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28 Patterns of Fruit–Frugivore Interactions in Two Atlantic Forest Bird Communities of South-eastern Brazil: Implications for Conservation

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Introduction

Plant–frugivore interactions are key components of complex forest communities. For several reasons, the modification or loss of such interactions may have profound implications for conservation, especially in the tropics. First, some species of fruiting plant may be critical for maintaining frugivore populations during periods when other species are not producing fruit (Howe, 1977, 1981; Terborgh, 1986a,b; Peres, 2000). Secondly, some plant species are likely to experience changes in dispersal and recruitment if populations of frugivores are reduced (Pizo, 1997; Asquith *et al.*, 1999; Wright *et al.*, 2000). In fact, because frugivores appear to be especially sensitive to habitat fragmentation (Loiselle and Blake, 1992; Kattan *et al.*, 1994), long-term maintenance of fruiting plants in habitat fragments may be especially difficult. Thirdly, seed dispersal by frugivores can contribute to the restoration and management of degraded habitats. For example, fruit-eating birds are

readily attracted to remnant trees and even artificial perches in degraded areas, thereby facilitating regeneration by increasing seed rain (McDonnell and Stiles, 1983; Guevara and Laborde, 1993; McClanahan and Wolfe, 1993; Silva *et al.*, 1996; Holl, 1998; Duncan and Chapman, 1999).

Despite the importance of fruit–frugivore interactions on a community level, there are few conservation-orientated studies that include more than several species of fruiting plants and frugivores (Silva and Tabarelli, 2000; Galetti, 2001). Thus, most studies overlook a myriad of interactions (e.g. by inconspicuous species) that contribute to the recruitment dynamics of plants and to the food-web structure of frugivores. Here we present a community-level study of fruit–frugivore interactions in the Atlantic Forest of Brazil. This biome, formerly widespread along the Brazilian coast, represents one of the most threatened in the world and is reduced to a series of fragments (Fonseca, 1985; SOS Mata Atlântica and INPE, 1992; Ranta *et al.*, 1998),

jeopardizing endemic species of fauna and flora (Terborgh, 1992; Brooks and Balmford, 1996).

We focus on frugivorous birds because they are important mutualists to fruiting plants, are diurnal, have conspicuous foraging behaviour and can be easily captured. We quantified general patterns of frugivory in two nearby communities, one suffering greater impact by humans than the other. In each, we recorded observations of fruit consumption by birds. A record of a fruit species eaten by a bird species constitutes an ‘interaction’ between those species. We tallied and analysed the number of unique interactions in each community. Our goal was to assign a conservation value to each species of plant and bird, under the assumption that the more interactions a species is part of, the more important it is in the community-wide maintenance of fruit–frugivore interactions.

Study Site and Methods

Study site

Data were collected at Intervalles State Park, a 50,000 ha preserve in south-eastern São Paulo State. Intervalles is part of a reserve network that totals 120,000 ha of continuous Atlantic Forest. It is characterized by a mosaic of pristine forest and second-growth vegetation along an altitudinal gradient of 60–1200 m. Our study sites are 7 km apart and at the same altitudinal range (800–1000 m). They are connected by forest vegetation but differ in the degree of disturbance. The first site (Sede) houses the park’s administration facilities and is covered by second-growth vegetation and open areas, surrounding some tracts of mature forest, mostly dominated by bamboo thickets, with many roads and trails crossing the different habitats. The second site (Barra Grande) is mainly composed of mature forest with less dense bamboo thickets. The occurrence of a few trails does not seem to have a severe impact on this area. The sites exhibit similar seasonality: December to February are the hottest and wettest months, June to August are the coldest and driest. The frequency of frost varies among years; some frosts are

extremely severe. Previous studies in Intervalles have revealed that its avian species composition is largely intact, especially with respect to frugivores (Galetti, 1996; Aleixo and Galetti, 1997; Vielliard and Silva, 2001).

Feeding data

We visited Intervalles monthly from January 1999 to March 2000, spending 3–5 days censusing each site. A 5–8 km transect along trails crossing different habitats was walked slowly by a trained person for approximately 8 non-consecutive hours daily. During the censuses, we recorded bird-feeding behaviour at understorey and canopy fruiting trees, as sight permitted. In addition to these transects, we conducted observations on focal trees. To avoid sampling biases towards more conspicuous plant species, we limited observations on focal trees to a maximum of 3 non-consecutive hours. We also captured birds in mist nets (2700 and 4500 net-hours for Sede and Barra Grande, respectively) to collect seeds from faecal samples. Seeds were identified using a reference collection. These three procedures have been widely used to identify interactions between species of frugivorous birds and plants, although they are each subject to sampling biases (see Wheelwright *et al.*, 1984).

The relative importance of a seed-disperser species to a plant is a function of several qualitative and quantitative variables (*sensu* Schupp, 1993). We considered an ‘interaction’ as our sample unit. A feeding record of one bird species on one plant species generates an interaction. Interactions are binary; either a given bird species eats a given fruit species or it does not. Although we made no distinction among frugivores that are likely to vary in their efficiency as seed-dispersers (Moermond and Denslow, 1985; Levey, 1987), we eliminated all feeding records involving probable seed predators (e.g. parrots and parakeets) (Janzen, 1981; Galetti and Rodrigues, 1992), as well as those in which birds consistently took very small portions of fruit pulp without ingesting seeds.

All interactions were arranged in a bird species by plant species matrix, which was used to calculate the number of interactions and an

'importance index' for both plant and bird species. The importance index, I_j , developed by Murray (2000), weights the contribution of each bird species relative to that of the alternative dispersers of each of its food plants, and is given by the equation

$$I_j = \sum_{i=1}^s \left(\frac{C_{i,j} / T_i}{S} \right)$$

where T_i is the total number of bird species feeding on plant species i and S is the total number of plant species included in the sample. $C_{i,j} = 1$ if bird species j consumes fruits of plant species i or 0 if it does not. Note that this index allows one to estimate the community-level contribution of a species as a function not only of the number of interactions it performs, but also of the number of other taxa interacting with the same species. Thus, for example, if two bird species in a community of frugivores take part in exactly the same number of interactions, their potential importance as seed-dispersers will differ according to how many other frugivores feed on the same set of plant species. Values of I_j can range from 0.0 for a bird that consumes no fruits whatsoever to 1.0 for a bird that is the sole consumer of all plant species in its community.

