 194	6.9 \pm 0.1	P
<i>Miconia</i> sp. 2	F, G	L	1.5 \pm 8.7	43 \pm 7	3.2 \pm 0.1	W
<i>Ossaea</i>						
<i>micrantha</i>	F, H	ST	22,7 \pm 79.9	171 \pm 42	9.0	W
<i>Henriettella</i>						
<i>trachyphylla</i>	F	MT	55.0 \pm 114	8770 \pm 6477	5.6	O
<i>Leandra</i>						
<i>melanodesma</i>	E	S	2.5 \pm 14.5	510	6.7	P

of fruiting species, fruiting individuals, number of fruits and biomass) and overall fruit abundance (non-melastome species) in phase one, and between mean melastome fruit biomass and precipitation during both phases. The R statistical framework (R Development Core Team, v. 2.4.0) was used for all statistical analyses.

To determine whether melastome fruit consumption by birds was selective, we used Jacobs' index, which tests for the proportion of use of a resource in relation to its abundance (Loiselle & Blake 1990): $D_{fr} = (r - p)/(r + p - 2rp)$, where r is the proportion of the diet made up of melastome fruits (measured as feeding events) and p is the proportional abundance of melastome fruits (measured as fruit biomass) with respect to the overall fruit abundance. For this analysis we only considered species for which we recorded consumption by birds at our study site. Negative values of D_{fr} indicate avoidance and positive values indicate preference. To interpret D_{fr} values we defined the following categories: from 0 to ± 0.15 = no preference; from ± 0.16 to ± 0.40 = slight preference or avoidance; from ± 0.41 to ± 0.80 = moderate preference or avoidance; and from ± 0.81 to ± 1.00 = strong preference or avoidance (Morrison 1982).

RESULTS

Melastome fruiting patterns

We found 19 species of melastomes producing fleshy fruits in the SFFOQ, 14 of which belong in the genus *Miconia*,

two in *Blackea* and one each in *Henriettella*, *Ossaea* and *Leandra*. Six species were represented by few individuals and did not produce fruit during the study. Of the other 13 species, ten produced fruit during phase one and nine during phase two, six of them in common between the two sampling periods. All the melastome species included in the sample produced small and juicy berries, but they differed in several ecological and morphological traits such as habitat, habit, abundance, crop size, and fruit colour and size (Table 1). During phase one *Miconia theizans* (56.2%), *M. aeruginosa* (20.5%) and *M. wurdackii* (6.5%) made the highest contribution to melastome fruit biomass. During phase two *M. acuminifera* (44.1%), *M. wurdackii* (28.0%) and *H. trachyphylla* (14.8%) made the highest contribution.

Melastome fruiting ($N = 15$ transects) exhibited temporal variation in the number of fruiting individuals ($F_{23,14} = 6.3$, $P < 0.0001$), number of fruits ($\chi^2 = 87.3$, $df = 23$, $P < 0.0001$) and biomass ($\chi^2 = 88.3$, $df = 23$, $P < 0.0001$) (Figure 1). The null model indicated that in the 2-y sampling period, both fruiting periods and fruiting peaks were temporally aggregated ($P = 0.0001$ and $P = 0.0002$, respectively; Figure 2). Melastome fruit abundance, as measured by the three variables, exhibited two annual peaks, one in March–May and the second one in August–October. The lowest melastome fruit abundance was observed during January–February, but there was always some fruit available (Figures 1, 2).

Melastome fruit abundance was correlated with non-melastome fruit abundance for number of fruits ($r_s = 0.27$, $P = 0.005$) and fruit biomass ($r_s = 0.23$, $P = 0.01$). Mean monthly melastome fruit biomass was not

