Chapter 3.4
Fruit Characteristics: Fruit Selection, Animal Seed Dispersal and Conservation Matters in the Sainte Luce Forests

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Abstract

This study represents a community-wide approach to primary seed dispersal in a Malagasy forest. No evidence could be found for close co-evolutionary relationships between fruits and frugivores. Regarding food selection, fruit and seed size appear to be the most determining physical traits for all consumer species. However, frugivores display a large dietary flexibility and for most traits they select according to what is readily available. As such, fruit traits seem more likely to be the result of abiotic conditions rather than strong interactions between frugivores and their food. Nevertheless, the local frugivore species have different impacts on seed dispersal. The littoral forest is expected to lose numerous endemic plant and animal species in the near future due to deforestation and the disruption of plant-animal exchanges. The database presented here on fruit-frugivore interactions should help to improve conservation management plans. The planting of several important fruiting species within corridors, plantations, or even clearings is a very useful application. These trees will attract several frugivores with species-specific dispersal services, which will contribute to forest regeneration.

Résumé

Caractéristiques des fruits: sélection des fruits et dispersion des graines par les animaux et enjeux de conservation dans les forêts de Sainte Luce. Cette étude portant sur la dispersion principale des graines dans une forêt malgache s'est déroulée à l'échelle d'une communauté. Nos travaux n'ont pas fait ressortir de relations étroites de co-évolution entre des fruits et des frugivores. Quant à la sélection des fruits, il apparaît que la taille du fruit et de la graine constituent les traits physiques les plus déterminants pour toutes les espèces consommant des fruits. Par contre, les frugivores montrent une grande flexibilité en matière de régime alimentaire, de sorte que la disponibilité prime sur l'ensemble des traits caractérisant les fruits et les graines. Ainsi, les traits des fruits sembleraient être davantage le résultat de conditions abiotiques plutôt que de fortes interactions entre les frugivores et l'aliment qu'ils consomment. Il n'en reste pas moins que les espèces frugivores ont des impacts différents sur la dispersion des graines. Il est prévu que les forêts littorales perdent de nombreuses espèces endémiques de plantes et d'animaux dans les années à venir suite au déboisement et à la rupture des interactions entre les plantes et les animaux. La base de données présentée ici sur les interactions entre fruit et frugivore devrait permettre d'améliorer les projets de gestion de la protection de la nature. La plantation de quelques espèces fruitières importantes dans des corridors boisés, des parcelles arborées ou même des clairières et zones ouvertes constituera une application très utile. Ces arbres attireront plusieurs frugivores en même temps que se mettront en place les mécanismes de dispersion spécifiques qui contribueront finalement à la régénération de la forêt.

Introduction

Interactions between fleshy-fruited plant species and the community of vertebrate frugivores have been studied in the tropics worldwide (e.g., Leighton 1982, Gautier-Hion *et al*. 1985, Dowsett-Lemaire 1988), where zoochorous plant species make up the majority of the flora (Howe and Smallwood 1982). The fleshy pulp of endozoochorous fruits attracts its

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consumers with a wide array of morphological traits and offers a nutritional reward for potential seed dispersers.

The study of fruit-frugivore interactions is particularly relevant for Madagascar, as this island has a high percentage of botanical and faunal endemism, (Lowry *et al*. 1997, Schatz 2001, Goodman and Benstead 2005) and at the same time a rather depauperate frugivore community (Langrand 1990, Goodman *et al*. 1997a). Several studies have compiled data on fruit and frugivore interactions in different dry and wet forest sites of Madagascar (Phillipson 1996, Birkinshaw 1999, 2001, Ganzhorn *et al*. 1999, Bleher and Böhning-Gaese 2001, Rakotonirainy 2001, Birkinshaw and Colquhoun 2003, Voigt *et al*. 2004).

This chapter summarizes interactions between the community of vertebrate frugivores present in the littoral forests of Sainte Luce, north of Tolagnaro, and the plant species they consume, with emphasis on fruit morphology and nutrient content, and with respect to the individual roles of consumers as seed dispersers, droppers, or predators (Bollen and van Elsacker 2002, 2004, Bollen *et al*. 2004a, 2004b, 2005). An attempt is made to unravel aspects of animal-plant interactions that determine the dynamics of the littoral forest, which presently suffers from severe fragmentation and degradation. Given this, it is important to understand these interactions and to integrate them in conservation management plans for this area.

The following questions are addressed in this chapter: 1) What are the morphological and biochemical traits of the zoochorous fruits in Sainte Luce?, 2) How do these traits influence food selection of the different frugivores?, 3) What is the impact of these frugivores on the fruits they eat?, and 4) How can data on fruit-frugivore interactions be useful for conservation actions?

Methods

This research was conducted from November 1999 through January 2001 in a 275 ha littoral forest fragment (S9) of Sainte Luce (24º45'S 47º11'E; in previous publications the size of this forest fragment has been given as 377 ha. Recent analyses of the old aerial photographs resulted in a much reduced size estimate). This forest is characterized by a relatively open or non-continuous canopy, which is 6 - 8 m in height with emergent trees up to 18 m (Dumetz 1999). The diameter at breast height (DBH) of trees rarely exceeds 30 to 40 cm (Rabevohitra *et al*. 1996, Dumetz 1999). At this site, mean monthly temperature is 23°C and average annual rainfall is about 2690 mm. There is a marked rainy season from November through February, but no well-defined dry season. Fruit production is seasonal, with a peak in abundance of ripe fruits in December and January, and with periods of fruit scarcity that show noted inter-annual differences (Bollen and Donati 2005).

Fruit traits

Ripe zoochorous fruits were collected in the study area throughout the research period. Herbarium specimens of all taxa were collected and identified at the Missouri Botanical Garden of Antananarivo (Appendix I). Consequently, morphological characteristics were measured at the field station and biochemical components were analyzed in the lab of the Department of Animal Ecology and Conservation, Hamburg University.

Discrete variables used to characterize fruits morphologically are growth form (large trees, small trees and shrubs, others), fruit type (berry, drupe, others), pulp type (juicy, soft or aril, fibrous, no pulp), color (yellow-orange, red, purple, brown, green, other), odor (absent, present), fruit skin protection (dehiscent, indehiscent with thin husk, indehiscent with thick husk), and seed protection (absent, present). The stage of ripeness of the consumed fruits was scored, which was also based on changes in size, color, and consistency. Continuous variables include the number of seeds per fruit, and fruit and seed weight and length. Fresh fruits and seeds were weighed using spring scales or electronic balances, and measured using scales and calipers with 0.01 g and 0.01 mm precision, respectively. All characterizations are based on the original classifications by Gautier-Hion *et al*. (1985) and Lambert and Garber (1998).

Water content was calculated by comparing fresh and dry weight of the fruit pulp after three days of drying in an oven. Dry samples of ripe fruits were analyzed in the lab for crude protein (total nitrogen x 6.25; though the conversion factor might have to be adjusted for different parts of plants; see Ortmann *et al*. 2006 for a review), extractable protein, lipids, sugar, neutral (NDF) and acid (ADF) detergent fiber, and tannins (Bollen *et al*. 2004a, 2004b).