The same equation was used to estimate the relative importance of the different plant species in the birds' diet (I_j), in which case T_i is the total number of plant species fed on by bird species i , S is the total number of bird species included in the sample, and $C_{i,j} = 1$ if plant species j is included in the diet of bird species i or 0 if it is not. Plant species with the highest values of I are those that produce fruit consumed by many bird species that eat few other species of fruits.

Fruiting plant and frugivorous bird species compositions in both study sites were compared using Sorensen's similarity coefficient (Krebs, 1989). This index ranges from 0 (no species are found in both communities) to 1.0 (all species are found in both communities). Differences in the average number of interactions per bird and plant family were tested by Mann-Whitney tests and differences in the frequency distribution of interactions between families of frugivores by a chi-square non-parametric test.

Bird nomenclature follows Sick (1993) and plant taxonomy follows Cronquist (1981).

Results

The frugivores

The frugivorous birds recorded in this study comprise the typical suite of frugivores for Intervales (Vielliard and Silva, 2001). A total of 68 species of frugivores accounted for 397 interactions unevenly distributed between sites (Table 28.1). Similarity in species composition between sites was relatively high (Sorensen index = 0.70) and the average number of interactions per bird species was also very similar (Sede = 4.1 ± 4.2 , $n = 233$; Barra Grande = 3.8 ± 4.0 , $n = 178$; Mann-Whitney test, $P > 0.05$).

The number of Emberizidae species was quite similar between the sites (18 in Sede and 19 in Barra Grande), although the species composition was slightly different. Tyrant flycatchers (Tyrannidae) had significantly more species in Sede than in Barra Grande (17 vs. 6, respectively; $\chi^2 = 6.9$, d.f. = 1, $P = 0.01$).

Five of 13 families (Emberizidae, Muscicapidae, Pipridae, Tyrannidae and Cotingidae) accounted for 83% of total interactions ($n = 397$). Excluding those families and subfamilies with records in only one site, the difference in the distribution of frequencies of interactions among bird families between sites was significant ($\chi^2 = 27.2$, d.f. = 9, $P = 0.01$). Tyrannidae and Emberizidae had more interactions than expected by chance in the more disturbed site (Sede), whereas Cotingidae and Ramphastidae had more interactions in the less disturbed site (Barra Grande). Less than 5% of total interactions were by species rarely seen eating fruit (Table 28.1), although some species contributing to these interactions were fairly common. This reflects an opportunistic pattern of fruit exploitation, at least for our sites.

The fruiting plants

A total of 103 plant species took part in 397 interactions with birds in both sites (Table 28.2). Similarity of species composition

Table 28.1. Number of species in families of frugivorous birds and total number of interactions observed between bird and fruiting-plant species in each bird family, performed in Barra Grande and Sede, Intervalles State Park, south-east Brazil.

Bird families	No. of species				No. of interactions			
	Unique to Sede	Unique to Barra Grande	Common to both sites	Total	Unique to Sede	Unique to Barra Grande	Common to both sites	Total
Columbidae	–	–	1	1	1	1	1	3
Cotingidae	2	2	2	6	16	25	–	41
Cracidae	–	–	2	2	10	9	1	20
Emberizidae	–	–	1	1	6	4	–	10
(Cardinalinae)								
Emberizidae	–	1	–	1	–	1	–	1
(Coerebinae)								
Emberizidae	–	1	–	1	–	1	–	1
(Emberizinae)								
Emberizidae	–	1	1	2	1	2	–	3
(Icterinae)								
Emberizidae	3	1	13	17	86	45	7	138
(Thraupinae)								
Mimidae	1	–	–	1	2	–	–	2
Muscicapidae	–	–	4	4	22	24	2	48
Phasianidae	–	1	–	1	–	1	–	1
Picidae	–	1	–	1	–	1	–	1
Pipridae	1	1	2	4	21	21	3	45
Ramphastidae	1	–	2	3	4	9	–	13
Trogonidae	–	1	2	3	8	8	–	16
Tyrannidae	12	1	5	18	36	7	–	43
Vireonidae	–	–	2	2	6	5	–	11
Total	20	11	37	68	219	164	14	397

was low (Sorensen index = 0.28). Despite the difference in plant species composition and total number of interactions between the two communities, the average number of interactions per plant species was very similar between sites (Sede = 3.5 ± 3.3 , $n = 233$; Barra Grande = 3.4 ± 3.6 , $n = 178$; Mann–Whitney, $P > 0.05$).

Proceeding the same way as with birds and excluding those families with records in only one site, the difference in the distribution of interactions among families between sites was marginally significant ($\chi^2 = 25.7$, d.f. = 15, $P = 0.05$), but only *Euphorbiaceae* and *Rosaceae* accounted for more interactions than expected by chance in Sede.

Species of *Melastomataceae* accounted for most records of fruit consumption in both sites

(19.7% in Sede, $n = 233$; 23.5% in Barra Grande, $n = 178$). Melastomes in Sede were more abundant along forest edges and in second growth, whereas in Barra Grande they were mainly trees and shrubs of the canopy and understorey. Among other plant families, pioneer and second-growth species formed the bulk of interactions in Sede (*Anacardiaceae*, *Flacourtiaceae*, *Euphorbiaceae*, *Rosaceae*, *Myrsinaceae*, *Solanaceae* and *Ulmaceae*), whereas canopy and shade-tolerant tree species contributed the most interactions in Barra Grande (*Lauraceae*, *Myrtaceae*, *Sapindaceae*, *Symplocaceae*, *Loranthaceae*). Five families (*Anacardiaceae*, *Aquifoliaceae*, *Flacourtiaceae*, *Piperaceae* and *Ulmaceae*) interacted with birds only in Sede, where they accounted for 19.7% of the local interactions ($n = 233$).

