# Linking frugivore activity to early recruitment of a bird dispersed tree, *Eugenia umbelliflora* (Myrtaceae) in the Atlantic rainforest

MARINA CORRÊA CÔRTES,[1,2] ELIANA CAZETTA,[1]★
VANESSA GRAZIELE STAGGEMEIER[3] AND MAURO GALETTI[1]
[1]*Departamento de Ecologia, Laboratório de Biologia da Conservação, Universidade Estadual Paulista
(UNESP), CP 199, 13506-900, (Email: eliana.cazetta@gmail.com),* [3]*Departamento de Botânica,
Grupo de Fenologia e Dispersão de Sementes, UNESP, Rio Claro, SP, Brazil; and* [2]*Department of
Ecology, Evolution and Environmental Biology, Columbia University, New York, New York, USA*

**Abstract** Seed dispersal by animals is a complex process involving several distinct stages: fruit removal by frugivores, seed delivery in different microhabitats, seed germination, seedling establishment, and adult recruitment. Nevertheless, studies conducted until now have provided scarce information concerning the sequence of stages in a plant's life cycle in its entirety. The main objective of this study was to evaluate the immediate consequences of frugivore activity for *Eugenia umbelliflora* (Myrtaceae) early recruitment by measuring the relative importance of each fruit-eating bird species on the establishment of new seedlings in scrub and low restinga vegetation in the Atlantic rainforest, Brazil. We conducted focal tree observations on *E. umbelliflora* trees recording birds' feeding behaviour and post-feeding movements. We also recorded the fate of dispersed seeds in scrub and low restinga vegetation. We recorded 17 bird species interacting with fruits in 55 h of observation. Only 30% of the handled fruits were successfully removed. From 108 post flight movements of exit from the fruiting trees, 30.6% were to scrub and 69.4% to low restinga forest. Proportion of seed germination was higher in low restinga than in the scrub vegetation. Incorporating the probabilities of seeds' removal, deposition, and germination in both sites, we found that the relative importance of each frugivorous bird as seed dispersers varies largely among species. *Turdus amaurochalinus* and *Turdus rufiventris* were the best dispersers, together representing almost 12% probability of seed germination following removal. Our results show the importance of assessing the overall consequence of seed dispersal within the framework of disperser effectiveness, providing a more comprehensive and realistic evaluation of the relative importance of different seed dispersers on plant population dynamics.

**Key words:** frugivory, gape width, seed dispersal effectiveness, seed germination, seed size.

## INTRODUCTION

Fruit-eating birds play a major role in seed dispersal of plants in tropical forests, acting as the link between plant reproduction and the recruitment of new individuals (Godínez-Alvarez *et al*. 2002; Jordano & Godoy 2002; Wang & Smith 2002). The integrative approach that considers the outcome of frugivore activity and its effects on post dispersal stages within the plant's life cycle, including seed germination, seedling establishment, juvenile and adult recruitment, is important to completely understand the process of seed dispersal in plant populations (Jordano & Herrera 1995; Russo 2005; Godínez-Alvarez & Jordano 2007).

Seed shadow acts as a template upon which early recruitment processes operate (Janzen 1970; Schupp

& Fuentes 1995; Nathan & Mueller-Landau 2000). Patterns of seed deposition and subsequent plant establishment are moulded by a range of ecological processes operating at different spatial scales (Kollmann 2000). This general ecological principle (Levin 1992) has been demonstrated in several plant-frugivore systems (e.g. García & Ortiz-Pulido 2004), especially in spatially heterogeneous environments in which fleshy-fruited plants are patchily distributed (Santos *et al*. 1999; Jordano & Schupp 2000; Calviño-Cancela 2002; Revilla *et al*. 2004). Nevertheless, studies conducted until now have provided scarce information concerning the entire sequence of stages in the seed dispersal process (but see Jordano & Schupp 2000; Wenny 2000; Godínez-Alvarez *et al*. 2002; Alcántara & Rey 2003).

This integrative approach can be conducted under the perspective of seed dispersal effectiveness, which is the contribution a disperser makes to plant fitness,

determined by components of quantity (frequency of visits and fruit removal rates) and quality (treatment given to the seed in the gut or mouth/bill, and quality of seed deposition) (Schupp 1993). In this framework, the first step towards understanding the scenario of seed dispersal is the assessment of fruit removal by fruit-eating animals (Jordano & Godoy 2002; Wang & Smith 2002). Fruit removal is a successful attempt by a frugivore to take the seed away from the parental tree (i.e. fruit is swallowed or carried on the bill), but can also include fruit thieving, which is an unsuccessful attempt by a frugivore to disperse the seed (i.e. seeds are damaged, fruits are dropped or regurgitated beneath the tree or are pecked for pulp consumption, without being detached from the peduncle and becoming susceptible to pathogens attack). Whether fruit handling results in effective seed dispersal depends on differences in the bird taxonomic group, life history traits (e.g. diet composition), bird feeding behaviour (e.g. fruit selection) (Francisco & Galetti 2002; Clark *et al.* 2005; Tellería *et al.* 2005), and fruit processing (e.g. treatment given to seed) (Traveset *et al.* 2008). Yet, it also depends on the post-feeding movements of birds (Herrera 1989) and microhabitat use (Schupp 1993; Jordano & Schupp 2000). Although this fact is widely acknowledged, it has rarely been placed in the context of disperser effectiveness (Spiegel & Nathan 2007).

The movements of frugivores after feeding on fruits are frequently non-random since they are usually sensitive to vegetation traits and spatial conditions (Jordano & Schupp 2000; Hasui *et al.* 2007). As microhabitats differ considerably in abiotic (e.g. light levels, water availability, soil composition) and biotic conditions (e.g. seed predation, competition, herbivory), the patterns of seed shadow generated by frugivores might lead to distinct delayed effects on the establishment of new seedlings and, consequently, on the plant demography (Jordano & Schupp 2000; Jordano & Godoy 2002; Schupp *et al.* 2002). In this context, the central objective of this study was to evaluate the immediate consequences of frugivore activity for *Eugenia umbelliflora* O. Berg (Myrtaceae) early recruitment in the Atlantic rainforest. We evaluated: (i) the relative importance of each fruit-eating bird species to the establishment of new seedlings in distinct habitat patches; and (ii) the probability that a removed seed is efficiently delivered to a suitable microhabitat where it can germinate.