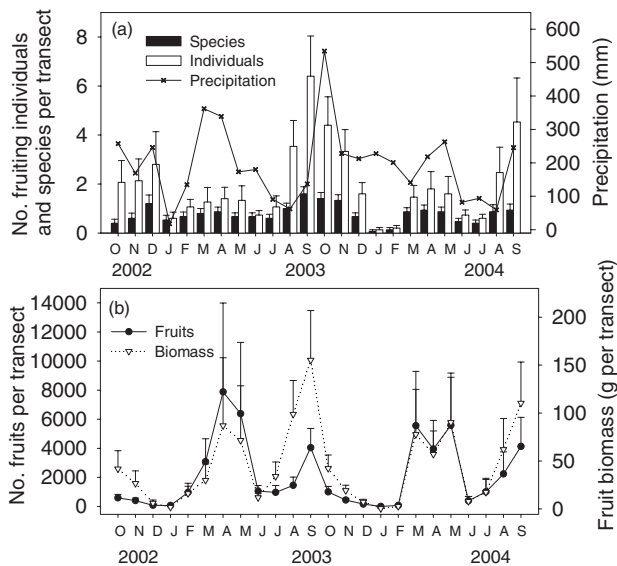


Figure 1. Monthly rainfall and fruiting phenologies of melastomes evaluated in 15 transects (50 × 4 m) at the Santuario de Fauna y Flora Otún Quimbaya, Colombia. Graphs show mean number of fruiting individuals and species per transect (a), and mean number of fruits and fruit biomass per transect (b). The horizontal axis represents the period October 2002–September 2004. Error bars represent 1 SE.

significantly correlated with the rainfall recorded for that period during phase one ($r_s = 0.65$, $N = 18$, $P = 0.17$) nor phase two ($r_s = 0.11$, $N = 24$, $P = 0.60$). However, the months of maximum fruit abundance coincided with the months of highest precipitation and the periods of low fruit abundance coincided with the dry season as well.

Patterns of fruit consumption by birds

A total of 75 shrub and tree species belonging to 34 families produced bird-dispersed fruits over the first phase

of this study (Appendix 1). Species with the highest fruit production were *Cecropia telealba* (Cecropiaceae), *Trema micrantha* (Ulmaceae), *Miconia theizans* and *Satyria* aff. *breviflora* (Ericaceae). We recorded fruit consumption by birds for 27 plant species and 1044 fruit feeding events by 61 species of bird during phase one (Appendix 2). Birds mostly fed on the fruits of ten species of melastome (37.4% of feeding events), *C. telealba* (19.7%), *T. micrantha* (18.0%) and *S. aff. breviflora* (10%).

Melastome fruits contributed 61.1% of total number of fruits (25.7% of ripe fruits) during phase one. In terms of biomass, however, melastomes contributed only 23.7% (8.4% of ripe fruit biomass) of overall fruit availability. This contribution ranged from a low of 3.5% in February to 38.6% in April (Figure 3). Birds fed on melastome fruits in all months, with the highest consumption rates observed in November–December and April ($\chi^2 = 13.9$, $df = 5$, $N = 18$, $P = 0.016$; Figure 3). In all months, consumption of melastome fruits was higher than expected in relation to their abundance ($\chi^2 = 1430$, $df = 5$, $P < 0.001$). Jacobs' index indicated that birds showed a moderate to strong preference for melastome fruits (Table 2). The most often consumed melastomes were *M. theizans* (58% of melastome consumption and 21.9% of overall fruit consumption) and *M. wurdackii* (23.2% of melastome consumption and 8.6% of overall fruit consumption).

Fruit-eating birds in the SFFOQ comprised species of 19 different families (Appendix 2). Of the 61 fruit-eating bird species recorded, 47 (77.0%) fed on melastomes. The main melastome consumers belonged to the families Thraupidae (36.2% of feeding events), Parulidae (10.6%), Turdidae (8.5%) and Emberizidae (8.5%). Overall, feeding observations were dominated by several tanagers (*Ramphocelus flammigerus*, *Tangara arthus*, *T. heinei*, *Thraupis episcopus*), a thrush (*Turdus ignobilis*)