Table 28.2. Number of species in families of bird-dispersed plants and total number of interactions observed between bird and fruiting-plant species in each plant family in Sede and Barra Grande, Intervalos State Park, south-east Brazil.

Plant families	No. of species				No. of interactions			
	Unique to Sede	Unique to Barra Grande	Common to both sites	Total	Unique to Sede	Unique to Barra Grande	Common to both sites	Total
<i>Anacardiaceae</i>	2	—	—	2	15	—	—	15
<i>Annonaceae</i>	—	1	—	1	—	1	—	1
<i>Apocynaceae</i>	1	—	—	1	1	—	—	1
<i>Aquifoliaceae</i>	1	—	—	1	8	—	—	8
<i>Araliaceae</i>	—	1	—	1	—	4	—	4
<i>Arecaceae</i>	1	1	—	2	4	2	—	6
<i>Boraginaceae</i>	1	—	—	1	3	—	—	3
<i>Burseraceae</i>	—	1	—	1	—	4	—	4
<i>Cactaceae</i>	—	1	—	1	—	3	—	3
<i>Cecropiaceae</i>	1	1	—	2	1	4	—	5
<i>Celastraceae</i>	—	1	—	1	—	3	—	3
<i>Commelinaceae</i>	1	—	—	1	1	—	—	1
<i>Euphorbiaceae</i>	2	—	1	3	20	7	—	27
<i>Flacourtiaceae</i>	2	—	—	2	5	—	—	5
<i>Lauraceae</i>	4	7	—	11	12	16	—	28
<i>Liliaceae</i>	1	—	—	1	1	—	—	1
<i>Loranthaceae</i>	1	1	3	5	8	14	1	23
<i>Melastomataceae</i>	8	4	6	18	40	36	6	82
<i>Moraceae</i>	1	—	1	2	10	8	—	18
<i>Myrsinaceae</i>	—	1	1	2	12	7	4	23
<i>Myrtaceae</i>	5	6	2	13	13	17	1	31
<i>Nyctaginaceae</i>	—	—	1	1	2	2	—	4
<i>Onagraceae</i>	—	—	1	1	2	1	1	4
<i>Phytolaccaceae</i>	1	—	—	1	3	—	—	3
<i>Piperaceae</i>	3	—	—	3	6	—	—	6
<i>Rosaceae</i>	1	—	1	2	8	—	1	9
<i>Rubiaceae</i>	4	3	—	7	8	7	—	15
<i>Rutaceae</i>	1	—	—	1	1	—	—	1
<i>Sapindaceae</i>	1	2	—	3	11	17	—	28
<i>Solanaceae</i>	5	2	—	7	9	6	—	15
<i>Symplocaceae</i>	1	2	—	3	1	5	—	6
<i>Ulmaceae</i>	1	—	—	1	12	—	—	12
<i>Zingiberaceae</i>	1	—	—	1	2	—	—	2
Total	51	35	17	103	219	164	14	397

Patterns of interactions

Twenty per cent of all recorded bird and plant species in both communities were responsible for the majority of the interactions.

The rank distribution of interactions among bird species was right-skewed; the vast majority of bird species took part in a few interactions, whereas a few bird species took part in many (Fig. 28.1). The hooded berry-eater, *Carpornis cucullatus*, a canopy and mid-level

species, had the highest number of interactions for both sites combined ($n = 34$), followed closely by an understorey species, the blue manakin, *Chiroxiphia caudata* ($n = 32$). The ruby-crowned tanager, *Tachyphonus coronatus* ($n = 28$), and the rufous-bellied thrush, *Turdus rufiventris* ($n = 24$), were also commonly seen eating fruit, most often along forest edges or in second growth.

The same pattern of rank distribution was observed for plant species (Fig. 28.1), except

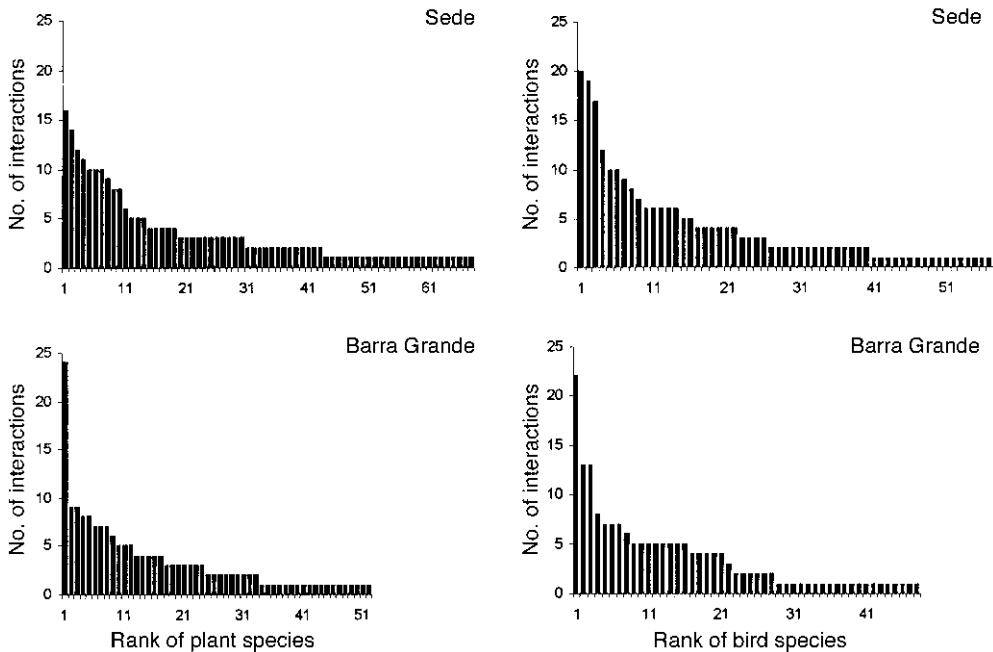


Fig. 28.1. Rank-ordered distribution of interactions for plant species (left panel) and bird species (right panel) in the Sede and Barra Grande regions of Intervalos State Park.

that one melastome species, *Miconia pusilliflora*, in Barra Grande had more than twice the number of interactions ($n = 24$) than any of its co-occurring species. In Sede, *Myrsine coriacea* (Myrsinaceae) and *Schinus terebenthifolius* (Anacardiaceae) ranked first and second in interactions with frugivores ($n = 16$ and 14 , respectively).