## METHODS

### Study site

The study was carried out during the fruiting period of *E. umbelliflora* from late July to early November 2005

in an inshore island, Ilha do Cardoso (25°03′ S and 48°53′ W), in the south of São Paulo state, Brazil. Ilha do Cardoso is a 15 100-ha protected land-bridge island encompassing several types of Atlantic rainforest, including lowland and montane tropical rainforests, mangroves, dune vegetation and restinga forest (Barros *et al.* 1991).

The present study was conducted in scrub and low restinga vegetation, which make up two different habitats of restinga forest (sandy forest). Restinga forest is distributed over a quaternary coastal plain and constitutes a heterogeneous ecosystem (Lima & Capobianco 1997) including a mosaic of vegetation types that varies from open areas to forest formations. Moving away from the seashore, the vegetation becomes denser and diversified due to substrate consolidation and salinity decrease. This habitat is named scrub vegetation because the vegetation is sparse and dominated by shrubs ranging from 1.5 to 2.0 m, such as *Dalbergia ecastaphyllum*, *Dodonaea viscosa*, *Schinus terebinthifolius*, *Psidium cattleianum* and *Abarema brachystachya* (Couto & Cordeiro 2005). In sequence, the forest physiognomy (hereafter low restinga) reaches approximately 15 m height, presents a higher density of trees and a more continuous canopy strata compared with scrub vegetation (Sugiyama 1998). At this site we can find many species of epiphytes (e.g. bromeliads and orchids) and trees, such as *Ilex theazans*, *Clusia criuva* and *Myrcia bicarinata* (Sugiyama 1998; Bernardi *et al.* 2005; Couto & Cordeiro 2005).

The climate at Ilha do Cardoso is generally warm and wet throughout the year without a marked dry season (Furnari *et al.* 1987; Castro *et al.* 2007). Total rainfall in 2005 was 2131.1 mm; the minimum rainfall was recorded in August (48.2 mm) and the maximum in January (459.2 mm). The highest temperature occurred in February and March (28.8°C) and the lowest temperature occurred in July (14.1°C). The mean temperature recorded for the whole period was 21.9°C. The climate data were obtained from the meteorological station located at the study site that belongs to the Escola Superior de Agricultura 'Luiz de Queiroz' from University of São Paulo (ESALQ-USP).

### Study species

*Eugenia umbelliflora* (Myrtaceae) is a small tree (4–7 m height) that grows in low elevations under ocean influence on the eastern coast of Brazil. It is a common species found in the transition between scrub and low restinga vegetation in Atlantic rainforest (Delgado & Barbedo 2007). Flowering is annual and occurs from March to May, and fruiting begins in June and extends to October (Staggemeier *et al.* 2007). Fruits are berries containing one to three seeds, red when unripe and

purple when ripe, 13.98 mm ± 2.33 long (mean ± SD) and 11.54 mm ± 1.23 wide ($n = 164$ fruits, nine trees). Seeds are 11.09 mm ± 1.85 long and 9.15 mm ± 1.02 wide ($n = 164$ seeds, nine trees). Mean fruit weight is 1.38 g ± 0.34 and mean pulp weight is 0.75 g ± 0.21 ($n = 164$ seeds, nine trees). Fruit crops of individual trees range between 192 and 1390 fruits, with a mean of 500 ripe fruits ($n = 8$). Chemical analyses of fruit pulp yielded 2.83% lipids, 2.58% protein, and 2.69% soluble carbohydrates (glucose and fructose) (Eliana Cazetta, unpubl. data, 2008). *Eugenia umbelliflora* fruits are intensively consumed by several birds and mammals, such as the crab-eating fox *Cerdocyon thous* (Cazetta & Galetti, unpubl. data, 2008).

## Quantitative component of seed dispersal effectiveness

We sampled nine *E. umbelliflora* individuals located within an area of $100 \times 30$ m on the transition between scrub and low restinga vegetation. We selected this area because it allowed us to have a wide-ranging vision of bird behaviour and post-feeding movements. We conducted focal observations (see Francisco & Galetti 2001; Galetti *et al.* 2004) at periods varying from 0630 h to 1100 h and from 1430 h to 1730 h, totalling 55 h. To assess the feeding behaviour of birds and seed dispersal we recorded bird species, time of arrival in the plant, and number of fruits handled according to avian feeding behaviour. Birds that are legitimate seed dispersers remove seeds by successfully swallowing the whole fruit or carrying it in the bill to distinct places, whereas seed thieves peck the fruit for pulp pieces, detach the fruit, and drop or regurgitate it beneath the tree where the mortality rate is usually higher than in micro-sites far from the reproductive tree (Jordano & Schupp 2000).

Birds are able to select fruits based on their sizes and, usually, swallowing is constrained by fruit width (Wheelwright 1985, 1993). Hence, for better understanding of avian feeding behaviour, we measured fruit width, mass, and pulp mass of 164 fruits from nine *E. umbelliflora* individuals. We compared fruit width with gape sizes of the primary frugivorous birds.

We carried out a Student's *t*-test to compare width, mass, and pulp mass, between 120 fruits collected from six tree crowns and 81 fruits dropped beneath each canopy. Since we did not have a sufficient sample size of dropped fruits for all trees, data were pooled in one single test for the population. To assure that fruits were dropped by birds and not naturally, we only selected fruits with conspicuous beak marks.

## Qualitative component of seed dispersal effectiveness

In order to estimate the probability of seed deposition by each fruit-eating bird in each site, we recorded flight direction and habitat (scrub or low restinga) where each bird perched after feeding on *E. umbelliflora* fruits.

We estimated seed predation in low restinga and scrub habitats by placing 50 stations, 10 m apart, containing one seed of *E. umbelliflora*. In scrub vegetation we placed the seeds in two microhabitats: open areas, and below common species of scrub mid and low shrubs (e.g. *Dodonaea viscosa*, *Dalbergia ecastaphyllum*, *Myrsine* spp.) that are perches to birds and might act as 'nurse plants' which facilitate seed survival and seedling establishment (Valiente-Banuet & Ezcurra 1991). We monitored the seeds monthly over 3 months (August to November 2005), recording whether the seeds disappeared (i.e. predated), germinated (i.e. successfully established), or were still intact.