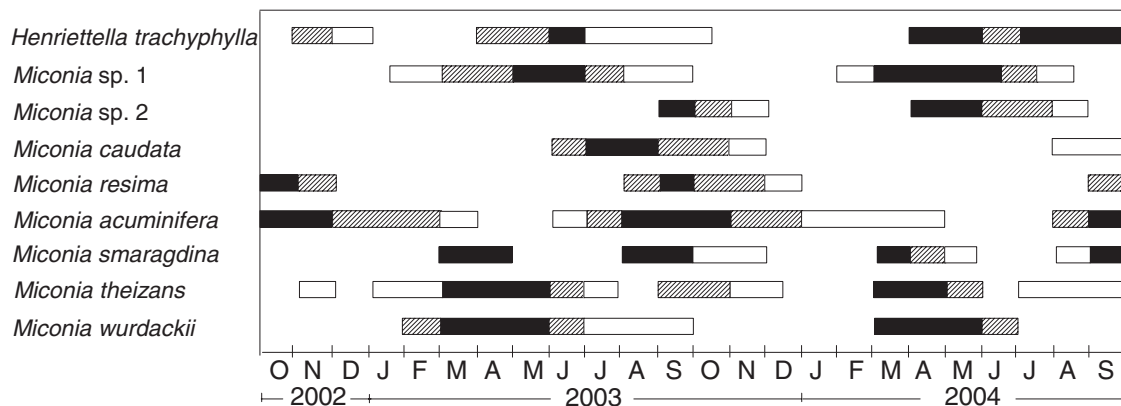


Figure 2. Fruiting phenologies of nine melastome species in the Santuario de Fauna y Flora Otún Quimbaya, Colombia, that produced fruits in sampling transects during the study period. The length of the bar indicates the duration of the fruiting season. Black bar portions represent > 50% of individuals fruiting (fruiting peak), shading represents between 30% and 40% of individuals fruiting, and white < 25%. The horizontal axis represents the period October 2002–September 2004.

Table 2. Jacobs' index (D_{fr}) as a measure of consumption preferences of melastome fruits by frugivorous birds in the Colombian Andes, for the period November 2001–April 2002. P = Proportional availability of melastome fruits for each month, r = consumption of melastome fruits by birds.

Month	P	r	D_{fr}
November	0.14	0.72	0.88
December	0.30	0.75	0.75
January	0.01	0.13	0.84
February	0.003	0.07	0.93
March	0.03	0.23	0.80
April	0.10	0.54	0.83
Total			0.81

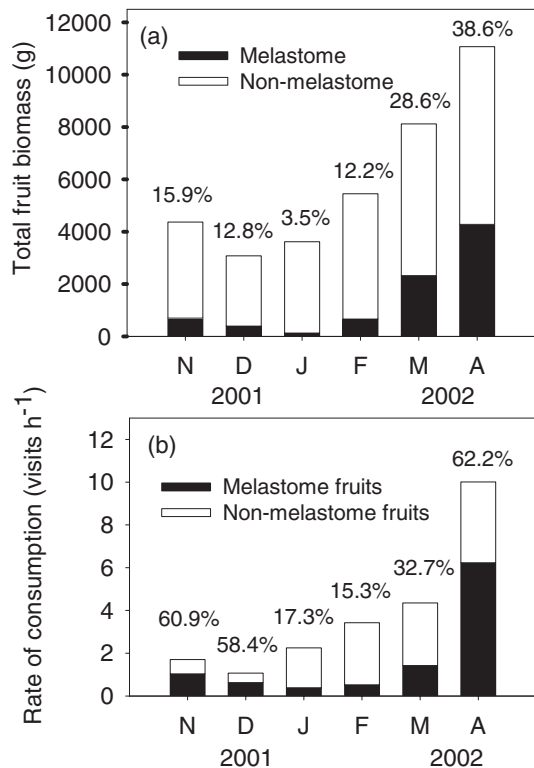


Figure 3. Melastome fruit biomass and consumption by birds evaluated in 18 transects (30 × 4 m) at the Santuario de Fauna y Flora Otún Quimbaya, Colombia, between November 2001 and April 2002. Total fruit biomass available in transects (a); black bars represent the contribution of melastome fruits to total fruit abundance each month. Rates of consumption by birds of melastomes and other fleshy fruits during the same period (b); black bars represent the contribution of melastome fruits to the total rate of consumption. Numbers above bars represent the percentages contributed by melastomes to biomass and consumption.

and a cotinga (*Pyroderus scutatus*). Melastome fruits were particularly important for five species of tanager (*Anisognathus sumptuosus*, *Tangara heinei*, *T. labradorides*, *T. arthus*, *Ramphocelus flammigerus*), a migratory thrush (*Catharus ustulatus*) and a migratory warbler (*Dendroica fusca*), each of which accounted for more than 5% of the melastome feeding records (Appendix 3).