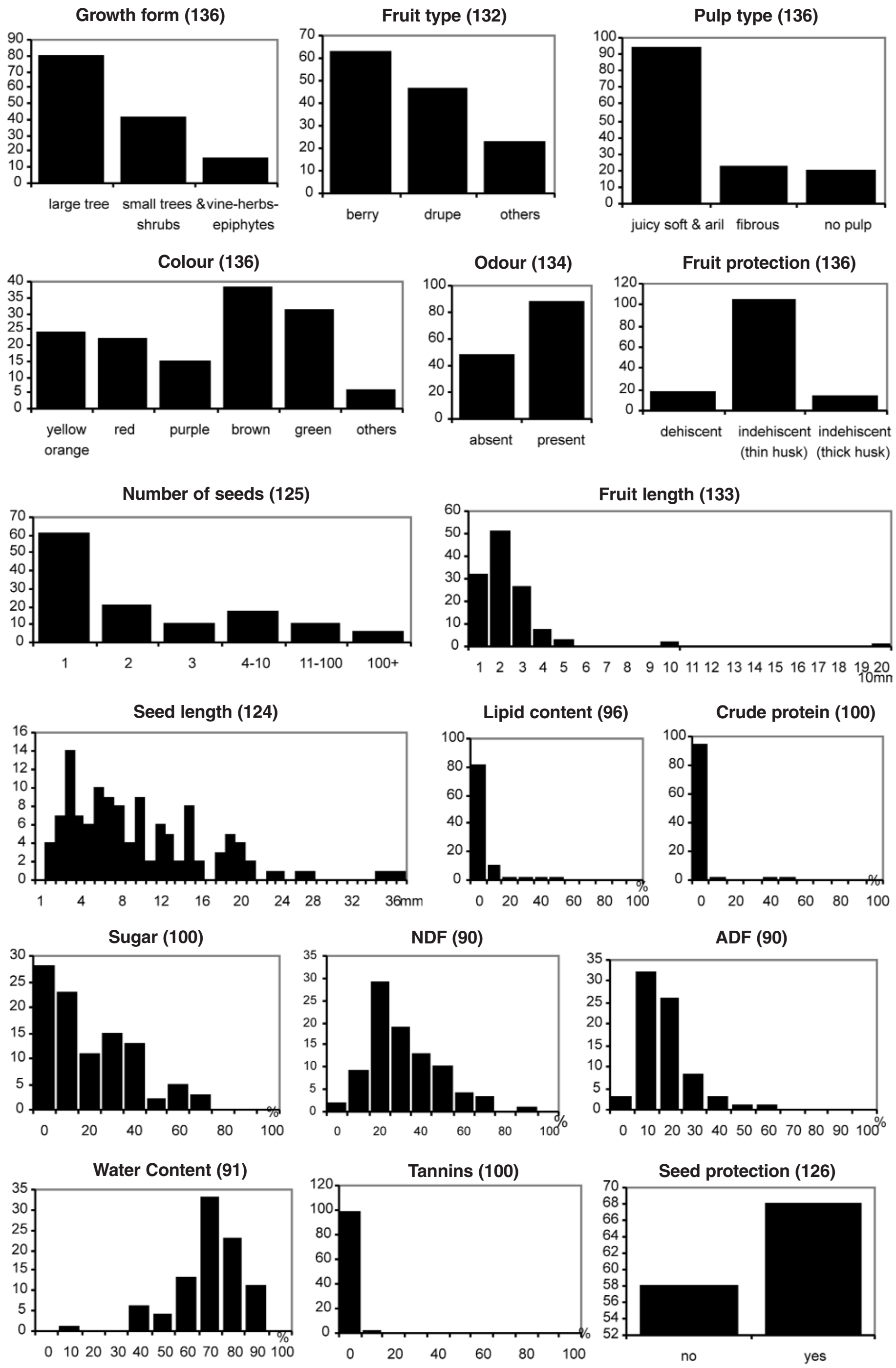

Figure 1. Frequency distribution of the fruit characteristics of the littoral forest of Sainte Luce. The number of species used for the different analyses are listed in parentheses. The y-axis indicates the number of species.

Frugivore diet

Diets of frugivore animal species were assessed by direct feeding observations through tree watches and casual encounters, as well as by more indirect methods such as analyses of fruit trap contents and macroscopical fecal analyses (Bollen *et al*. 2004a, 2004b). At Sainte Luce, the trophic guild of frugivores consists of 13 strictly or partially frugivorous birds, rodents (one of which is introduced), fruit bats, and lemurs (Table 1).

Role of the different frugivores in the ecosystem

Fruit-eating vertebrates can be classified into the following categories: seed dispersers or fruit consumers (D), neutral seed droppers or pulp consumers (N), and seed predators (P) (cf. Gauthier-Hion *et al*. 1985, Debussche and Isenmann 1992; Table 1). The first group disperses intact seeds by endozoochory (droppings) or synzoochory (regurgitation), while the second group eats fruit pulp but drops the seeds under the parent plant. The last group eats and destroys the seeds. Based on observations and the results from fruit trap and fecal analyses, it was possible to assign each fruit-frugivore interaction to one of these categories (Bollen *et al*. 2004a).

Results

Fruit traits

The complete data set of all fruit species (n=136) consists mainly of large, canopy tree species (59%). The most common plant families are Rubiaceae (10%), Euphorbiaceae (5%), and Flacourtiaceae, Myrtaceae, Annonaceae, and Areceae (4% each). Morphologically, berries and drupes are the most common fruit types (83%) with a soft and juicy pulp (62%). Dull colored fruits (green, brown, yellow-orange) (68%) with an odor (65%) make up the majority of the fruits. Other dominant features are indehiscence and a thin husk (77%). Seeds can be either protected (54%) or not (46%). The median number of seeds per fruit is 2 (quartiles 1-4), median fruit weight is 1.2 g (0.49-5.23 g), fruit length is 15.4 mm (0.49-5.23 mm), and seed length is 8.4 mm (4.85–14.42 mm; Fig. 1). Water is the dominant constituent of fresh pulp (median 76.0%). On a dry mass basis, both acid (22.6%) and neutral (32.0%) detergent fiber contents are high. The median sugar content is 19.2%. Median lipid content of fruits is 3.1%, crude protein is 5.6%, and extractable protein 2.8%. Tannin values are very low in our dataset with a median of 0.2% (Fig. 1).

Fruit diet and food selection

Lemurs feed on most fruit species. Their diet included 119 plant species. Birds, rodents, and the fruit bat *Pteropus rufus* consume 55, 50, and 39 plant species, respectively. Different methods of collecting dietary data influence the outcome of diet lists (Fig. 2). In general, direct observations result in the largest number of feeding records. Due to hunting pressure, observations of *P. rufus* at night using a headlight are difficult (Bollen and Van Elsacker 2002). This bias could be limited by systematically collecting fecal droppings under the roost sites. Both rodent species are rarely observed as they detect the observer by smell, but gnaw marks on feeding remains are easily recognizable (Bollen *et al*. 2004b).