## Probability of seed dispersal

To completely understand seed dispersal by frugivores we would need detailed information about the effects of frugivore activity on the subsequent stages of the plant life cycle, which includes seed germination, establishment of seedling, juvenile, and adult survival (Godínez-Alvarez & Jordano 2007). In the present study we only evaluated the effect of frugivore activity on seed germination at different sites. Thus, hereafter, the term seed dispersal encompasses the probability that a fruit-eating bird successfully removes a fruit and delivers the seed to a habitat where it germinates.

To dissect the frugivore effects on seed dispersal we estimated three probabilities, as defined by Godínez-Alvarez and Jordano (2007): (i) the probability of seed removal by each fruit-eating bird (i.e. relative proportion of the product of the frequency of visits, number of seeds handled, and the proportion of fruits successfully removed away from the parent tree); (ii) the probability of delivering the seed to a particular habitat (low restinga and scrub) (i.e. proportion of flights to a specific patch); (iii) the probability of germination (i.e. proportion of germinated seeds after 3 months).

These three estimates are incorporated in the formula of seed dispersal probability (SDP) (modified from Godínez-Alvarez & Jordano 2007):

$$SDP = P_s \sum_{m=1}^{y=2} (D_{sm}T_m)$$

where, $P_s$ is the probability of seed removal by frugivore $s$, $D_{sm}$ is the probability that seeds are deposited in habitat $m$ by frugivore $s$, $T_m$ is the probability of transition from seed to seedling in habitat $m$, and $y$ is equivalent to the total number of patches that seeds are deposited.

**Table 1.** Visitation patterns to *Eugenia umbelliflora* (Myrtaceae) and characteristics of frugivorous bird species recorded at Ilha do Cardoso, Atlantic rainforest, Brazil

| Family | Species | No. visits (%) | No. visits with fruit handling (%) | Body size (cm)† | Gape width (mm)‡ |
|---|---|---|---|---|---|
| Cotingidae | *Procnias nudicollis* | 2 (0.6) | 2 (1.4) | 27‡ | 24.53 |
| Emberizidae | *Sicalis flaveola* | 1 (0.3) | – | 13.5 | – |
| Parulidae | *Parula pitiayumi* | 4 (1.2) | 3 (2.0) | 9.8 | – |
| Thraupidae | *Ramphocelus bresilius* | 4 (1.2) | 1 (0.7) | 19 | – |
| | *Tachyphonus coronatus* | 6 (1.9) | 4 (2.7) | 17.7 | 9.14 |
| | *Tangara peruviana* | 15 (4.7) | 8 (5.4) | – | 7.6 |
| | *Thraupis cyanoptera* | 13 (4.0) | 4 (2.7) | 18 | 10.40§ |
| | *Thraupis palmarum* | 3 (0.9) | 3 (2.0) | 18‡ | 10.55 |
| | *Thraupis sayaca* | 66 (20.6) | 36 (24.5) | 17.5‡ | 10.11 |
| | *Thraupis* sp.¶ | 3 (0.9) | – | – | – |
| Turdidae | *Turdus flavipes*†† | 66 (20.6) | 10 (6.8) | 20.5 | 12.13 |
| | *Turdus albicollis* | 10 (3.1) | 7 (4.76) | 22 | 13.08 |
| | *Turdus amaurochalinus* | 26 (8.1) | 20 (13.6) | 21.9 | 11.41 |
| | *Turdus leucomelas* | 3 (0.9) | 1 (0.7) | 22 | 11.86 |
| | *Turdus rufiventris* | 29 (9.0) | 15 (10.2) | 25 | 12.14 |
| | *Turdus* sp.¶ | 28 (8.7) | 11 (7.5) | – | – |
| Tyrannidae | *Elaenia obscura* | 3 (0.9) | 1 (0.7) | 15 | 9.01 |
| | *Myiozetetes similis* | 2 (0.6) | 2 (1.4) | 17.5 | 10.16 |
| | *Myiarchus tyrannulus* | 8 (2.5) | 7 (4.8) | 19.5 | – |
| | *Pitangus sulphuratus* | 19 (5.9) | 9 (6.1) | 22.5 | 15.43 |
| Indeterminated | Indeterminated | 10 (3.1) | 3 (2.0) | – | – |
| | Total | 321 | 147 | | |

†Data from Sick (1997). ‡Mean and gape width/body sizes measured from specimens of the Museum of Zoology at São Paulo (*n* = 10). §Data from Hasui (2003). ¶Species not identified. ††Genus *Platycichla* has been recently subsumed into *Turdus* (Voelker *et al.* 2007). Nomenclature and bird species order after CBRO (Comitê Brasileiro de Registros Ornitológicos 2008).

# RESULTS

## Quantitative component of seed dispersal effectiveness

Eighteen species of birds were recorded visiting *E. umbelliflora* trees (Table 1). However, only 46% of the 321 visits included fruit handling, thereby reducing the number of species observed interacting with *E. umbelliflora* fruits to 17 (Table 1).

*Thraupis sayaca*, *Turdus amaurochalinus* and *Turdus rufiventris* were the most frequent birds interacting with *E. umbelliflora* fruits, representing 48% of the total 147 visits (Table 2). These three species and *Tangara peruviana* handled 66% of the total fruits manipulated. In contrast, the number of fruits handled per visit showed a distinct pattern. *Tangara peruviana* and *Procnias nudicollis,* followed by *Myiarchus tyrannulus,* presented the highest fruit handling rates, exceeding four fruits manipulated per visit (Table 2).

Almost 70% of the total handled fruits were thieved (Table 2). *Thraupis sayaca* and *Tangara peruviana*, species presenting high visit frequencies and fruit handling rates, showed the lowest probabilities of handling a fruit successfully; less than 1% and 4% of removal, respectively (Table 2, Fig. 1). *Turdus albicollis*, *Turdus flavipes* and *Pitangus sulphuratus* presented the highest

probabilities of handling success, reaching 90%, 80% and 100% of successful removal (swallowing and carrying), respectively (Table 2, Fig. 1).

We found a large variability in fruit width (F = 20.78, d.f. = 8, *P* < 0.0001) and fruit mass (F = 29.22, d.f. = 8, *P* < 0.0001) among trees. Birds from the Thraupidae family presented the smallest body size and gape width (Table 1) and were able to swallow less than 30% of the fruits (Fig. 2). At one extreme is *Tangara peruviana* with the smallest gape width among the recorded avian frugivores and smaller than the measured fruits in the *E. umbelliflora* population. At the other extreme, *Pitangus sulphuratus*, has one of the largest body masses and gape widths among frugivorous birds and is able to swallow almost the entire range of fruit sizes available (Fig. 2).