We captured 70 individual birds in 930 net-h, but only 23 produced faecal samples (12 *Myadestes ralloides*, 5 *Euphonia xanthogaster*, 4 *Mionectes striaticollis*, 1 *Xenopipo flavicapilla* and 1 *Ramphocelus flammigerus*). Twelve samples (52.2%) contained melastome seeds. We identified the seeds of 26 species in all faecal samples, including six melastomes (20.7%). When counting the presence of seeds as a consumption event, we had 49 such events, with melastomes representing 32.6%, Rubiaceae 14.3% and Ericaceae 12.2%. Most of the samples containing melastome seeds (83.3%) included more than one fruit species and 33.3% included at least two different melastome species.

DISCUSSION

The melastome fruiting pattern

Fruiting periods of melastomes are aggregated at our study site in the Central Andes of Colombia. Aggregated fruiting suggests a high potential of competition for dispersal agents. However, depending on the community context, the advantages of synchronous fruiting may balance or outweigh the costs of potential competition for dispersers (Lortie *et al.* 2004, Saracco *et al.* 2004). For example, multispecific fruiting neighbourhoods have been reported to attract more frugivores than those with a single fruiting species (Blendinger *et al.* 2008, Carlo 2005, Sargent 1990). Likewise, fruit consumption and seed dispersal of species with small crops, low densities, or less-preferred fruits may be facilitated by the presence of species with large crops, high densities, or more preferred or more rewarding fruits (Blendinger *et al.* 2008, Thompson & Willson 1979).

Although faecal samples underestimate the amplitude of bird diets, the presence of seeds of several melastome species in some samples is evidence that birds feed from different plant species in a single feeding foray. Thus, synchronous fruiting may be beneficial by (1) increasing the probability that seeds are dispersed away from conspecifics (Poulin *et al.* 1999), (2) broadening the dispersal pattern (Carlo 2005), or (3) providing directed dispersal (Carlo & Aukema 2005). For instance, for species with particular germination and establishment requirements, as occurs in several melastome species (Ellison *et al.* 1993), the overlapping fruiting periods may attract a wider spectrum of dispersers, which increases the chances of seeds being dispersed into spatially unpredictable germination sites that have suitable conditions for each species (Thies & Kalko 2004).

Aggregated fruiting patterns seem to be widespread. In a review of phenological patterns of terrestrial plants, Rathcke & Lacey (1985) found that in general, fruiting times of animal-dispersed species tend to be aggregated or

random rather than temporally displaced. Similarly, in a meta-analysis of data from 14 biogeographic locations including temperate and tropical forest, Burns (2002) found a geographically consistent pattern of phenological synchrony in fruit production and bird abundances, in support of this hypothesis.

The temporally aggregated fruiting of melastomes in this Andean forest contrasts with the segregated pattern originally reported by Snow (1965) and supported by the findings of Hilty (1980) and Poulin *et al.* (1999). These studies were carried out in sites that differed in the magnitude and distribution of peaks and troughs in fruit abundance, which suggests that differences among sites are probably related to the community context. Species interactions exhibit spatial and temporal variability in their nature and outcomes (Peres 2000, Thompson 1982). Variation in the community context in which melastomes are immersed, such as the type and diversity of mutualists and competitors, probably plays a role in melastome phenology. For example, manakins, the most important dispersers of melastome fruits in Neotropical lowland forests, are poorly represented in our study area, whereas other frugivores such as tanagers and thrushes strongly interact with melastomes at our site.