Taxonomically, Rubiaceae is the dominant plant family in most diets. Euphorbiaceae, Areceae, and Annonaceae are important as well, but to a lesser extent. There were no clear taxonomic preferences within the diet of all frugivores. The dominant plant families seem to be equally represented in the individual diets and the overall sample. Because of the interaction of different variables, logistic regressions were used to assess the importance of different traits for food selection of different frugivores (Bollen *et al*. 2004b). For *Eulemur collaris*, growth form and seed protection seem to be most important in determining whether a fruit is eaten. The diet of this lemur is characterized by hard kernelled fruits from large trees. For *Cheirogaleus* spp., fruit length is the only significant determinant, whereas for *Microcebus rufus*, it is seed length. Obviously, small fruits and seeds constitute the diets of both lemur species. Conspicuous colors and high fat contents influence whether frugivore birds eat a certain fruit. *Coracopsis nigra* prefers small, odorless fruits. Fat content and seed length seem to determine the presence of fruits in the diet of *P. rufus*. In particular, fruits with low lipid content and small seed length are most abundant. Finally, the diet of rodents is characterized by a significant interaction between seed length and protection indicating that large seeds, which often have a hard kernel, dominate their diet. These results show that mainly size characteristics such as fruit and seed length determine feeding preferences of most frugivores, whereas biochemical traits are less important (Bollen *et al*. 2004a, 2004b). Similar results were found when conducting multiple univariate tests, but for *Cheirogaleus* spp. there was a clear selection for fruits with high sugar content.

Seed dispersal and seed predation

It is difficult to assign certain frugivores to a single category, as a species may have different impacts on seeds within and between plant species. However, we can conclude that the 'true' frugivorous bird species (*Alectroenas madagascariensis*, *Treron australis*, and *Hypsipetes madagascariensis*) disperse seeds of most of the species they feed on. Ripe fruits are almost always swallowed and thus dispersed (Table 1). *Streptopelia picturata* is considered a seed predator feeding on seeds on the ground, but due to its shy nature, feeding behavior could not be observed in detail and the fate of consumed seeds remains unclear. *Coracopsis nigra* occasionally drops fruits under the parent plant or carries away intact fruits, but for the majority of their food resources they act as seed predators, either destroying seeds directly with their beak or feeding on unripe fruits (Bollen and van Elsacker 2004). In contrast, *Eulemur collaris* is an important seed disperser for a large number of plant species (Table 1, Fig. 1). When feeding, this species is messy, swallowing numerous seeds and dropping others under the parent plant; this occurs for a third of their consumed plant species (Table 1). Furthermore, it eats the fruit of some plant species unripe, thus destroying the seeds. *Cheirogaleus* spp., *M. rufus*, and *P. rufus* act as seed dispersers for small seeds and as seed droppers for larger ones. *Pteropus rufus* may participate in both short and long distance dispersal (Bollen and van Elsacker 2002). Rodents often tear off and do not consume the fibrous flesh which surrounds nuts. Both rodent species clearly prey on seeds of numerous plant species, but intact and even germinated seeds of four species were found at feeding sites. No secondary seed dispersal through caching could be detected (Table 1).

Table 1. Overview of mainly frugivorous vertebrate species at Sainte Luce with indication of their diet (F: frugivorous, G: granivorous, O: omnivorous), body mass, and length. Abbreviations for the species used in text and appendix are given in parentheses. The number of plant species for which the frugivores act as dispersers (D), droppers (N = Neutral), or predators (P) is indicated. The category '?' refers to plant species for which the seed fate is unknown. The same frugivorous species may play more than one role for the same plant species.

Family	Species	English name	Diet	Body mass (g)[a]	Body length (cm)[ab]	Effect on seeds D	N	P	?
Aves									
Columbidae	*Treron australis* L. (*Ta*)	Malagasy green pigeon	F	236	32	9	0	0	0
Columbidae	*Alectroenas madagascariensis* L. (*Am*)	Malagasy blue pigeon	F	173	28	18	1	0	0
Columbidae	*Streptopelia picturata* Temminck (*Sp*)	Madagascar turtle dove	G	190	28	0	0	0	13
Psittacidae	*Coracopsis nigra* L. (*Cn*)	Lesser vasa parrot	G	246	35	4	8	36	0
	Coracopsis vasa (Cv)	Greater vasa parrot	G	525	50				
Pycnonotidae	*Hypsipetes madagascariensis* Muller (*Hm*)	Madagascar bulbul	F	45	24	21	2	0	0
Mammalia									
Rodentia	(rod)					4	2	49	0
Muridae	*Rattus rattus* L. (Rr)	Black rat	O	100	15-23				
Nesomyinae	*Eliurus webbi* Ellerman (Ew)	Webb's tuft-tailed rat	G	88	10-16				
Chiroptera									
Pteropodidae	*Pteropus rufus* Tiedemann (*Pr*)	Madagascar flying fox	F	500-750	23-27	37	12	0	1
Primates									
Lemuridae	*Eulemur collaris* E. Geoffrey (*Ec*)	Collared brown lemur	F	2000-2300	40-47	100	36	27	0
Cheirogaleidae	*Microcebus rufus* E. Geoffrey (*Mr*)	Brown mouse lemur	O	42	12.5	27	20	0	4
	Cheirogaleus spp. (*Ch*)					28	24	0	0
	Cheirogaleus major E. Geoffrey (*Cmaj*)	Greater dwarf lemur	O	443	25				
	Cheirogaleus medius E. Geoffrey (*Cmed*)	Fat-tailed dwarf lemur	O	119-282	20				

[a] Data from Fietz and Ganzhorn (1999), Ganzhorn *et al.* (1999), Goodman *et al.* (2003), Langrand (1990), Ravokatra *et al.* (2003), G. Donati (pers. comm., 2002).
[b] Body length is total length for birds and bats but head/body length for lemurs and rodents.

Conservation

As frugivores face periods of fruit scarcity, it is important to collect long-term data on phenology to understand inter-annual patterns and predict periods of fruit abundance and scarcity. It is also good to identify keystone plant species that bear fruit during periods of fruit scarcity and supply much of the diets of the frugivores in this forest (Terborgh 1986). Given the short duration of our studies, we are unable to identify true 'keystone species' (definition according Terborgh 1986, Mills *et al*. 1993), however *Syzigium* sp. 2 (Myrtaceae), and to a lesser extent *Dypsis prestoniana* (Arecaceae), may be potential candidates. Both species fruit when fruit availability is low. *Syzigium* sp. 2 is a large canopy tree species that is very common in the littoral forest (Razafimizanilala 1996) with numerous odoriferous purple berries. This species constituted 80% of the diet of *Eulemur collaris* in June 2000 (Donati 2002). *Dypsis prestoniana* is much less abundant than it used to be due to human exploitation, but can still be found in the intact parts of S9. This tall palm species has a relatively large fruit crop considering its small canopy, and comprises 20% of the diet of *E. collaris* during the month of April (Donati 2002). The overall importance of these potential keystone species increases if we consider that they are eaten by all frugivorous species present in Sainte Luce. *Vaccinium emirnense* (Ericaceae), *Sarcolaena multiflora* (Sarcolaenaceae), *Uapaca littoralis* (Euphorbiaceae), and *Apodytes dimidiata* (Icacinaceae) are also eaten by 9 of the 13 frugivore species and thus, may be important as well (Appendix I). Plant species with large seeds are most vulnerable as they have to rely on a very limited number of species in the already depauperate frugivore community of Madagascar (Ganzhorn *et al*. 1999). Therefore, special care has to be given to the regeneration of *Canarium boivinii* (Burseraceae), *Dypsis fibrosa*, *Crataeva obovata* (Capparaceae), *Salacia madagascariensis* (Hippocrateaceae), and *Brochoneura madagascariensis* (Myristicaceae, Appendix I).