We found significant differences in fruit width (t = 3.54, d.f. = 199, *P* = 0.0005), fruit mass (t = 3.69, d.f. = 199, *P* = 0.0003), and pulp mass (t = 2.64, d.f. = 199, *P* = 0.009) between fruits dropped beneath the trees by frugivorous birds and those collected from *E. umbelliflora* crowns. Dropped fruits presented greater width (dropped: 11.99 mm ± 1.45, *n* = 81; crown: 11.27 mm ± 1.34, *n* = 120), fruit mass (dropped: 1.33 g ± 0.38, *n* = 81; crown: 1.14 g ± 0.33, *n* = 120), and pulp mass (0.69 g ± 0.22, *n* = 81; crown: 0.60 g ± 0.23, *n* = 120) than fruits collected in the

**Table 2.**    Data on visits and feeding behaviour of frugivorous birds on *Eugenia umbelliflora* in Ilha do Cardoso, Brazil. Feeding behavior summarized as mean ± SD of fruits handled per visit, and total number of fruits handled, removed and thieved

| Species | No. visits per hour | No. fruits per visit | No. fruits handled | No. fruits removed | No. fruits thieved |
|---|---|---|---|---|---|
| *Procnias nudicollis* | 0.04 | 6.5 ± 6.4 | 13 | 8 | 5 |
| *Parula pitiayumi* | 0.05 | 2.0 ± 1.0 | 6 | 0 | 6 |
| *Ramphocelus bresilius* | 0.02 | 1.0 | 1 | 0 | 1 |
| *Tachyphonus coronatus* | 0.07 | 3.7 ± 3.2 | 15 | 1 | 14 |
| *Tangara peruviana* | 0.15 | 7.2 ± 6.7 | 58 | 2 | 56 |
| *Thraupis cyanoptera* | 0.07 | 1.2 ± 0.5 | 5 | 2 | 3 |
| *Thraupis palmarum* | 0.05 | 3.3 ± 2.1 | 10 | 0 | 10 |
| *Thraupis sayaca* | 0.65 | 4.0 ± 3.1 | 142 | 1 | 141 |
| *Turdus flavipes* | 0.18 | 2.1 ± 1.9 | 21 | 17 | 4 |
| *Turdus albicollis* | 0.13 | 4.0 ± 2.9 | 28 | 25 | 3 |
| *Turdus amaurochalinus* | 0.36 | 3.4 ± 5.0 | 68 | 29 | 39 |
| *Turdus leucomelas* | 0.02 | 1.0 | 1 | 0 | 1 |
| *Turdus rufiventris* | 0.27 | 3.1 ± 3.1 | 47 | 25 | 22 |
| *Turdus* sp. | 0.20 | 1.3 ± 0.6 | 14 | 10 | 4 |
| *Elaenia obscura* | 0.02 | 1.0 | 1 | 0 | 1 |
| *Myiozetetes similis* | 0.04 | 1.0 ± 0 | 2 | 2 | 0 |
| *Myiarchus tyrannulus* | 0.13 | 4.6 ± 2.4 | 32 | 16 | 16 |
| *Pitangus sulphuratus* | 0.16 | 1.2 ± 0.4 | 11 | 11 | 0 |
| Indeterminated | 0.05 | 1.3 ± 0.6 | 4 | 1 | 3 |
| Total (%) | | | 479 | 150 (33.2) | 329 (68.8) |
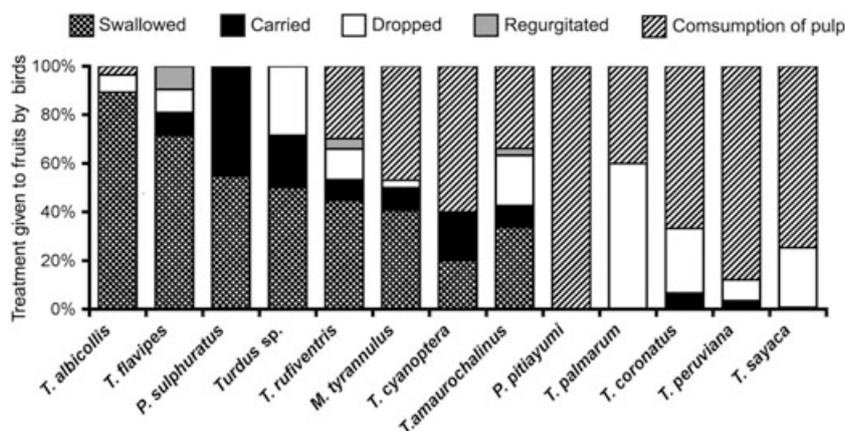


**Fig. 1.**    Treatment given to *Eugenia umbelliflora* fruits by frugivorous birds in Ilha do Cardoso, Brazil.

trees. To account for fruit size and mass, and pulp mass variability among trees, we repeated these analyses to one *E. umbelliflora* individual for which we had enough sample size of dropped fruits ($n = 29$) and we found the same pattern. All fruits collected beneath the tree had the seeds intact, indicating that bird species that dropped the fruits did not prey upon the seeds.

### Qualitative component of seed dispersal effectiveness

Considering all studied frugivorous birds, 108 exit flights from *E. umbelliflora* trees were recorded: 33 to

scrub habitat (30.6%) and 75 to low restinga habitat (69.4%). Considering only birds that handled *Eugenia* fruits and provided adequate data to calculate the frequency of exit flights, we found that *Pitangus sulphuratus*, *Thraupis cyanoptera* and *Tachyphonus coronatus* showed 100% of exit flights towards low restinga habitat (Fig. 3). In contrast, *Thraupis palmarum* showed 100% of exit flights to scrub habitats (Fig. 3).