A variety of factors, therefore, may be interacting to determine melastome phenology. First, the broad spectrum of ecological characteristics of melastomes such as fruit display, habitat and spatial distribution (Table 1), in addition to requirements for seed germination and seedling establishment, may dilute competition by attracting different sets of dispersers (Stiles & Rosselli 1993). Second, because fruiting is only one component of fitness, selection acting on time of flowering, germination, or seasonal avoidance of herbivores may override selection on fruiting time (Sloan *et al.* 2007, van Schaik *et al.* 1993). Third, although there is no strong evidence that fruiting phenologies are phylogenetically conserved (Smith-Ramírez & Armesto 1994), aggregated fruiting may reflect a physiological response of closely related species to similar environmental conditions. Although we found no correlation between monthly melastome fruit abundance and rainfall, peaks of melastome fruit production coincided with rainfall maxima. Thus, abiotic factors may also determine the melastome fruiting pattern by synchronizing fruiting time with the optimal conditions for seed dispersal and germination. Hilty (1980) and Stiles & Rosselli (1993) also reported strong seasonality in melastome fruiting.

The role of melastome fruits for frugivorous birds

Melastomataceae were the most important plant family in the diet of frugivorous birds at the SFFOQ, both in terms

of the number of consumed species and consumption frequency. Two of the top five species in the diets of birds belonged to this family and its fruits were a preferred food both during times of high and low fruit abundance.

Melastome fruit availability exhibited two peaks. One peak occurred in March–May, in coincidence with the breeding season of many bird species in mid-elevation Andean forest sites (Beltrán & Kattan 2001, Miller 1963, Rios *et al.* 2006). The second peak, in August–October, coincides with the moulting season for some species (Beltrán & Kattan 2001). Although birds fed on melastome fruits throughout the year, they particularly relied on these fruits during the March–May breeding season, when melastomes constituted 54% of the feeding records. Additionally, we recorded adults of several bird species feeding fledglings with melastome fruits (*Tangara arthus*, *T. heinei*, *Chlorochrysa nitidissima* and *Ramphocelus flammigerus*) and juveniles of several species were also observed feeding on melastome fruits (*Pyroderus scutatus*, *Chamaepetes goudotii*, *Penelope perspicax* and *Pipraeidea melanonota*). The breeding season is the most energy-demanding time for these birds and melastome fruits may supply an important part of their energetic requirements, both for adults and juveniles.

Melastomataceae, and particularly the tribe Miconieae, are a diverse taxon in Andean forest. At our study site, melastomes are locally abundant and some species exhibit extended fruiting periods. Their fruits are moderately abundant and are eaten by many frugivorous birds, particularly during the breeding season. Even when melastome fruits were scarce, birds showed a moderate preference for these fruits. Some species, such as *Miconia theizans*, were particularly important food sources for frugivorous birds. Although this species exhibited discrete peaks of fruit abundance, some ripe fruits were available throughout the year. A large number of bird species fed on fruits of this species, and its seeds were present in 35% of the faecal samples analysed. Muñoz *et al.* (2007) found that *M. theizans* constituted 22% of the feeding events of the Cauca guan (*Penelope perspicax*) in April 2003, when fruits of other species were also abundant.

The plants that produce fleshy fruits eaten by birds, and the birds that disperse their seeds, constitute mutualistic interaction networks. The resilience of such networks depends on their architecture, represented in features such as the strength and asymmetry of the interactions (Bascompte & Jordano 2007). Melastomes constitute an important module of these networks in Neotropical forests because they are highly connected, i.e. they interact with a large number of bird species. In addition, birds strongly depend on melastomes throughout their annual cycles. Highly connected species are critical elements of interaction networks, because their disappearance may cause networks to collapse (Bascompte & Jordano 2007). Projects that seek to conserve or restore Neotropical

forests should include fleshy-fruited melastomes as pivotal elements that greatly influence community dynamics.

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Appendix 1. Plant species (nomenclature according to Tropicos. Missouri Botanical Garden <http://www.tropicos.org>) with fleshy fruits potentially consumed by birds, that fruited in the Santuario de Fauna y Flora Otún Quimbaya, Colombia, during November 2001–April 2002. The table indicates fruits consumed by birds during the first (a) and second (b) phases of the study.