Discussion

Fruit diet and food selection

The main food preferences of all consumers are related to the morphological traits of the fruit., In studies on fruit-frugivore interactions throughout the world, size, color, and fruit protection seem to be the most important factors in fruit selection (see

Table 2. An indication of niche differentiation among the different frugivorous species found in the Sainte Luce forest. FBS: Frugivorous bird species; for species abbreviations see Table 1.

		Birds			Mammals				
		FBS	Sp	Cn / Cv	Ec	Ch	Mr	Pr	rod
Seed size	Small	+	+		+	+	+	+	
	Medium	+		+	+	+	+	+	
	Large				+				+
	Max seed diameter (mm)	6.1-10.6	3.8	6.8	16.7	10.5	11.6	10.0	12.1
Ripeness	Ripe	+	?	+	+	+	+	+	+
	Unripe			+	(+)				
Activity	Diurnal	+	+	+	+				
	Nocturnal				+	+	+	+	+
	Year round	+	+	?	+			+	+
	Seasonal			?		Sep-Apr	Sep-Apr		
Forest type	Primary	+	+	+	+	+	+	+	+
	Secondary	+	+	+		+	+	+	+
Feeding height	Ground		+						+
	Canopy	+		+	+	+	+	+	+
Role	Seed dispersal	+		(+)	+	+	+	+	(+)
	Seed dropping				(+)	+	+	+	
	Seed predation		+?	+					+
Dispersal distance	Within fragment				+	+	+		
	Beyond fragment	+						+	

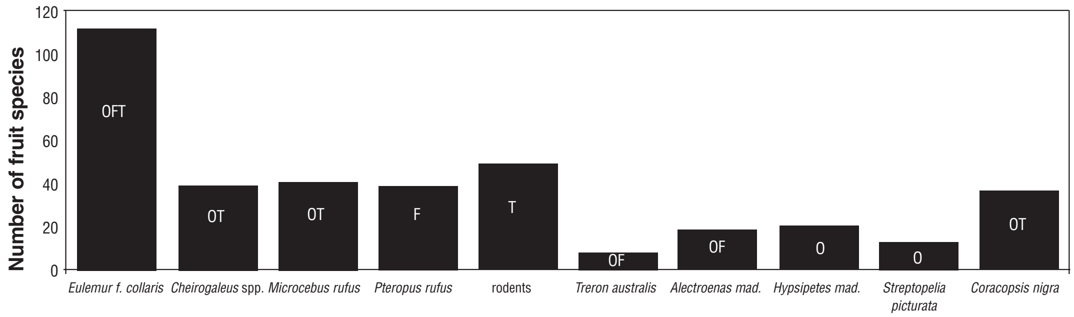

Figure 2. Diversity of the fruit diet of the different frugivore species, with indication of the method by which most feeding records were obtained (O: observations, F: fecal droppings, T: feeding traces).

contributions in Dew and Boubli 2005). Among these, fruit and/or seed size is found to be most significant and correlated to the body size of the consumer. In our study, as in most studies, birds seem to select significantly smaller fruits than mammals (Janson 1983, Knight and Siegfried 1983, Gautier-Hion *et al*. 1985, Herrera 1987, Jordano 1995, Bollen *et al*. 2004a, 2004b). In this respect, *Eulemur collaris* is very important in the local community as it is the only seed disperser for the plant species with large seeds, both in Saint Luce and in other forests (Birkinshaw 1999, 2001, Ganzhorn *et al*. 1999). As for biochemical traits, which are rarely considered, the most common finding is that mammals in general avoid lipid-rich fruits whereas birds may favor them (McKey 1975, Debussche and Isenmann 1989, Jordano 1995). This differential preference for lipids matches our findings on fruit selection by frugivorous birds and mammals (*E. collaris*, *Pteropus rufus*). The only other trend found was that *Cheirogaleus* favor sugar-rich fruit pulp. For *C. medius*, this preference during pre-hibernation fattening was already described by Bonnaire and Simmen (1994) and Fietz and Ganzhorn (1999).

In general, few traits consistently determine food selection of the 13 consumer species in the littoral forest. Most frugivores in Sainte Luce seem to be flexible and eat what is available. This leads to diffuse mutual relationships between plant and consumer species, which is similar to findings at most other study sites (Terborgh 1983, Gautier-Hion *et al*. 1985, Dowsett-Lemaire 1988, Debussche and Isenmann 1989). Thus, this current study did not provide evidence for co-evolution. Instead, we found that there is substantial dietary overlap between frugivore species, and that dispersal is achieved through redundant systems. Most frugivores seem to eat according to what is available, given the limitation of fruit and seed size and certain feeding preferences.

The lack of close co-evolutionary relationships is further confirmed when trying to fit tree dispersal strategies to three existing hypotheses (Bollen *et al*. 2004a). In Sainte Luce, there is no evidence for species specific co-evolution, or for the low-high investment model (McKey 1975). However, for dispersal syndromes, (Van der Pijl 1969) diaspores dispersed by birds, mammals, or both groups differ in fruit and seed size, fruit shape, and seed number, but not in biochemical traits. No evidence for co-evolution was found in an intersite comparison of fruit traits and feeding selection between a Malagasy dry deciduous forest and the humid littoral forest. Both sites have an almost identical set of frugivores, but differ substantially in abiotic conditions. Fruit characteristics differ substantially between these two sites. This suggests that abiotic factors (i.e. water availability), rather than strong specific interactions and co-evolution with frugivores, are driving the evolution of fruit traits (Bollen *et al*. 2005). Obviously, the same frugivore species can switch its diet to what is available at a certain site. This allows them to survive in different forest types on frugivorous diets with different nutrient compositions and different morphological traits.

Dispersal role

Fruit pigeons only feed on ripe fruits and always swallow the entire fruit, digesting the fleshy parts and excreting the seeds. As such, they seem to be efficient seed dispersers of numerous plant species. Further, they cover considerable distances (Dowsett-Lemaire 1988, Fleming 1992) and use secondary and disturbed habitats when dispersing seeds from pioneer and heliophilic species. *Hypsipetes madagascariensis* is an important seed disperser as well, feeding at lower heights than fruit pigeons and parrots. This species swallows ripe fruits entirely and excretes the seeds unharmed (Bollen 2003). Bulbuls are very tolerant of disturbance and can be encountered in intact forest as well as on forest edges. In contrast, *Coracopsis nigra* destroys seeds of many endemic plant species and can be considered a pre-dispersal seed predator in this ecosystem (Bollen and Van Elsacker 2004). Occasional seed dispersal may occur, but for few species and on rare occasions, which may be important from an evolutionary perspective (Böhning-Gaese *et al*. 1999). *Streptopelia picturata* was most often observed feeding on the ground and is suspected to be a post-dispersal seed predator destroying most seeds as reported by Goodman *et al*. (1997b).