Importance indices

The 15 bird species with highest indices at Sede and Barra Grande are shown in Fig. 28.2. They performed 63.4% of all interactions in the matrix and comprised three different groups: (i) canopy or mid-level species that feed on a wide variety of fruit types, but mainly large drupes, berries and arillate seeds (e.g. *C. cucullatus*, *Penelope obscura*, *Pipile jacutinga*, *Turdus albicollis*, *Platycichla flavipes*, *Selenidera maculirostris*, *Trogon* spp., *Euphonia pectoralis*); (ii) understorey species that feed mainly on small drupes and berries (e.g. *C. caudata*, *Ilicura militaris*, *Schiffornis virescens*, *Trichothraupis melanops*); and (iii) forest-edge and second-

growth species that feed on small drupes, berries and arillate seeds (e.g. *T. rufiventris*, *T. coronatus*, *Thraupis* spp., *Stephanophorus diadematus*, *Cissopis leveriana*, *Saltator similis*). Among these 15 species, seven are common to both sites. The remaining eight species in Sede are mostly edge species, whereas in Barra Grande they are mostly understorey or mid-level species (Fig. 28.2). Although abundant and speciose, tanagers (Thraupinae) had their importance diluted by more strictly frugivorous taxa, such as cotingids, manakins, thrushes, guans and toucans. In general, bird species with more strictly frugivorous diets had higher values in the less disturbed site, as shown remarkably by the hooded berry-eater (*C. cucullatus*) (Fig. 28.2).

The 15 most important plant species are shown in Fig. 28.3. They accounted for 60.4% of all interactions in the matrix and, like the bird species, can be classified into three groups: (i) canopy or mid-level species, usually shade-tolerant, with a wide variety of fruit types (e.g. *M. pusilliflora*, *Matayba guianensis*, *Cupania vernalis*, *Euterpe edulis*, *Ocotea puberula*, *Persea pyrifolia*, *Myrcia grandiflora*); (ii) forest-edge

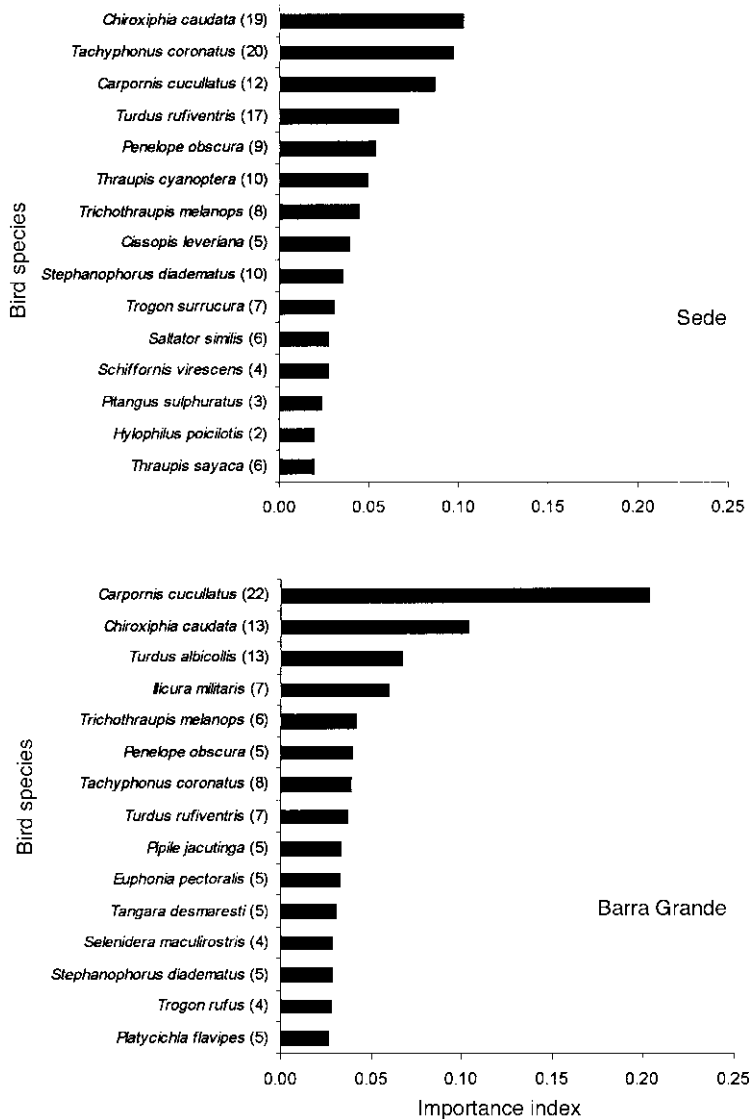


Fig. 28.2. Importance values for the 15 frugivorous birds with highest importance indices in the Sede and Barra Grande regions of Intervalas State Park. The number of interactions of each species is given in parentheses.

and second-growth species, with small to medium drupes, berries and arillate seeds (e.g. *Trema micrantha*, *M. coriacea*, *S. terebinthifolius*, *Sapium glandulatum*, *Alchornea triplinervia*, *Tetrorchidium rubrivenium*, *Leandra dasytricha*, *Ossaea amygdaloides*, *Ficus luschnatiana*, *Allorhaphis edulis*, *Ilex brevicuspis*); and (iii) hemi-parasitic mistletoes with small tough-skinned, mucilaginous fruits (e.g. *Struthanthus* spp.). The higher values were assigned

to the plant species of the first group in the less disturbed site (Barra Grande).