After 3 months we found 133 seeds in the field, from these 18 (13.5%) germinated, 51 (38.3%) were predated, and 64 (48.1%) remained intact. Low restinga showed the highest proportion of germinated seeds, representing 66.6% ($n = 12$) of the total of germinated seeds in all micro-habitats ($\chi^2 = 19.37$, d.f. = 2, $P = $
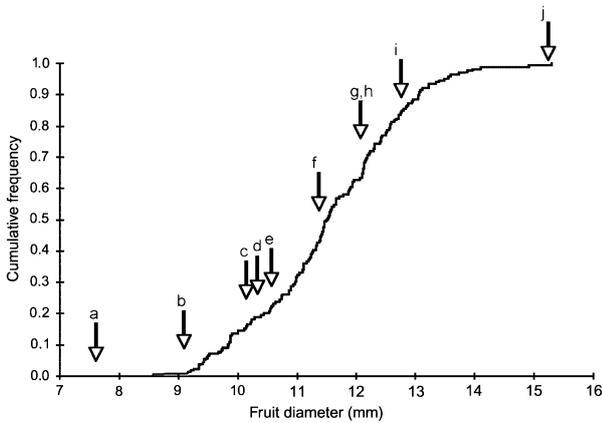
**Fig. 2.** Cumulative frequency of *Eugenia umbelliflora* fruits width sampled at Ilha do Cardoso, Brazil (*n* = 164). Mean gape sizes of frugivorous birds are indicated with arrows, as follow: (a) *Tangara peruviana*, (b) *Tachyphonus coronatus*, (c) *Thraupis sayaca*, (d) *Thraupis cyanoptera*, (e) Thraupis palmarum, (f) *Turdus amaurochalinus*, (g) *Turdus flavipes*, (h) *Turdus rufiventris*, (i) *Turdus albicollis*, (j) *Pitangus sulphuratus*. *Procnias nudicollis* presents gape size far wider than the maximum fruit diameter and, thus, is not indicated in the figure.



**Fig. 3.** Frequency of exit flights of frugivorous birds from *Eugenia umbelliflora* to low restinga and scrub habitats in Ilha do Cardoso, Brazil.

0.001) (Fig. 4). There was no difference in seed fate (germinated, predated and intact) when comparing open scrub and under-perch in scrub vegetation ($\chi^2$ = 1.239, d.f. = 4, $P$ = 0.538). Thus, hereafter, data from these two microhabitats will be pooled and considered as scrub.

**Probability of seed dispersal**

We obtained enough data to estimate the seed dispersal probability for nine bird species. The birds with the highest probabilities of seed removal were *Turdus amaurochalinus* and *Turdus rufiventris*, followed by
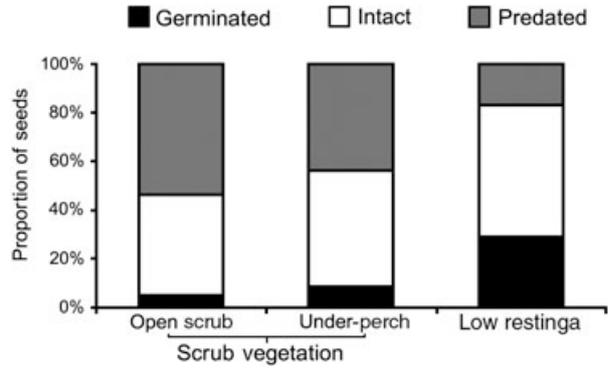
**Fig. 4.** Proportion of seeds germinated, predated, and remaining intact after 3 months of exposure in two micro-habitats in scrub vegetation (open areas and under-perch) and in low restinga forest, at Ilha do Cardoso, Brazil.

*Turdus flavipes*. *Thraupis palmarum* showed no seed removal since its probability of fruit handling success is null (Table 3). The feeding behaviour of this species was observed to be 60% dropping fruits and seeds beneath the tree canopy and 40% pulp consumption (Fig. 1).

When considering the effects of each disperser, the value of the probability of seed dispersal is very low; in most cases lower than 5% (Table 4). *Turdus amaurochalinus* and *Turdus rufiventris* were the best dispersers among the birds studied. The fruits eaten by these two birds have an almost 12% chance to germinate (Table 4). *Turdus flavipes* was the third most important bird and had half the probability of dispersing *E. umbelliflora* fruits compared with *T. rufiventris* (Table 4).

**DISCUSSION**

The sequential stages studied within the *Eugenia umbelliflora* life cycle proved to be extremely complex. First, fruit-eating birds differed considerably in their effectiveness as seed dispersers, presenting varying degrees of seed dispersal quantity and quality. Second, although the frequency of frugivorous visits is often considered the best predictor of high seed dispersal quantity (Schupp 1993; Vásquez *et al.* 2005), we found that this relationship was not always true in the *E. umbelliflora* system. In fact, the primary visitor, *Thraupis sayaca*, is an inefficient seed disperser. It presents a low likelihood of successful removal, and probably poses a negative effect on plant reproduction (Vásquez *et al.* 2005).

The pattern of seed dispersal of *E. umbelliflora* can be described as presenting many visitors, but is also characterized by numerous inefficient dispersal events. Almost half of the visits to the fruiting plants did not present fruit-frugivore interactions, and in those visits

**Table 3.** Relative proportion of the probability of seed removal by each frugivorous bird in Ilha do Cardoso, Brazil

| Species | No. fruits per visit (1) | No. visits per hour (2) | Dispersal probability (3) | Product of 1, 2 and 3 | Relative proportion ($Ps$) |
|---|---|---|---|---|---|
| *Tachyphonus coronatus* | 3.7 | 0.07 | 0.07 | 0.02 | 0.01 |
| *Tangara peruviana* | 7.2 | 0.15 | 0.03 | 0.03 | 0.02 |
| *Thraupis cyanoptera* | 1.2 | 0.07 | 0.40 | 0.03 | 0.02 |
| *Thraupis palmarum* | 3.3 | 0.05 | 0.00 | 0.00 | 0.00 |
| *Turdus flavipes* | 2.1 | 0.18 | 0.81 | 0.31 | 0.17 |
| *Turdus rufiventris* | 3.1 | 0.27 | 0.53 | 0.44 | 0.24 |
| *Turdus amaurochalinus* | 3.4 | 0.36 | 0.43 | 0.53 | 0.28 |
| *Myiarchus tyrannulus* | 4.6 | 0.13 | 0.50 | 0.30 | 0.16 |
| *Pitangus sulphuratus* | 1.2 | 0.16 | 1.00 | 0.19 | 0.10 |
| | | | Total | 1.85 | 1.00 |