Eulemur collaris is possibly the most important seed disperser in this ecosystem. Its relatively large home range (up to 100 ha) and extensive day range lengths (1500-3500 m, Donati 2002) indicate that long distance seed dispersal within a fragment is likely. They eat large amounts of fruit throughout the year (Donati *et al*. 2007) and are the only local native vertebrates that are able to swallow larger seeds (Table 2). The smaller nocturnal lemurs eat less, have a less diverse fruit diet, occupy limited ranges (1-4 ha; Fietz 1999, Atsalis 2000, Lahann *et al*. 2006), and have a rather limited gape size. Furthermore, in Sainte Luce, as in other Malagasy forests (Fietz and Ganzhorn 1999, Schmid 2000, Dausmann *et al*. 2005), *Cheirogaleus* spp. and *M. rufus* go into prolonged torpor or hibernation from May through October, which restricts their feeding and thus their dispersal activity to the austral summer. These species are often found at forest edges and in secondary forests throughout Madagascar (Petter *et al*. 1977), including Sainte Luce. This makes them important seed dispersers for small-seeded plant species that fruit during the austral summer. *Pteropus rufus* feeds on a wide array of endemic plant species in Sainte Luce and is the most important long distance seed disperser in the littoral forest. A colony of about 300 *P. rufus* eats large quantities of fruit each night, defecates during flight, and covers long distances between sleeping and feeding roosts (up to 50 km; Bollen and Van Elsacker 2002). By bridging isolated forest fragments, *P. rufus* helps to ensure genetic exchange between plant populations in forest fragments and even regeneration in clearings. For the rodents, evidence of post-dispersal predation of 50 plant species was found. Only a few seeds escape total destruction when germinating from the rodents' food piles.

As mentioned above, the dispersal quality within this community of frugivores differs substantially. While birds may defecate from nearby or far away perches either within primary forest or in the clearings, fruit bats defecate during flight or under feeding or sleeping roosts, rodents concentrate seeds at burrows or feeding sites, and lemurs move seeds within a given forest fragment. The combined activities of a variety of fruit-eating vertebrates produce very heterogeneous means to transport seeds, which are important to ensure regeneration in the severely fragmented and degraded littoral forest (Table 2). In terms of conservation, *E. collaris* is of crucial importance for the dispersal and regeneration of large-seeded plant species, *P. rufus* for long distance dispersal across fragment boundaries, and frugivore bird species for enhancing succession and regeneration of plants in the clearings and degraded areas.

Conservation

Plant-frugivore interactions are important components of complex forest communities. Vertebrate seed dispersal is key in the processes of natural vegetation and vegetation recovery (Wallace and Painter 2002). Losses of ecologically interdependent species will be permanent to an increasing extent as forest fragments become more isolated, particularly for arboreal lemur species. Consequently, gene flow and seed dispersal between patches become more critical for long term survival of many plant species. However, deforestation, forest degradation, and fragmentation have a drastic impact on the food chain of the frugivorous fauna, which will affect the long-term survival of animal species. Madagascar already has a depauperate, avian frugivore community (Langrand 1990), lacks larger frugivores such as ruminants, ungulates, and elephants, and a significant percentage of lemur species have been extinct for centuries (Godfrey *et al*. 1997). This emphasizes even more the importance of the remaining seed dispersers. Local extinction of these frugivorous species could ultimately lead to the lack of regeneration of a number of plant species.

Since degradation and fragmentation are quite advanced in the littoral forest, active protection of the remaining intact forest and control of hunting, logging, and fires are not enough to conserve and restore this ecosystem. Natural regeneration via secondary forests is too slow to counteract the loss of relatively intact forests and, therefore, it is necessary to accelerate the natural recovery process. The creation of corridors that connect isolated primary forest remnants with thin strips of habitat is considered important for conservation activities. Corridors are valuable conservation tools, promoting increased plant and animal movement between forest fragments, which enhances population viability and the likelihood of recolonization, as well as facilitation of pollination and seed dispersal (Beier and Noss 1998, Tewksbury *et al.* 2002). Planting specific fruiting trees in corridors, plantations or clearings will improve the process of reforestation by attracting frugivores and the seed dispersal they provide. Thus, fruit trees can be used to accelerate regeneration and enrich certain aspects of biodiversity. Our dietary data on frugivores should influence the choice of fruit species to be used in these planting projects. Perches or trees in clearings may further attract birds and fruit bats, which bring seeds into these open areas (Holl *et al*. 2000), thus facilitating regeneration, reforestation and vegetation succession of the tropical forest. Since large-seeded plant species (for example *Canarium boivinii*, *Diospyros* sp., *Apodytes* sp. nov.; Appendix 1) are less easily dispersed than small seeds and because they have fewer dispersers, they require planting in subsequent efforts (Terborgh 1983, Janzen 1988, Wunderle 1997).

Conclusion

This study provides an extensive dataset involving numerous plant species, and their phenological, morphological, and biochemical traits, in the Sainte Luce Forest. The precise composition of the fruit diets of all frugivore species is known, as well as the main traits determining that food selection. These data reveal that the diet choices of frugivores show a remarkable flexibility towards variations in fruit supply. Based on these results, it can be concluded that in the littoral forest of Sainte Luce, fleshy-fruited plants engage in diffuse mutualisms with their dispersal agents. These interactions are quite generalized, very ancient, and extraordinarily frequent in certain communities (Willson and Traveset 2000). High unpredictability and asymmetry of interactions, coupled with the important influence of abiotic factors, signal that mutual selection pressures between plants and seed dispersers are greatly constrained (Levey and Benkman 1999). In Sainte Luce, fruit-eating animals tend to consume many fruit species and thus the fruits of many plants are consumed by a wide range of animals, possibly to minimize the effect of the loss of a dispersal agent. Abiotic factors seem to be more responsible than biotic ones in shaping fruit characteristics. If frugivore preference had influenced the evolution of fruit traits at all, it would most likely have been based on general characteristics, such as fruit size. Nevertheless, insight into fruit-frugivore interactions is a valuable tool to integrate into conservation action plans that focus both on the regeneration of vulnerable plant species as well as on important fruiting species, which influence the long term survival of frugivores.

Future research should concentrate more on the animal side of these interactions, which is essential to understand how niche separation among frugivores is organized. Data on the post-dispersal phase are needed as well to complete the dispersal cycle and to comprehend how the assembly and recruitment of plant communities are organized in space and time. Since the clear patterns of one year may disappear in the next, long-term data on phenology are needed. Even though there is still a lot to explore and investigate, now is the time to act in order to preserve the littoral forest, and to prevent the permanent disappearance of this precious ecosystem (Bollen and Donati 2006).

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Appendix 1. All plant species that are included in the diet lists of the consumer species with indication of the method how these data were gathered (O: observation, T: feeding marks; F: fecal droppings). Abbrevations of the species are Ec for *Eulemur collaris*, Ch for *Cheirogaleus* spp., Cmed for *C. medius*, Cmaj for *C. major*, Mr for *Microcebus rufus*, Am for *Alectroenas madagascariensis*, Ta for *Treron australis*, Sp for *Streptopelia picturata*, Cn for *Coracopsis nigra*, Hm for *Hypsipetes madagascariensis*, Pr for *Pteropus rufus*, rod for both rodent species, Rr for *Rattus rattus* and Ew for *Eliurus webbi*. Nomenclature was based on the Flora Madagascar, the database of the Missouri Botanical Garden (http://mobot.mobot.org/W3T/Search/vast.html). The main morphological and biochemical traits are also indicated. Growth form (GF): 1 = large trees, 2 = small trees or shrubs, 3 = vine, herbs, epiphytes; Fruit type (FT): 1 = berry, 2 = drupe, 3 = others; Pulp type (PT): 1 = soft & juicy or arillate, 2 = fibrous, 3 = no pulp; Color (Col): 1 = green, 2 = yellow-orange, 3 = red, 4 = brown, 5 = purple, 6 = other; Odor (Od): 1 = absent, 2 = present; Fruit skin protection (FSP): 1 = dehiscent, 2 = indehiscent with thin husk, 3 = indehiscent with thick husk; Seed protection (SP): 1 = absent, 2 = present; Number of seeds per fruit (NS); Fruit weight (FW) in g; Fruit length (FL) in mm; Seed length (SL) in mm; Water content; percentages of dry weight of crude protein (CP), extractable protein (EP), fat, soluble sugar, neutral detergent fiber (NDF), acid detergent fiber (ADF) and tannins (Tann) content are given.