Discussion

The frugivore profile

The average number of interactions that we recorded between frugivorous birds and

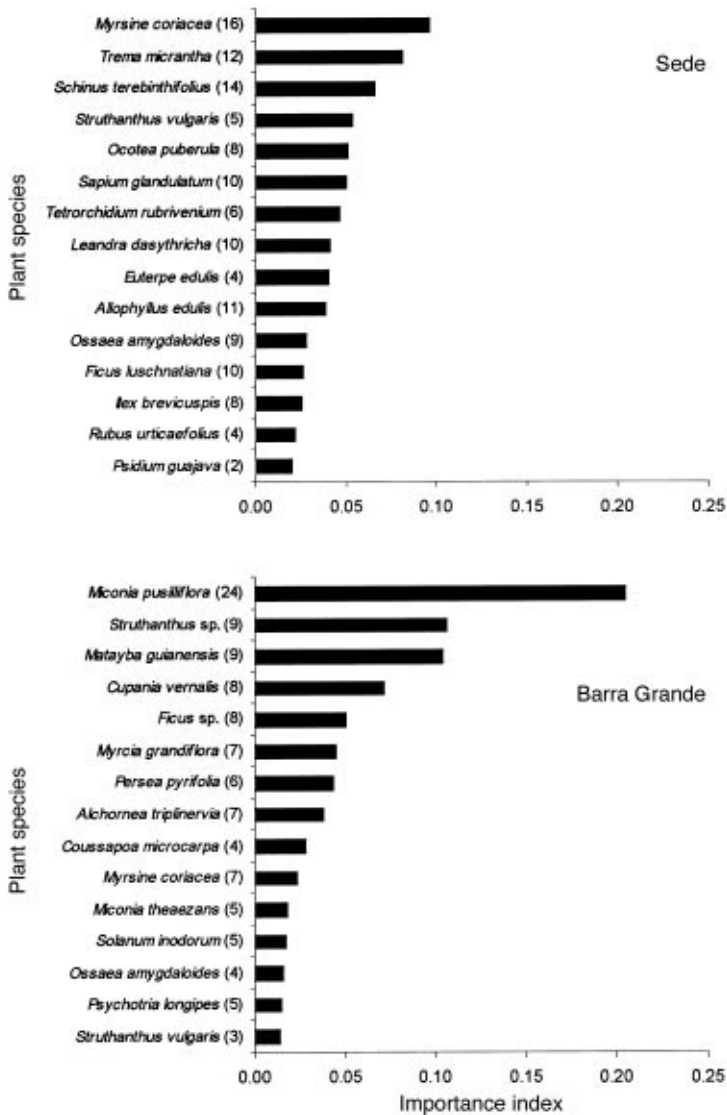


Fig. 28.3. Importance values for the 15 ornithochorous plants with highest importance indices in the Sede and Barra Grande regions of Intervaes State Park. The number of interactions of each species is given in parentheses.

fruiting plants was similar to other studies conducted with equivalent methods (Galetti and Pizo, 1996), but lower than reported in a study of a more species-rich community (Wheelwright *et al.*, 1984). However, the average number of interactions and number of species in a community may vary independently from each other (Jordano, 1987). Although our dietary records for each bird species are not exhaustive, we assume that the

interactions we report are an unbiased sample and thus that the patterns we found provide an accurate picture of how interactions are organized in both communities.

Fruit-eating bird communities may change in species composition and dynamics according to variation in spatial and temporal components of the habitat (Levey, 1988; Loiselle and Blake, 1991). Despite the difference in plant composition and degree of disturbance

between Sede and Barra Grande, their bird communities were quite similar, indicating that frugivorous birds in the Atlantic Forest are flexible in habitat choice, at least within the range of habitats we studied. We detected no absence of large-bodied frugivorous species in the more disturbed site (Sede), as one might expect (Galetti and Aleixo, 1998). The major difference between sites was due to the dominance of edge-habitat tyrant-flycatchers in the Sede site (Table 28.1), a group that often relies heavily on fruit (Morton, 1977; Fitzpatrick, 1980; Sick, 1993). Together with tanagers, saltators and icterines, flycatchers play an important role in the seed-dispersal systems of several plant species in disturbed areas in the Atlantic Forest of Brazil (de Souza *et al.*, 1992; Rodrigues, 1995) and elsewhere in the neotropics (Snow and Snow, 1971).

The higher number of interactions involving cotingas and toucans in the more preserved site (Barra Grande) is difficult to explain, as these taxa were commonly seen in both sites. Some species of cotingas and toucans forage in open areas adjacent to forest (Estrada *et al.*, 1993; Guevara and Laborde, 1993). At Intervalles, however, these species seem to prefer fruiting plants associated with less disturbed habitats. The number of interactions performed by a cotingid, the hooded berry-eater (*C. cucullatus*), was especially high. Although some cotingid species are known to migrate altitudinally (Sick, 1993), *Carporhis* is probably a resident species, because we recorded it in both sites during the entire study period. Its diverse diet is probably a result of its permanent residency and its willingness to eat fruits of both primary and secondary forest (W.R. Silva, personal observation). This species is found in the lowlands of Intervalles only in severe winters (Galetti, 1996).

Thrushes and manakins were common frugivores in both sites. The rufous-bellied thrush (*T. rufiventris*) is an important seed-disperser in forest-edge habitats in Sede, whereas the white-necked thrush (*T. albicollis*) plays the same role in the forest understorey. The blue manakin (*C. caudata*), found mainly in the understorey, is one of the most active frugivores at both sites (W.R. Silva, personal observation).

Trogons usually include animal matter in their otherwise frugivorous diet (Remsen *et al.*,

1993) and sometimes seem to ignore nearby fruits while searching for animal prey (W.R. Silva, personal observation). Their number of interactions was equally distributed in the two study sites. Like the hooded berry-eater, the three trogon species at Intervalles foraged in a variety of habitats and strata, taking several fruit types. Vireos, although primarily insectivorous in Brazil (Sick, 1993), can also exploit fruit sources opportunistically (Greenberg *et al.*, 1995; Pizo, 1997).