**Table 4.** Dispersal probabilities by each of the frugivorous bird in Ilha do Cardoso, Brazil

| Species | $Ps$ 1 | $\Sigma(D_{sm}T_m)$ 2 | Probability of dispersal (product of 1 and 2) |
|---|---|---|---|
| *Tachyphonus coronatus* | 0.01 | 0.280 | $0.3 \times 10^{-2}$ |
| *Tangara peruviana* | 0.02 | 0.170 | $0.3 \times 10^{-2}$ |
| *Thraupis cyanoptera* | 0.02 | 0.280 | $0.6 \times 10^{-2}$ |
| *Thraupis palmarum* | 0.00 | 0.060 | 0.00 |
| *Turdus flavipes* | 0.17 | 0.170 | $2.9 \times 10^{-2}$ |
| *Turdus rufiventris* | 0.24 | 0.233 | $5.6 \times 10^{-2}$ |
| *Turdus amaurochalinus* | 0.28 | 0.221 | $6.2 \times 10^{-2}$ |
| *Myiarchus tyrannulus* | 0.16 | 0.170 | $2.7 \times 10^{-2}$ |
| *Pitangus sulphuratus* | 0.10 | 0.280 | $2.8 \times 10^{-2}$ |
| Total | 1.00 | 0.214 | 0.214 |

$D_{sm}$, probability that seeds would be deposited in habitat $m$ by frugivores; $Ps$, probability of seed removal by frugivores; $T_m$, probability of making the transition from seed to seedling in $m$.

with interaction ($n = 147$), only 30% of the fruits handled were successfully dispersed. This situation reflects the visitation of birds belonging to the Thraupidae and Parulidae families (see Levey 1987). Although these birds generally presented a high frequency of visits and fruit handling, they were unable to successfully remove *E. umbelliflora* fruits in most of the feeding events, therefore contributing to the amount of seeds fated to failure. On the contrary, birds from the Turdidae and Tyrannidae families proved to be excellent fruit removers. This behavioural dichotomy between these bird families is probably a result of the morphological traits of the species (Levey 1987; Jordano & Schupp 2000). It is well known that birds with larger body and gape sizes are able to ingest wider fruits and in larger quantities than smaller birds (Levey 1987; Jordano 2000). Small birds, such as those from the Thraupidae and Parulidae families, cannot swallow large seeds, therefore they simply peck pulp pieces, dropping seeds beneath the parent canopy or dropping the entire fruit (Levey 1987).

The fact that fruits dropped by birds beneath the tree canopy are larger than those collected directly from the plants is evidence of a birds' failure to remove larger fruits. Similar results were also found in other studies (Wheelwright 1985; Rey *et al*. 1997). Two behavioural situations are possible. Either birds actively select larger fruits to obtain greater pulp amount, as suggested by Martínez *et al*. (2007) for *Crataegus* fruits, or they do not select fruits based on their sizes but pick fruits indiscriminately (Wheelwright 1985). In both cases, birds that are unable to manage big fruits drop those wider than their gapes. Only *Procnias nudicollis* and *Pitangus sulphuratus* presented gape width wider than the largest fruits found in *E. umbelliflora* populations and, therefore, they are not constrained by the fruit sizes at Ilha do Cardoso.

Fruit discrimination by birds and the inability to disperse large seeds can result in both immediate and delayed consequences to *E. umbelliflora* fitness. Larger seeds can aggregate more reserve tissues that ameliorate the growing and vigour of seedlings, turning them into stronger survivors and competitors under distinct environmental adversities (Leishman *et al*. 2000; Alcántara & Rey 2003; Pizo *et al*. 2006). Furthermore, they become more tolerant to shade, burial, herbivory

and low soil moisture and nutrients (Leishman *et al.* 2000). In the scenario where frugivores disperse small to medium sized fruits, the establishment of seedlings is affected by the lack of individuals of greater vigour. In addition, fruit size is a heritable trait that can be maintained or shaped through generations (Wheelwright 1993). Therefore, selection pressures in the long term might decrease the mean fruit size in each individual tree, as well as the range of fruit size for the entire population. However, as shown by Alcántara and Rey (2003), there might be a trade-off between seed dispersal and survival that can reverse the selective pressure exerted by frugivores on seed size. Thus, although birds are dispersing a small number of large seeds, these seeds may be experiencing increased probability of survival during post-dispersal stages in the *E. umbelliflora* life cycle.

Low restinga received more avian post-feeding flights than scrub vegetation. Restinga also showed the highest rate of seed germination and the lowest rate of seed predation. Therefore, we suggest that low restinga is the best microhabitat for *E. umbelliflora* establishment. The post-feeding movements of birds are associated with their pattern of habitat use, which is strongly related to their vegetation preferences, including aspects of floristic composition, vegetation structure and availability of food resources (Hasui *et al.* 2007). Birds may prefer low restinga habitats over scrub due to its higher diversity of life forms, species and structural complexity (Souza & Capellari 2004; Bernardi *et al.* 2005).

*Eugenia umbelliflora* seeds are unlikely to survive in scrub vegetation because they are intolerant to desiccation, losing their viability at moisture levels lower than 15% (Delgado & Barbedo 2007). The severe conditions of intense exposure to sunlight and the high salinity of the scrub habitat might result in high seed desiccation, which is certainly a constraint to *E. umbelliflora* survival. In addition, the very abundant scrub crab *Ocypode quadrata*, which has an omnivorous diet including seeds (Nalesso 2004), probably acts as an intense fruit remover and post-dispersal seed predator, as described in studies with other species of crabs (Capistrán-Barradas *et al.* 2006).

The probability of seed germination after avian gut passage is also signed as an important factor contributing to the qualitative component of seed dispersal effectiveness (Godínez-Alvarez & Jordano 2007; Traveset *et al.* 2007). We have not measured its contribution to the final probability of seed dispersal; however, we suggest that in this case, this factor represents a weak effect. As found by Cazetta & Galetti, unpubl. data, 2008), *E. umbellifora* seeds do not need to pass through a frugivore gut to germinate. Few birds are able to swallow *E. umbelliflora* fruits, thus their major consequence on seed germination is the removal of the pulp enclosing the seed.

The importance of combining the three probabilities (seed removal, seed deposition, and seed germination) to calculate the seed dispersal probability is evident when we observe *Thraupis cyanoptera* and *Tachyphonus coronatus*. These species had the highest probabilities of delivering seeds in patches where seeds germinate, but a low probability of seed removal, resulting in low seed dispersal effectiveness.