	Lemurs					Birds					Flying Fox	Rodents		
Plant species	**Ec**	**Ch**	**Cmed**	**Cmaj**	**Mr**	**Am**	**Ta**	**Sp**	**Cn**	**Hm**	**Pr**	**rod**	**Rr**	**Ew**
Anacardiaceae *Campnosperma micranteum*	OF													
Anacardiaceae *Poupartia chapelieri*	OF	OT	OT	OT	OT				O			T		
Anacardiaceae *Protorhus cf. lecomtei*	F													
Annonaceae *Monanthotaxis* cf. *malacophylla*	OF	OT	OT			O						T		
Annonaceae *Polyalthia capuronii*	OT											T		
Annonaceae *Polyalthia madagascariensis*	OF	OT	OT		OT	OF			O	OF	F	T		
Annonaceae *Polyalthia* sp. 1	O													
Annonaceae *Polyalthia* sp. 2	OF													
Apocynaceae *Cabucala madagascariensis*					OT				O					
Araliaceae *Polyscias* sp.	OF					OF	O	O	O	O	F			
Araliaceae *Schefflera rainaliana*	O					O			O	O				
Areceae *Dypsis fibrosa*	OF											T	T	T
Areceae *Dypsis nodifera*	OF	OT	OT		OT						TF			
Areceae *Dypsis prestoniana*	OF	OT	OT	OT		OF		O	O	O	O			
Areceae *Dypsis saintelucei*	OF													
Areceae *Dypsis scottiana*	OF	OT	OT			F	F					T		
Bignoniaceae *Ophiocolea delphinensis*	F										T			
Bignoniaceae *Phyllarthron ilicifolium*	OF													
Bignoniaceae *Phyllarthron* sp.	F													
Burseraceae *Canarium boivinii*	O											T		T
Canellaceae *Cinnamosma madagascariensis* var. *namoronensis*	OTF										F			
Capparaceae *Crataeva obovata*	OTF											T		
Celastraceae *Mystroxylon aethiopicum*	OT											O		
Celastraceae *Polycardia phyllanthoides*	F													
Clusiaceae *Garcinia chapelieri*	OT													
Clusiaceae *Garcinia* cf/aff *madagascariensis*	OT											T		
Clusiaceae *Psorospermum revolutum*		T			OT					O				
Combretaceae *Terminalia fatraea*	OF	OT			OT	OF			O		OTF	T		
Connaraceae *Agelaea pentagyna*									O					
Dichapetalaceae *Dichapetalum* sp.	OF											T		
Ebenaceae *Diospyros* sp. 1	OT													
Ebenaceae *Diospyros* sp. 2	OTF													
Elaeocarpaceae *Elaeocarpus alnifolius**	O											T		
Elaeocarpaceae *Elaeocarpus alnifolius**	OF											OT	T	T
Ericaceae *Vaccinium emirnense*	OT	OTF	OTF		OTF		OF		O	O	F			
Erythroxylaceae *Erythroxylum buxifolium*	F								OF	O				
Erythroxylaceae *Erythroxylum nitidulum*	OF					OF			OF			T		
Euphorbiaceae *Anthostema madagascariensis*	OF													

GF	FT	PT	Col	Od	FSP	SP	NS	FW	FL	SL	W	CP	EP	Fat	Sugar	NDF	ADF	Tann
1	2	1	3	2	2	2	1	0.4	8.9	6.8	93	9.1	4.6	-	2.5	-	-	0.0
1	2	1	1	2	2	2	1	0.5	15.4	15.2	76	5.7	2.5	0.7	12.6	18.5	15.0	0.0
1	2	1	1	2	2	1	1	1.2	2.0	1.3	-	9.6	2.4	24.4	10.2	27.1	12.5	0.1
3	-	1	2	2	2	2	3	9.2	29.3	14.8	42	46.9	3.7	16.2	27.8	32.0	20.4	0.0
3	1	2	3	2	2	2	1	11.8	30.7	20.3	43	5.0	0.9	2.4	21.0	57.0	41.0	0.4
1	1	1	2	1	2	2	1	0.3	12.2	7.8	72	5.4	3.2	1.2	49.4	27.6	22.5	0.5
1	1	1	2	2	2	2	1	1.4	20.1	13.2	95	5.9	0.8	-	10.8	-	-	0.0
1	1	1	4	2	2	-	1	2.9	20.8	13.8	77	5.4	1.6	3.3	35.9	28.0	19.6	0.0
2	2	1	2	2	2	2	3	0.1	38.0	9.2	75	6.1	1.6	4.8	61.9	13.7	9.0	0.0
1	2	2	1	1	2	2	1	0.0	5.0	3.6	-	4.2	2.7	2.1	17.8	55.7	46.4	0.0
1	2	1	5	2	2	1	2	0.1	4.7	2.8	-	6.9	2.7	5.7	61.8	18.6	11.9	0.5
2	1	2	4	1	2	2	1	9.1	24.4	21.2	45	5.4	3.5	1.8	6.5	60.6	35.5	0.2
2	1	1	2	1	2	2	1	0.3	9.7	8.3	72	2.4	4.2	1.6	40.0	26.9	12.7	0.0
1	1	1	2	2	2	2	1	0.6	14.9	12.9	80	7.2	5.8	3.0	15.4	33.6	16.6	0.2
1	1	1	2	2	2	2	1	1.4	16.4	13.7	52	-	-	-	-	-	-	-
2	1	1	3	2	2	1	1	0.3	10.8	9.4	84	4.3	1.8	2.7	41.3	25.5	12.7	0.0
2	1	1	5	2	2	1	150	-	192.9	7.2	74	7.9	1.6	2.4	45.2	25.3	17.4	0.1
1	1	1	4	2	2	1	-	3.6	53.0	-	90	7.4	1.4	-	13.5	-	-	0.2
1	1	1	4	2	2	2	50	-	101.8	7.6	79	2.9	0.8	11.2	75.4	27.4	18.6	0.0
1	2	2	4	2	2	2	1	9.7	31.1	27.0	44	9.2	2.0	13.0	2.2	47.5	38.6	0.0
1	1	1	4	2	2	1	10	6.2	22.0	8.4	79	5.3	3.8	5.0	26.0	17.7	12.4	1.7
2	1	2	5	2	2	1	6	32.4	49.4	20.0	79	8.8	2.0	1.4	10.8	57.8	38.2	0.2
2	2	2	3	1	2	2	1	1.2	12.4	10.1	79	-	-	-	-	-	-	-
1	3	3	1	1	3	1	14	-	-	-	-	-	-	-	-	-	-	-
1	1	1	4	2	2	1	6	31.8	37.1	20.4	-	-	-	-	-	-	-	-
2	1	1	2	2	2	1	4	11.1	30.4	18.2	43	5.1	2.5	11.1	43.3	20.0	16.7	0.0
2	1	1	4	2	2	1	5	0.2	8.1	3.0	-	8.4	4.9	15.4	39.1	21.1	13.7	1.0
1	2	2	5	1	2	2	1	0.4	13.2	8.1	-	7.8	3.1	3.1	16.4	46.1	35.7	0.4
3	7	3	3	2	1	1	1	1.1	16.9	12.6	61	6.0	3.6	0.7	11.4	33.5	22.6	3.9
3	2	1	1	2	2	2	1	5.8	35.6	24.9	-	-	-	-	-	-	-	-
2	1	2	6	1	2	2	6	2.9	22.0	13.6	-	-	-	-	-	-	-	-
2	1	1	1	2	3	1	5	16.5	30.7	19.7	65	3.1	7.8	0.6	6.5	51.8	27.7	0.6
1	2	1	1	2	2	2	1	0.7	14.5	13.0	73	-	-	-	-	-	-	-
1	2	2	1	2	2	2	1	1.3	16.4	14.3	90	4.1	4.3	3.4	5.9	35.0	24.8	0.0
2	1	1	3	1	2	2	105	0.8	11.5	1.4	74	1.8	1.2	1.4	50.4	36.5	26.8	0.1
2	2	1	3	1	2	2	1	0.1	7.3	6.9	83	2.6	2.9	3.9	79.2	9.9	7.7	0.9
1	2	1	3	2	2	1	1	0.3	11.0	8.2	-	6.8	3.0	18.6	31.8	21.1	11.5	5.4
1	7	3	4	2	3	1	3	7.3	19.7	12.1	67	8.3	5.4	4.0	5.6	53.8	36.7	0.4