The number of interactions recorded for guans was certainly much lower than reported in a study that focused on guans in a nearby site (Galetti *et al.*, 1997). Like other frugivores recorded in this study, guans foraged for fruits in mature as well as in second-growth vegetation. This group, represented at Intervalles by the dusky-legged guan (*P. obscura*) and the jacutinga (*P. jacutinga*), is a key focus for conservation efforts, because they are often sensitive to hunting pressure and habitat degradation (Galetti *et al.*, 1997; reviewed in Strahl *et al.*, 1997). We found guans equally common at our two study sites.

Overall, the weak-to-moderate level of habitat degradation at one of our sites appears to have had little impact on the avifauna, although abundance of some species may be affected (Galetti and Aleixo, 1998). Given that most remaining Atlantic Forest in southeastern Brazil consists of a mosaic of different successional types similar to those that occur at Intervalles (Fonseca, 1985; Tabarelli and Mantovani, 1997), it is likely that the coteries of avian frugivores will be similar, with a pervasive influence of facultative frugivores, such as tyrant-flycatchers, tanagers, thrushes, trogons and manakins.

The fruiting plants

The richness of ornithochorous plant species in both Sede and Barra Grande is difficult to compare with that of other sites because we made no attempt to survey the entire plant community, leaving many ornithochorous species unreported because no interaction was assigned to them. This is a common bias when working in a very speciose community and

when depending on fortuitous observations of organisms that are often difficult to spot.

The plant families with the most interactions are commonly reported as important to birds in other neotropical sites (Leck, 1972; Snow, 1981; Wheelwright *et al.*, 1984; Blake and Loiselle, 1992). The difference in the species composition of the two plant communities used by birds in our study probably reflects the effect of human disturbance in the Sede site. However, despite the prevalence of second-growth species in Sede, those species were exploited by essentially the same bird species as in Barra Grande. This suggests that frugivorous birds in the Atlantic Forest readily forage across plant successional stages and can switch their food preferences according to local fruit availability.

The importance of fruiting *Melastomataceae* species to birds is well documented throughout the neotropics (Willis, 1966; Stiles and Rosselli, 1993; Galetti and Stotz, 1996). At our site, melastomes accounted for approximately 20% of all interactions and were eaten by almost all frugivorous species. The role of other plant families varied between sites. Although some families were consumed significantly more often in one site, a few accounted for the larger number of interactions in Sede. When families of edge and second-growth habitats, such as *Piperaceae*, *Rosaceae*, *Anacardiaceae*, *Flacourtiaceae* and *Ulmaceae*, are removed from the sample, the number of interactions becomes roughly equivalent between the two sites (Table 28.2), suggesting that the differences in the patterns of frugivory among Atlantic Forest sites are shaped by habitat structure.

The meaning of asymmetry in the interaction pattern

We found asymmetrically shaped distributions of interactions, in which a few species of birds or plants were responsible for the vast majority of interactions. Such a distribution seems typical of other tropical frugivore communities (Pérez, 1976; Wheelwright *et al.*, 1984; Blake and Loiselle, 1992; Galetti and Pizo, 1996; Murray, 2000). Asymmetry in interactions among species is expected for mutualistic

systems and is a characteristic feature of multi-species assemblages (Herrera, 1984; Jordano, 1987). No matter what metric of interaction is used (*sensu* Herrera and Jordano, 1981), some plant or bird species will be disproportionately important to their counterparts in the community. Thus, a plant species can be of great significance to a bird species, which in turn can be unimportant as a seed-disperser to the plant because its contribution is ‘diluted’ by that of other frugivores exploiting the same species. Likewise, the long tail of the distribution suggests that a plant species can be relatively unimportant to birds but may none the less be highly dependent on a given species for dispersal.

The asymmetrical distribution persists even when applying the ‘importance index’ to a small fraction of the plant/bird community. This trend not only reinforces the occurrence of ‘diffuse coevolution’ among sets of fruits and frugivores (Herrera, 1985; Jordano, 1987), but also has implications in the conservation of such communities, because it suggests alternative routes for system response in cases where one interacting partner becomes extinct (Jordano, 1987).

Conservation Perspective

Frugivory in the neotropics is often portrayed as an interaction between spectacular birds and conspicuous fruits. This is a misconception, based on narrowly focused case-studies (e.g. D.W. Snow, 1962; B.K. Snow, 1970; Skutch, 1980; Wheelwright, 1983). On a community level, the role of dull-coloured and inconspicuous fruits and frugivores is not fully appreciated (Westcott and Graham, 2000). The importance rankings of the birds and plants that we report make it clear that many fruit–frugivore mutualisms in neotropical forests involve relatively inconspicuous species, as also noted by Murray (2000) in Costa Rica. For birds, these species are usually small, facultative frugivores that are widespread in second-growth habitats. For plants, many are widespread shrubs of successional habitats, bearing small berries and drupes with small and often numerous seeds, or species of mistletoes using particular sets of small frugivores. Perhaps

none of them would fit into a category used to justify conservation efforts (Noss, 1990).

The importance values we assigned to species indirectly reflect the lack of redundancy in the interacting systems to which they belong (Walker, 1992), because higher values are a function of the interactions not shared with other species. Therefore, from a functional standpoint, species with high values are important for maintaining the resilience of their communities. This resilience may be particularly important during times of general fruit scarcity (e.g. the dry season at our site), when bird species with different degrees of fruit dependence rely on the fruits of several melastomes and other plant species that grow along edge and successional vegetation, a type of habitat that represents an important source of resources in tropical areas (Foster, 1980; Levey, 1988, 1990).

Our approach does not ignore the value of keystone resources but rather offers an alternative way to detect the 'mobile links' (*sensu* Gilbert, 1980) within a fruit–frugivore community and to evaluate their importance from a conservation perspective.