The relative importance of each frugivorous bird species as a seed disperser varies largely between species (Jordano & Schupp 2000; Francisco & Galetti 2001; Cazetta *et al.* 2002; Godínez-Alvarez *et al.* 2002; Jordano *et al.* 2007). In this context, *Turdus* species showed to be the best dispersal agents. Their larger bodies and wider gapes allow them to disperse larger fruits. They are frequent visitors and successful fruit removers and they also deliver seeds into suitable microhabitats. The association of all of these aspects leads to high probabilities of successful seed dispersal, making these birds fundamental to the maintenance of the *E. umbelliflora* population, especially in endangered sites such as restinga vegetation, which historically have been the first areas in the Atlantic rainforest to suffer the consequences of human expansion (Souza & Capellari 2004).

We conclude that assessing the overall consequence of seed dispersal within the framework of disperser effectiveness can provide a more comprehensive and realistic evaluation of different seed dispersers. This approach represents a better understanding of plant-frugivore interactions and their fundamental ecological and evolutionary processes. Only linking detailed information on the outcome of frugivore activity and their potential effects on critical stages of the life cycles of plants can allow the evaluation of the effects of seed dispersal on plant population dynamics.

## ACKNOWLEDGEMENTS

## REFERENCES

Alcántara J. M. & Rey P. J. (2003) Conflicting selection pressures on seed size: evolutionary ecology of fruit size in a bird-dispersed tree, *Olea europaea*. *J. Evol. Biol.* **16,** 1168–76.

Barros F., Melo M. M. R. F., Chiea S. A. C., Kirizawa M. G. L., Wanderley M. & Jung-Mendaçolli S. L. (1991) Flora Fanerogâmica da Ilha do Cardoso. São Paulo. *Bol. Inst. Bot.* **1,** 1–184.

Bernardi J. V. E., Landim P. M. B., Barreto C. L. & Monteiro R. C. (2005) Estudo especial do gradiente de vegetação do Parque Estadual da Ilha do Cardoso, SP, Brasil. *Holos Environ.* **5,** 1–22.

Calviño-Cancela M. (2002) Spatial patterns of seed dispersal and seedling recruitment in *Corema album* (Empretaceae): the importance of unspecialized dispersers for regeneration. *J. Ecol.* **90,** 775–84.

Capistrán-Barradas A., Moreno-Casasola P. & Defeo O. (2006) Postdispersal fruit and seed removal by the crab *Gecarcinus lateralis* in a coastal forest in Veracruz, México. *Biotropica* **32,** 203–9.

Castro E. R., Galetti M. & Morellato L. P. C. (2007) Reproductive phenology of *Euterpe edulis* (Arecaceae) along a gradient in the Atlantic rainforest of Brazil. *Aust. J. Bot.* **55,** 725–35.

Cazetta E., Rubim P., Lunardi V. O., Francisco M. R. & Galetti M. (2002) Frugivoria e dispersão de sementes de *Talauma ovata* (Magnoliaceae) no sudeste brasileiro. *Ararajuba* **10,** 199–206.

Clark C. J., Poulsen J. R., Boulker B. M., Connor E. F. & Parker V. T. (2005) Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology* **86,** 2684–94.

Comitê Brasileiro de Registros Ornitológicos (2008) Listas das aves do Brasil. Versão 5 Oct 2008 [Cited 17 Nov 2008.] Available from URL: ⟨http://www.cbro.org.br⟩.

Couto O. S. & Cordeiro R. M. S. (2005) *Manual do reconhecimento das espécies vegetais da restinga do Estado de São Paulo.* Secretaria do Meio Ambiente, Departamento Estadual de Proteção dos Recursos Naturais – DEPRN, São Paulo.

Delgado L. F. & Barbedo C. J. (2007) Tolerância à dessecação de sementes de espécies de *Eugenia*. *Pesq. Agrop. Bras.* **42,** 265–72.

Francisco M. R. & Galetti M. (2001) Frugivoria e dispersão de sementes de *Rapanea umbellata* (Myrsinaceae) no cerrado de São Paulo, sudeste do Brasil. *Ararajuba* **9,** 13–19.

Francisco M. & Galetti M. (2002) Aves como potenciais dispersores de *Ocotea pulchella* (Lauraceae) numa área de vegetação de cerrado do sudeste brasileiro. *Rev. Bras. Bot.* **25,** 11–17.

Furnari F. L., Struffaldi-de-Vuono Y. & Salum S. T. (1987) Balanço hídrico de duas áreas de Mata Atlântica: Reserva Biológica de Paranapiacaba e Parque Estadual da Ilha do Cardoso (São Paulo). *Anais do Congresso da Sociedade Brasileira de São Paulo* **4,** 95–101.

Galetti M., Pizo M. A. & Morellato L. P. C. (2004) Métodos para estudo da fenologia, frugivoria e dispersão de sementes. In: *Manual para Manejo da Vida Silvestre no Brasil* (eds L. Cullen, C. Pádua & R. Rudram) pp. 395–422. Editora da UFPR, Paraná.

García D. & Ortiz-Pulido R. I. (2004) Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales. *Ecography* **27,** 187–96.

Godínez-Alvarez H. & Jordano P. (2007) An empirical approach to analyzing the demographic consequences of seed dispersal by frugivores. In: *Seed Dispersal: Theory and its Application in a Changing World* (eds A. Dennis & D. Westcott) pp. 391–406. CABI Publishing, Wallingford, UK.

Godínez-Alvarez H., Valiente-Banuet A. & Rojas-Martinez A. (2002) The role of seed dispersers in the population dynam-

ics of the columnar cactus *Neobuxbaumia tetetzo*. *Ecology* **83,** 2617–29.

Hasui E. (2003) Influência da variação fisiológica da vegetação sobre a composição de aves frugívoras na Mata Atlântica. PhD Thesis. Universidade Estadual de Campinas, Campinas.

Hasui E., Gomes V. S. M. & Silva W. R. (2007) Effects of vegetation traits on habitat preferences of frugivorous birds in Atlantic Rain Forest. *Biotropica* **39,** 502–9.

Herrera C. M. (1989) Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics in undisturbed *Mediterranean habitats*. *Oikos* **55,** 250–62.

Janzen D. H. (1970) Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104,** 501–28.