Appendix 1. Comtinued

	Lemurs					Birds					Flying Fox	Rodents		
Plant species	**Ec**	**Ch**	**Cmed**	**Cmaj**	**Mr**	**Am**	**Ta**	**Sp**	**Cn**	**Hm**	**Pr**	**rod**	**Rr**	**Ew**
Euphorbiaceae *Euphorbia tetraptera*												T		
Euphorbiaceae *Macaranga perrieri*	F								O	O				
Euphorbiaceae *Suregada baronii*								O	O					
Euphorbiaceae *Uapaca ferruginea*	OF	OTF	OT	OT	OT						OF	T		
Euphorbiaceae *Uapaca littoralis*	OF	OTF	OT	OT	OT				OT		OTF	T	T	T
Euphorbiaceae *Uapaca thouarsii*	TF	OTF		OT	OTF						F	T		T
Fabaceae *Cynometra* cf. *cloiselii*	O											T		
Fabaceae *Phylloxylon xylophylloides*												T		
Flacourtiaceae *Aphloia theiformis*					O			O		O				
Flacourtiaceae *Bembicia uniflora*	OF	O	O						O					
Flacourtiaceae *Homalium louvelianum*									O					
Flacourtiaceae *Ludia antanosarum** (*hazofotsy*)	OT				OT						F			
Flacourtiaceae *Ludia antanosarum** (*zorafotsy*)	OT	OT			OT				OT		F			
Flacourtiaceae *Scolopia orientalis*	OT	OT	OT		OT			O			OF	T		T
Grossulariaceae *Brexia* sp.	OF	OF	OF		F						F	T		
Hammamelidaceae *Dicoryphe stipulacea fa transiens*												T		
Hippocrateaceae *Salacia madagascariensis*	OT											T		
Icacinaceae *Apodytes dimidiata*	OF	O	O	O	O	OF	O		T	O		T		
Icacinaceae *Apodytes* sp. nov.	T											T		
Lauraceae *Beilschmiedia madagascariensis** (*tavolohazo*)	F				T							T	T	T
Lauraceae *Beilschmiedia madagascariensis** (*resonzo*)					T						T	T		
Lauraceae *Cryptocarya* sp.	O				T	OF								
Lauraceae *Ocotea* sp.	O					OF					F			
Lecythidaceae *Barringtonia butonica*										O				
Liliaceae *Dracaena reflexa* var. *nervosa** (*falinandro*)	O				T						F			
Liliaceae *Dracaena reflexa* var. *nervosa** (*tavolobotroka*)	O										F			
Loganiaceae *Anthocleista longifolia*	OTF	OT			F						F	T		
Loganiaceae *Anthocleista madagascariensis*											F			
Loranthaceae *Bakerella ambongoensis*		OF							O		F			
Loranthaceae *Bakerella* sp.		OF			OF	F			O	O	F			
Melastomataceae *Tristemma mauritianum*												T		
Meliaceae *Malleastrum mandenense*	O													
Menispermaceae *Burasaia madagascariensis*	F	OT		OT								T	T	T
Monimiaceae *Tambourissa castri-delphinii*	OF									O				
Monimiaceae *Tambourissa purpurea** (*ambora*)	OF				O	OF				O	F	T		T
Monimiaceae *Tambourissa purpurea** (*amboralahy*)	O										F	T		
Moraceae *Ficus baroni*	O										F			
Moraceae *Ficus guatteriifolia*	F										F	T		
Moraceae *Ficus pyrifolia*	O	O			O	O	O				O	F		
Moraceae *Trilepisium madagascariense*	OF	O	O											
Myricaceae *Myrica spathulata*						OF	OF			O				
Myristicaceae *Brochoneura acuminata*	O											T		
Myristicaceae *Brochoneura madagascariensis*	O											T		
Myrsinaceae *Embelia incumbens*	O													
Myrtaceae *Eugenia cloiselii*	OF	OT	OT											
Myrtaceae *Eugenia* sp.	OF													