Family	Species
Anacardiaceae	<i>Toxicodendron striatum</i> ^a
Arecaceae	<i>Aiphanes simplex</i>
	<i>Chamaedorea pinatifrons</i> ^b

Appendix 1. Continued.

Family	Species
Araliaceae	<i>Oreopanax floribundum</i> ^a <i>Dendropanax macrophyllum</i> ^b
Boraginaceae	<i>Cordia bogotensis</i> ^b
Caprifoliaceae	<i>Viburnum cornifolium</i> ^a
Cecropiaceae	<i>Cecropia telealba</i> ^a
Celastraceae	<i>Celastrus liebmanii</i> ^a
Clusiaceae	<i>Chrysoclamys colombiana</i> ^a <i>Chrysoclamys dependens</i> ^b
Cucurbitaceae	<i>Cayaponia bureavii</i> ^a <i>Melothria pendula</i>
Ericaceae	<i>Psammisia</i> aff. <i>aberrans</i> ^b <i>Satyria</i> aff. <i>breviflora</i> ^a <i>Alchornea glandulosa</i> ^a
Euphorbiaceae	<i>Xylosma benthamii</i> ^b
Flacourtiaceae	<i>Besleria solanoides</i>
Gesneriaceae	<i>Besleria florida</i> ^{a,b}
Lauraceae	<i>Aniba muca</i> ^a <i>Nectandra lineatifolia</i> ^{a,b}
Malpighiaceae	<i>Bunchosia</i> cf. <i>armeniaca</i> ^b
Melastomataceae	<i>Miconia acuminifera</i> ^a <i>Miconia smaragdina</i> ^a <i>Ossaea micrantha</i> ^a <i>Miconia</i> sp. 1 ^a <i>Miconia wurdackii</i> ^a <i>Leandra melanodesma</i> ^a <i>Miconia aeruginosa</i> ^a <i>Miconia notabilis</i> ^a <i>Miconia theizans</i> ^a <i>Henriettella trachyphylla</i> ^a <i>Cissampelos andromorpha</i>
Menispermaceae	<i>Mollinedia repanda</i> ^b
Monimiaceae	<i>Ficus hartwegii</i> ^b
Moraceae	<i>Otoba lehmani</i> ^b
Myristicaceae	<i>Ardisia foetida</i> ^b
Myrsinaceae	<i>Myrsine coriacea</i> ^b <i>Myrsine pellucida</i> ^b
Myrtaceae	Indet. sp.
Passifloraceae	<i>Passiflora</i> sp. ^b
Polygalaceae	<i>Monnina phytolaccifolia</i> ^a
Rosaceae	<i>Rubus guianensis</i> ^a
Rubiaceae	<i>Palicourea angustifolia</i> ^a <i>Palicourea acetosoides</i> ^a <i>Psychotria hazenii</i> <i>Psychotria fortuita</i> <i>Psychotria longirostris</i> ^b <i>Palicourea ovalis</i> ^a
Sapindaceae	<i>Cupania</i> sp. ^b
Saurauiaceae	<i>Saurauia brachybothrys</i> ^b
Simaroubaceae	<i>Picramnia gracilis</i> ^b
Siparunaceae	<i>Siparuna laurifolia</i> ^b <i>Siparuna equinata</i> ^b
Solanaceae	<i>Cestrum</i> aff. <i>macrophyllum</i> ^b <i>Lycianthes radiata</i> ^b <i>Solanum aphodendrum</i> ^b <i>Solanum lepidotum</i> <i>Cestrum</i> sp.
Thymelaeaceae	<i>Daphnopsis bogotensis</i>
Ulmaceae	<i>Trema micrantha</i> ^a
Vitaceae	<i>Cissus sycioides</i> ^b 11 spp. indet.

Appendix 2. Bird species (nomenclature according to Remsen *et al.* A classification of the bird species of South America. American Ornithologists' Union <http://www.museum.lsu.edu/~Remsen/SACCBaseline.html>) eating melastome fruits between November 2001–April 2002 at the Santuario de Fauna y Flora Otún Quimbaya, Colombia. The table indicates species recorded feeding on melastomes during the first phase of the study (a), and species recorded feeding on *Miconia acuminifera* (b) and *M. theizans* (c) during the first and second phases.