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References

- Aleixo, A. and Galetti, M. (1997) The conservation of the avifauna in a lowland Atlantic forest in south-east Brazil. *Bird Conservation International* 7, 235–261.
- Asquith, N.M., Terborgh, J., Arnold, A.E. and Riveros, C.M. (1999) The fruits the agouti ate: *Hymenaea courbaril* seed fate when its disperser is absent. *Journal of Tropical Ecology* 15, 229–235.
- Blake, J.G. and Loiselle, B.A. (1992) Fruits in the diets of neotropical migrant birds in Costa Rica. *Biotropica* 24, 200–210.
- Brooks, T. and Balmford, A. (1996) Atlantic forest extinctions. *Nature* 380, 115.
- Cronquist, A. (1981) *An Integrated System of Classification of Flowering Plants*. Columbia University Press, New York, 1262 pp.
- de Souza, F.L., Roma, J.C. and Guix, J.C. (1992) Consumption of *Didymopanax pachycarpum* unripe fruits by birds in southeastern Brazil. *Miscellanea Zoologica* 16, 246–248.
- Duncan, R.S. and Chapman, C.A. (1999) Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications* 9, 998–1008.
- Estrada, A., Coates-Estrada, R., Meritt, D., Jr, Montiel, S. and Curiel, D. (1993) Patterns of frugivore species richness and abundance in forest islands and agricultural habitats at Los Tuxtlas, Mexico. In: Fleming, T.H. and Estrada, A. (eds) *Frugivores and Seed Dispersal: Ecological and Evolutionary Aspects*. Kluwer Academic Publishers, Dordrecht, pp. 245–257.
- Fitzpatrick, J.W. (1980) Foraging behavior of neotropical tyrant flycatchers. *Condor* 82, 43–57.
- Fonseca, G.A.B. (1985) The vanishing Brazilian Atlantic forest. *Biological Conservation* 34, 17–34.
- Foster, R.B. (1980) Heterogeneity and disturbance in tropical vegetation. In: Soulé, M.E. and Wilcox, B.A. (eds) *Conservation Biology, an Evolutionary–Ecological Perspective*. Sinauer, Sunderland, pp. 75–92.
- Galetti, M. (1996) Fruits and frugivores in a Brazilian Atlantic forest. PhD thesis, University of Cambridge, Cambridge.
- Galetti, M. (2001) The future of the Atlantic Forest. *Conservation Biology* 14, 4.
- Galetti, M. and Aleixo, A. (1998) Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil. *Journal of Applied Ecology* 35, 286–293.
- Galetti, M. and Pizo, M. (1996) Fruit eating by birds in forest fragment in southeastern Brazil. *Ararajuba* 4, 71–79.
- Galetti, M. and Rodrigues, M. (1992) Comparative seed predation on pods by parrots in Brazil. *Biotropica* 24, 222–224.
- Galetti, M. and Stotz, D. (1996) *Miconia hypoleuca* (Melastomataceae) como espécie-chave para aves frugívoras no sudeste do Brasil. *Revista Brasileira de Biologia* 56, 435–439.

- Galetti, M., Martuscelli, P., Olmos, F. and Aleixo, A. (1997) Ecology and conservation of the jacutinga *Pipile jacutinga* in the Atlantic forest of Brazil. *Conservation Biology* 82, 31–39.
- Gilbert, L.E. (1980) Food web organization and the conservation of neotropical diversity. In: Soulé, M.E. and Wilcox, B.A. (eds) *Conservation Biology: an Evolutionary–Ecological Perspective*. Sinauer, Sunderland, Massachusetts, pp. 11–33.
- Greenberg, R., Foster, M.S. and Marquez-Vadellamar, L. (1995) The role of the White-eyed Vireo in the dispersal of *Bursera* fruit on the Yucatan Peninsula. *Journal of Tropical Ecology* 11, 619–639.
- Guevara, S. and Laborde, J. (1993) Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. In: Fleming, T.H. and Estrada, A. (eds) *Frugivores and Seed Dispersal: Ecological and Evolutionary Aspects*. Kluwer Academic Publishers, Dordrecht, pp. 319–338.
- Herrera, C.M. (1984) A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Monographs* 54, 1–23.
- Herrera, C.M. (1985) Determinants of plant–animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos* 44, 132–141.
- Herrera, C.M. and Jordano, P. (1981) *Prunus mahaleb* and birds: the high efficiency seed dispersal system of a temperate fruiting tree. *Ecological Monographs* 51, 203–221.
- Holl, K.D. (1998) Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? *Restoration Ecology* 6, 253–261.
- Howe, H.F. (1977) Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* 58, 539–550.
- Howe, H.F. (1981) Dispersal of a neotropical nutmeg (*Virola sebifera*) by birds. *The Auk* 98, 88–98.
- Janzen, D.H. (1981) *Ficus ovalis* seed predation by an Orange-chinned Parakeet (*Brotogeris jugularis*) in Costa Rica. *The Auk* 98, 841–844.
- Jordano, P. (1987) Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *American Naturalist* 129, 657–677.
- Kattan, G.H., Alvarez-Lopez, H. and Giraldo, M. (1994) Forest fragmentation and bird extinctions: San Antonio 80 years later. *Conservation Biology* 8, 138–146.
- Krebs, C.J. (1989) *Ecological Methodology*. Harper Collins Publishers, New York, 654 pp.
- Leck, C.F. (1972) Seasonal changes in feeding pressures of fruit- and nectar-eating birds in Panama. *Condor* 74, 54–60.
- Levey, D.J. (1987) Seed size and fruit-handling techniques of avian frugivores. *American Naturalist* 129, 471–485.
- Levey, D.J. (1988) Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58, 251–269.
- Levey, D.J. (1990) Habitat-dependent fruiting behaviour of an understory tree, *Miconia centrodesma*, and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. *Journal of Tropical Ecology* 6, 409–420.
- Loiselle, B.A. and Blake, J.G. (1991) Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72, 180–193.
- Loiselle, B.A. and Blake, J.G. (1992) Population variation in a tropical bird community. *BioScience* 42, 838–845.
- McClanahan, T.R. and Wolfe, R.W. (1993) Accelerating forest succession in a fragmented landscape: the role of bird and perches. *Conservation Biology* 7, 279–288.
- McDonnell, M.J. and Stiles, E.W. (1983) The structural complexity of old field vegetation and the recruitment of bird dispersed plant species. *Oecologia* 56, 109–116.
- Moermond, T.C. and Denslow, J.S. (1985) Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. In: Buckley, P.A., Foster, M.S., Morton, E.S., Ridgely, R.S. and Buckley, F.G. (eds) *Neotropical Ornithology*. Ornithological Monographs No. 36, American Ornithologist Union, Washington, DC, pp. 865–897.
- Morton, E.S. (1977) Intratropical migration in the Yellow-green Vireo and Piratic Flycatcher. *The Auk* 94, 97–106.
- Murray, K.G. (2000) The importance of different bird species as seed dispersers. In: Nadkarni, N.M. and Wheelwright, N.T. (eds) *Monteverde: Ecology and Conservation of a Tropical Cloud Forest*. Oxford University Press, New York, pp. 294–295.
- Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 44, 335–364.
- Peres, C.A. (2000) Identifying keystone plant resources in tropical forests: the case of gums from *Parkia* pods. *Journal of Tropical Ecology* 16, 287–317.
- Pérez, L.T. (1976) Diseminación de semillas por aves en ‘Los Tuxtlas’, Ver. In: Gómez-Pompa, A., Vázquez-Yanes, C., Rodríguez, S.A. and Cervera, A.B. (eds) *Regeneración de selvas*. Compañía Editorial Continental, Mexico, pp. 447–470.
- Pizo, M.A. (1997) Seed dispersal and predation in two populations of *Cabralea canjerana* (*Meliaceae*) in the Atlantic Forest of southeastern Brazil. *Journal of Tropical Ecology* 13, 559–578.