Jordano P. (2000) Fruits and frugivory. In: *Seeds: The Ecology of Regeneration in Natural Plant Communities* (ed. M. Fenner) pp. 125–66. Commonwealth Agricultural Bureau International, Wallingford.

Jordano P. & Godoy J. A. (2002) Frugivore-generated seed shadows: a landscape view of demographic and genetic effects. In: *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D. J. Levey, W. R. Silva & M. Galetti) pp. 305–21. CAB International, Wallingford.

Jordano P. & Herrera C. M. (1995) Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Ecoscience* **2,** 230–37.

Jordano P. & Schupp E. W. (2000) Seed dispersal effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecol. Monogr.* **70,** 591–615.

Jordano P., García C., Godoy J. A. & García-Castaño J. L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proc. Natl Acad. Sci. USA* **104,** 3278–82.

Kollmann J. (2000) Dispersal of fleshy-fruited species: a matter of spatial scale? *Perspect. Plant Ecol. Evol. Syst.* **3,** 29–51.

Leishman M. R., Wright I. J., Moles A. T. & Westoby M. (2000) The evolutionary ecology of seed size. In: *Seeds: The Ecology of Regeneration in Natural Plant Communities* (ed. M. Fenner) pp. 31–57. Commonwealth Agricultural Bureau International, Wallingford.

Levey D. J. (1987) Seed size and fruit-handling techniques of avian frugivores. *Am. Nat.* **129,** 471–85.

Levin S. A. (1992) The problem of pattern and scale in ecology. *Ecology* **73,** 1943–67.

Lima A. R. & Capobianco J. P. (1997) *Mata Atlântica: avanços legais e institucionais para sua conservação*. Documento do ISA No. 4, São Paulo.

Martínez I., García D. & Obeso J. R. (2007) Allometric allocation in fruit and seed packaging conditions the conflict among selection pressures on seed size. *Evol. Ecol.* **21,** 517–33.

Nalesso R. C. (2004) Os decápodos Brachyura e Anomura da Estação Ecológica Juréia-Itatins. In: *Estação Ecológica Juréia-Itatins: ambiente físico, flora e fauna* (eds O. A. V. Marques & W, Duleba). pp. 189–97. Ribeirão Preto, Holos.

Nathan R. & Mueller-Landau H. C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* **15,** 278–85.

Pizo M. A., Von Allmen C. & Morellato L. P. C. (2006) Seed size variation in the palm *Euterpe edulis* and the effects of seed predators on germination and seedling survival. *Acta Oecol.* **29,** 311–15.

Revilla E., Wiegand T., Palomares F., Ferreras P. & Delibes M. (2004) Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. *Am. Nat.* **164,** E130–53.

Rey P. J., Gutiérrez J. E., Alcántara J. & Valera R. (1997) Fruit size in wild olives: implications for avian seed dispersal. *Func. Ecol.* **11,** 611–18.

Russo S. E. (2005) Linking seed fate to natural dispersal patterns: factors affecting predation and scatter-hoarding of *Virola calophylla* seeds in Peru. *J. Trop. Ecol.* **21,** 243–53.

Santos T., Tellería J. L. & Virgós E. (1999) Dispersal of Spanish juniper *Juniperus thurifera* by birds and mammals in a fragmented landscape. *Ecography* **22,** 193–204.

Schupp E. W. (1993) Quantity, quality, and the effectiveness of seed dispersal by animals. In: *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects* (Eds T. H. Fleming & A. Estrada) pp. 15–29. Kluwer Academic Publishers, Dordrecht.

Schupp E. W. & Fuentes M. (1995) Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* **2,** 267–75.

Schupp E. W., Milleron T. & Russo S. E. (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. In: *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D. J. Levey, W. R. Silva & M. Galetti) pp. 19–34. CAB International, Wallingford.

Sick H. (1997) *Ornitologia Brasileira*. Nova Fronteira Editora, Rio de Janeiro.

Souza V. C. & Capellari L. Jr. (2004) A vegetação das dunas e restingas da Estação Ecológica Juréia-Itatins. In: *Estação Ecológica Juréia-Itatins: Ambiente Físico, Flora e Fauna* (eds O. A. V. Marques & W, Duleba) pp. 103–14. Ribeirão Preto, Holos.

Spiegel O. & Nathan R. (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecol. Lett.* **10,** 718–28.

Staggemeier V. G., Morellato L. P. C. & Galetti M. (2007) Fenologia reprodutiva de Myrtaceae em uma ilha continental de Floresta Atlântica. *Rev. Bras. Bioc.* **5,** 423–5.

Sugiyama M. (1998) Estudo de florestas da restinga da Ilha do Cardoso, Cananéia, São Paulo, Brasil. *Bol. Inst. Bot.* **11,** 119–59.

Tellería J. L., Ramírez A. & Pérez-Tris J. (2005) Conservation of seed-dispersing migrant birds in Mediterranean habitats: shedding light on patterns to preserve processes. *Biol. Conserv.* **124,** 493–502.

Traveset A., Robertson A. W. & Rodríguez-Pérez J. (2007) A review on the role of endozoochory on seed germination. In: *Seed Dispersal: Theory and its Application in a Changing World* (eds A. Dennis & D. Westcott) pp. 78–108. CABI Publishing, Oxon.

Traveset A., Rodríguez-Pérez J. & Pías B. (2008) Seed trait changes in dispersers' guts and consequences for germination and seedling growth. *Ecology* **89,** 95–106.

Valiente-Banuet A. & Ezcurra E. (1991) Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse-plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *J. Ecol.* **79,** 961–71.

Vázquez D. P., Morris W. F. & Jordano P. (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol. Lett.* **8,** 1088–94.

Voelker G., Rohwer S., Bowie R. C. K. & Outlow D. C. (2007) Molecular systematics of a speciose, cosmopolitan songbird genus: Defining the limits of, and relationships among, the Turdus thrushes. *Mol. Phylogenet. Evol.* **42,** 422–34.

Wang B. C. & Smith T. B. (2002) Closing the seed dispersal loop. *Tree* **17,** 379–85.

Wenny D. G. (2000) Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecol. Monogr.* **70,** 331–51.

Wheelwright N. T. (1985) Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* **63,** 808–18.

Wheelwright N. T. (1993) Fruit size in a tropical tree species: variation, preference by birds, and heritability. *Vegetatio* **107/108,** 163–74.