Family	Species	Common name
Cracidae	<i>Penelope perspicax</i> ^{a, b, c}	Cauca guan
Columbidae	<i>Patagioenas cayennensis</i>	Pale-vented pigeon
	<i>Patagioenas fasciata</i> ^a	Band-tailed pigeon
Psittacidae	<i>Pionus seniloides</i>	Speckle-faced parrot
Cuculidae	<i>Crotophaga ani</i>	Smooth-billed ani
	<i>Piaya cayana</i> ^{a, c}	Squirrel cuckoo
Momotidae	<i>Momotus momota</i> ^b	Blue-crowned motmot
Bucconidae	<i>Malacoptila mystacalis</i> ^{a, b}	Moustached puffbird
Capitonidae	<i>Eubucco bourcierii</i> ^{a, b, c}	Red-headed barbet
Ramphastidae	<i>Aulacorhynchus prasinus</i> ^{a, b, c}	Emerald toucanet
	<i>A. haematopygus</i> ^{a, b}	Crimson-rumped toucanet
Picidae	<i>Melanerpes formicivorus</i>	Acorn woodpecker
	<i>Colaptes rubiginosus</i> ^a	Golden-olive woodpecker
Pipridae	<i>Masius chrysopterus</i> ^a	Golden-winged manakin
	<i>Xenopipo flavicapilla</i>	Yellow-headed manakin
Cotingidae	<i>Pyroderus scutatus</i> ^{a, b}	Red-ruffed fruitcrow
Tyrannidae	<i>Myiarchus cephalotes</i>	Pale-edged flycatcher
	<i>Myiodinastes maculatus</i>	Streaked flycatcher
	<i>Myiozetetes cayanensis</i>	Rusty-margined flycatcher
	<i>Pitangus sulphuratus</i>	Great kiskadee
	<i>Mionectes striaticollis</i> ^a	Streak-necked flycatcher
Corvidae	<i>Cyanocorax yncas</i> ^{a, c}	Green jay
Turdidae	<i>Platycichla leucops</i> ^b	Pale-eyed thrush
	<i>Turdus ignobilis</i> ^{a, b, c}	Black-billed thrush
	<i>Myadestes ralloides</i> ^{a, b, c}	Andean solitaire
Parulidae	<i>Catharus ustulatus</i> ^{a, c}	Swainson's thrush
	<i>Parula pitiayumi</i> ^a	Tropical parula
	<i>Wilsonia canadensis</i> ^a	Canada warbler
	<i>Myioborus miniatus</i> ^a	Slate-throated redstart
	<i>Dendroica fusca</i> ^{a, c}	Blackburnian warbler
Thraupidae	<i>Mniotilta varia</i> ^{a, c}	Black-and-white warbler
	<i>Chlorophanes spiza</i>	Green honeycreeper
	<i>Chlorophonia cyanea</i> ^a	Blue-naped chlorophonia
	<i>Tangara arthus</i> ^{a, b, c}	Golden tanager
	<i>Tangara cyanicollis</i> ^{a, c}	Blue-necked tanager
	<i>Tangara gyrola</i> ^a	Bay-headed tanager
	<i>Tangara heinei</i> ^{a, c}	Black-capped tanager
	<i>Tangara labradorides</i> ^{a, b}	Metallic-green tanager
	<i>Tangara nigroviridis</i> ^a	Beryl-spangled tanager
	<i>Tangara ruficervix</i> ^a	Golden-naped tanager
	<i>Tangara vassorii</i> ^a	Blue-and-black tanager
	<i>Tangara vitriolina</i> ^{a, c}	Scrub tanager
	<i>Tangara xanthocephala</i> ^a	Saffron-crowned tanager
	<i>Chlorochrysa nitidissima</i> ^{a, b}	Multicoloured tanager
	<i>Thraupis episcopus</i> ^{a, c}	Blue-grey tanager
	<i>Thraupis palmarum</i> ^{a, c}	Palm tanager
	<i>Anisognathus somptuosus</i> ^{a, b, c}	Blue-winged mountain-tanager
	<i>Ramphocelus flammigerus</i> ^{a, c}	Flame-rumped tanager
	<i>Pipraeidea melanonota</i> ^{a, b, c}	Fawn-breasted tanager
	<i>Piranga flava</i>	Hepatic tanager
<i>Piranga rubra</i> ^{a, b}	Summer tanager	
<i>Hemispingus frontalis</i> ^{a, c}	Oleaginous hemispingus	
<i>Chlorospingus canigularis</i> ^{a, c}	Common bush-tanager	
<i>Hemithraupis flavicollis</i>	Yellow-backed tanager	
<i>Euphonia lanirostris</i> ^a	Thick-billed euphonia	
<i>Euphonia musica</i>	Antillean euphonia	
<i>Euphonia xanthogaster</i> ^a	Orange-bellied euphonia	