- Ranta, P., Blom, T., Niemela, J., Joensuu, E. and Siitonen, M. (1998) The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. *Biodiversity and Conservation* 7, 385–403.
- Remsen, J.V., Jr, Hyde, M.A. and Chapman, A. (1993) The diets of neotropical trogons, motmots, barbets and toucans. *Condor* 95, 178–192.
- Rodrigues, M. (1995) Spatial distribution and food utilization among tanagers in southeastern Brazil (Passeriformes: Emberizidae). *Ararajuba* 3, 27–32.
- Schupp, E.W. (1993) Quantity, quality and the effectiveness of seed dispersal by animals. In: Fleming, T.H. and Estrada, A. (eds) *Frugivores and Seed Dispersal: Ecological and Evolutionary Aspects*. Kluwer Academic Publishers, Dordrecht, pp. 15–29.
- Sick, H. (1993) *Birds in Brazil, a Natural History*. Princeton University Press, Princeton, New Jersey, 703 pp.
- Silva, J.M.C. and Tabarelli, M. (2000) Tree species impoverishment and the future of the Atlantic Forest of northeast Brazil. *Nature* 404, 72–74.
- Silva, J.M.C., Uhl, C. and Murray, G. (1996) Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conservation Biology* 10, 491–503.
- Skutch, A.F. (1980) Arils as food of tropical American birds. *Condor* 82, 31–42.
- Snow, B.K. (1970) A field study of the Bearded Bellbird in Trinidad. *Ibis* 114, 139–162.
- Snow, B.K. and Snow, D.W. (1971) The feeding ecology of tanagers and honeycreepers in Trinidad. *The Auk* 88, 291–322.
- Snow, D.W. (1962) A field study of the Golden-headed Manakin, *Pipra erythrocephala*, in Trinidad, W.I. *Zoologica (New York)* 47, 183–198.
- Snow, D.W. (1981) Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13, 1–14.
- SOS Mata Atlântica and INPE (1992) *Atlas da evolução dos remanescentes florestais e ecossistemas associados do domínio da Mata Atlântica no período de 1985–1990*. Fundação SOS Mata Atlântica, São Paulo.
- Stiles, F.G. and Rosselli, L. (1993) Consumption of fruits of the *Melastomataceae* by birds: how diffuse is coevolution? In: Fleming, T.H. and Estrada, A. (eds) *Frugivores and Seed Dispersal: Ecological and Evolutionary Aspects*. Kluwer Academic Publishers, Dordrecht, pp. 57–73.
- Strahl, S.D., Beajon, S., Brooks, D.M., Begazo, A.J., Sedaghatkish, G. and Olmos, F. (1997) *The Cracidae: their Biology and Conservation*. Hancock House, Surrey, 506 pp.
- Tabarelli, M. and Mantovani, W. (1997) Colonização de clareiras naturais na floresta atlântica do sudeste do Brasil. *Revista Brasileira de Botânica* 20, 57–66.
- Terborgh, J. (1986a) Keystone plant resources in the tropical forests. In: Soulé, M.E. (ed.) *Conservation Biology: the Science of Scarcity and Diversity*. Sinauer, Sunderland, Massachusetts, pp. 330–344.
- Terborgh, J. (1986b) Community aspects of frugivory in tropical forests. In: Estrada, A. and Fleming, T.H. (eds) *Frugivores and Seed Dispersal*. Dr W. Junk, Dordrecht, pp. 371–384.
- Terborgh, J. (1992) Maintenance of diversity in tropical forests. *Biotropica* 24, 283–292.
- Vielliard, J. and Silva, W.R. (2001) Avifauna. In: Secretaria de Estado do Meio Ambiente, Fundação para a Conservação e a Produção Florestal do Estado de São Paulo (eds) *Intervales*. Fundação Florestal, São Paulo, pp. 123–145.
- Walker, B.H. (1992) Biodiversity and ecological redundancy. *Conservation Biology* 6, 18–23.
- Westcott, D.A. and Graham, D.L. (2000) Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia* 122, 249–257.
- Wheelwright, N.T. (1983) Fruits and the ecology of the resplendent quetzals. *The Auk* 100, 286–301.
- Wheelwright, N.T., Haber, W.A., Murray, K.G. and Guindon, C. (1984) Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16, 173–191.
- Willis, E.O. (1966) Competitive exclusion and birds at fruiting trees in western Colombia. *The Auk* 83, 479–480.
- Wright, S.J., Zeballos, H., Domínguez, I., Galdardo, M.M., Moreno, M.C. and Ibáñez, R. (2000) Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology* 14, 227–239.