Appendix 2. Continued.

Family	Species	Common name
Emberizidae	<i>Atlapetes albinucha</i> ^a	White-naped brush-finch
	<i>Arremon brunneinucha</i> ^a	Chestnut-capped brush-finch
Fringillidae	<i>Pheucticus ludovicianus</i>	Rose-breasted grosbeak
	<i>Saltator atripennis</i> ^a	Black-winged saltator

Appendix 3. Matrix of fruiting plants and their main bird consumers recorded between November 2001–April 2002 at the Santuario de Fauna y Flora Otún Quimbaya, Colombia. Values in table are the number of consumption events recorded during this period. Ct (*Cecropia tealaba*), Sb (*Satyria* aff. *breviflora*), Tm (*Trema micrantha*), Ma (*Miconia acuminifera*), Me (*Miconia aeruginosa*), Mn (*Miconia notabilis*), Mt (*Miconia theizans*), Mw (*Miconia wurdackii*), M1 (*Miconia* sp. 1), Om (*Ossaea micrantha*), Nl (*Nectandra lineatifolia*), Am (*Aniba muca*), Rg (*Rubus guianensis*).

Bird/Plant	Ct	Sb	Tm	Ma	Me	Mn	Mt	Mw	M1	Om	Nl	Am	Rg
<i>Patagioenas fasciata</i>						8							14
<i>Pionus seniloides</i>								9					
<i>Piaya cayana</i>	1					5							
<i>Momotus momota</i>	7	2											
<i>Eubucco bourcierii</i>							12						
<i>Pyroderus scutatus</i>	16	17					1	10				8	
<i>Cyanocorax yncas</i>	1		1			9	1	4					3
<i>Turdus ignobilis</i>	10			1		28		5			3	3	48
<i>Myadestes ralloides</i>							1		2	2			
<i>Catharus ustulatus</i>	1		1		2	21						1	4
<i>Wilsonia canadensis</i>	1		1		1	11						2	
<i>Myioborus miniatus</i>						3						3	1
<i>Dendroica fusca</i>	7					24						1	2
<i>Chlorophonia cyanea</i>						6							
<i>Tangara arthus</i>	14		1		1	3	16					15	1
<i>Tangara cyanicollis</i>	2			4									
<i>Tangara heinei</i>	9			2	14	9					3	2	14
<i>Tangara labradorides</i>	8				1	1	18					2	
<i>Tangara vitriolina</i>				2	1	5					4		4
<i>Tangara xanthocephala</i>	2						6						
<i>Chlorochrysa nitidissima</i>	3						2					2	
<i>Thraupis episcopus</i>	14			1	2	9							23
<i>Thraupis palmarum</i>	7				1	1							3
<i>Anisognathus somptuosus</i>	3					16	13					7	
<i>Ramphocelus flammigerus</i>	46			4	2	21					17	1	19
<i>Pipraeidea melanonota</i>	1					13							
<i>Piranga rubra</i>	4					3						6	3
<i>Chlorospingus canigularis</i>	5		1		1	9	4					7	
<i>Euphonia xanthogaster</i>	10		4				10		3			9	2
<i>Atlapetes albinucha</i>	2					1					2		
<i>Pheucticus ludovicianus</i>													27
<i>Saltator atripennis</i>					1	3							1