GF	FT	PT	Col	Od	FSP	SP	NS	FW	FL	SL	W	CP	EP	Fat	Sugar	NDF	ADF	Tann
2	3	1	2	2	2	1	2	1.1	11.4	7.2	91	-	-	-	-	-	-	-
1	2	3	1	1	1	2	1	-	4.6	3.1	-	5.4	6.4	4.5	2.9	56.7	42.3	0.0
2	3	3	4	1	1	1	4	0.4	9.5	4.0	-	-	-	-	-	-	-	-
1	2	1	4	2	2	2	3	1.4	13.6	10.7	81	5.9	4.0	5.7	2.3	62.7	51.0	0.0
1	2	1	4	2	2	2	3	4.9	23.6	15.0	78	-	-	-	-	-	-	-
1	2	1	4	2	2	2	3	1.7	12.5	9.6	83	4.4	5.3	2.1	7.5	41.8	29.9	0.4
1	4	3	4	1	3	1	1	3.5	20.9	19.8	-	-	-	-	-	-	-	-
1	4	3	4	1	1	1	2	5.9	37.0	19.8	67	-	-	-	-	-	-	-
2	1	1	6	2	2	1	2	0.3	10.6	3.3	94	4.4	3.4	7.5	45.4	22.0	17.1	0.2
1	3	3	4	1	2	-	1	0.0	5.3	-	-	4.9	1.4	2.2	4.0	73.2	59.4	0.5
1	3	3	4	1	2	-	-	0.0	2.4	-	-	-	-	-	-	-	-	-
2	1	1	3	2	2	1	7	1.5	14.0	2.8	93	7.5	0.8	2.3	11.8	28.4	20.2	0.2
1	1	1	1	1	2	1	6	1.0	12.5	3.2	62	2.9	2.8	1.2	23.4	33.3	21.7	0.4
1	1	1	5	2	2	1	3	0.5	10.5	3.8	65	3.1	2.5	0.8	33.4	18.6	12.8	0.4
2	2	1	2	1	2	2	1	1.6	20.2	15.1	72	2.7	1.4	2.8	18.2	23.3	18.6	0.0
1	3	3	4	1	1	-	-	1.1	22.1	-	-	-	-	-	-	-	-	-
3	1	2	2	2	3	2	6	37.8	46.5	36.4	65	4.8	1.6	1.9	28.2	37.5	28.3	0.0
1	2	1	3	1	2	2	1	0.5	12.3	10.6	84	6.9	1.5	2.9	64.1	-	-	0.0
1	2	1	1	1	2	2	1	6.6	27.2	21.3	-	-	-	-	-	-	-	-
1	2	1	2	2	2	2	1	2.0	14.3	7.7	84	13.6	3.2	19.1	5.4	22.4	17.1	0.0
1	2	1	2	2	2	1	1	8.5	27.7	20.1	78	0.0	-	-	-	-	-	-
1	1	1	3	2	2	2	1	1.7	12.4	10.6	-	0.0	-	-	-	-	-	-
1	1	1	1	2	2	1	1	1.4	25.0	15.3	70	7.1	3.0	-	3.3	-	-	0.0
2	3	1	6	?	2	1	1	0.9	13.2	10.3	91	2.9	1.6	9.2	40.4	23.9	18.8	0.0
2	1	1	2	2	2	1	2	0.5	9.1	5.7	82	7.1	2.8	1.6	50.0	-	-	0.0
2	1	1	2	2	2	1	2	0.9	15.5	5.3	88	5.3	1.4	2.2	37.2	20.1	14.0	0.0
2	1	2	2	2	2	1	65	5.9	30.3	3.4	70	3.3	1.8	6.7	29.7	48.0	41.1	0.0
1	1	2	2	2	2	1	80	3.6	18.5	2.7	76	2.3	1.3	3.9	26.3	55.7	45.9	0.2
3	1	1	1	1	2	1	1	0.1	8.0	4.6	71	3.7	3.8	2.4	41.4	31.2	22.0	1.4
3	1	1	1	1	2	1	1	0.7	15.9	10.4	69	3.1	7.1	3.3	11.2	39.3	28.4	0.3
3	1	1	3	1	2	1	-	1.2	17.5	-	-	55.8	1.2	6.0	36.5	33.7	27.6	0.1
1	1	2	2	2	3	1	2	1.1	12.0	10.2	-	3.3	7.9	5.1	70.0	7.5	5.3	17.7
2	2	1	2	1	2	2	1	3.5	23.6	15.1	82	8.0	5.1	1.4	65.7	-	-	0.0
2	2	1	3	2	1	2	-	-	-	8.5	80	8.5	1.4	54.2	4.3	-	-	0.1
2	2	1	3	1	1	2	43	54.2	43.8	11.3	80	2.9	1.8	2.5	3.9	72.7	55.4	1.0
2	2	1	3	1	1	2	8	5.6	17.8	7.5	89	4.4	2.5	10.5	5.4	45.4	37.2	0.9
1	6	1	4	2	2	1	1000	1.2	13.0	-	-	5.0	3.6	2.4	6.6	50.8	36.1	0.9
1	6	1	4	2	2	1	1000	14.5	32.8	1.6	93	4.1	2.2	2.5	24.8	28.6	22.0	0.5
1	6	1	3	2	2	1	1000	0.1	6.3	1.0	-	7.3	5.0	5.6	2.8	51.6	40.5	0.4
1	2	2	2	2	2	2	1	2.4	21.5	13.0	-	-	-	-	-	-	-	-
2	2	3	4	2	2	2	1	0.0	3.4	3.1	-	4.0	2.5	54.6	2.4	28.8	28.6	0.1
1	1	2	4	1	1	2	1	9.5	43.4	19.6	73	0.0	-	-	-	-	-	-
1	1	2	4	1	1	2	1	7.7	44.8	23.8	-	4.3	2.9	5.2	7.5	42.4	32.8	0.5
3	1	1	5	2	2	-	1	-	4.2	3.1	-	-	-	-	-	-	-	-
1	1	1	2	2	2	1	1	1.6	13.2	11.6	88	7.3	4.3	2.1	31.2	24.2	19.6	0.2
1	1	3	4	2	2	1	1	4.2	23.8	15.3	-	3.9	3.7	1.2	18.5	31.9	24.8	0.0

Appendix 1. Comtinued

	Lemurs					Birds					Flying Fox	Rodents		
Plant species	**Ec**	**Ch**	**Cmed**	**Cmaj**	**Mr**	**Am**	**Ta**	**Sp**	**Cn**	**Hm**	**Pr**	**rod**	**Rr**	**Ew**
Myrtaceae *Psidium guajava*		T							O					
Myrtaceae *Syzygium* sp. 1	OF	O			O							T	T	T
Myrtaceae *Syzygium* sp. 2	OF	O	O		O	OF		O	O	O	O			
Ochnaceae *Campylospermum obtusifolium*						O	O	O	O					
Oleaceae *Jasminum kitchingii*	OF							O	O					
Oleaceae *Noronhia* cf. *lanceolata*									O	O				
Oleaceae *Noronhia* sp. 1	O								O			T	T	
Oleaceae *Noronhia* sp. 2												T		
Oleaceae *Olea* sp.	OF	OT		OT	OT				OT			T	T	T
Pandanaceae *Pandanus* aff. *longistylus*	O													
Pandanaceae *Pandanus dauphinensis*	OF													
Pandanaceae *Pandanus rollotii*	O													
Rubiaceae *Canthium* sp.					OT									
Rubiaceae *Canthium variistipula*	OF	OT			OT				O		F			
Rubiaceae *Ixora* sp.	OF	OT									F			
Rubiaceae *Mapouria aegialodes*	O									O	F			
Rubiaceae *Mapouria* sp.	OF				O						F			
Rubiaceae *Morinda* cf. *umbellata*	O								O					
Rubiaceae *Morinda rigida*	O								O					
Rubiaceae *Peponidium* sp.	F											T		
Rubiaceae *Plectronia densiflora*	O	O												
Rubiaceae *Psychotria* sp.	O				T									
Rubiaceae *Pyrostria* sp.	O													
Rubiaceae *Hyperacanthus mandenensis*	OTF										F	T		
Rubiaceae *Saldinia littoralis*	O	O			O			O		O				
Rubiaceae *Tarenna thouarsiana*	F													
Rubiaceae *Tricalysia* cf. *cryptocalyx*	F				O					O	F			
Rubiaceae *genus* indet. (*tainbarika*)	F										F			
Rutaceae *Vepris elliotii** (*ampoly*)	OF	OT	OT		O		F		O		F			
Rutaceae *Vepris elliotii** (*lahinampoly*)	OF	O			O							T		
Rutaceae *Vepris fitoravina*	OTF	OT	OT		OT				OT			T		
Sapindaceae *Macphersonia radlkoferi*	O	O			O									
Sapindaceae *Plagioscyphus jumellei*												T		
Sapindaceae *Tina thouarsiana*	O				OT			O	OT			O	OT	OT
Sapindaceae *Tinopsis conjugata*	OTF								OT					
Sapotaceae *Mimusops commersonii*	O													
Sapotaceae *Sideroxylon beguei* var. *saboureani*	O								OT		F			
Sarcolaenaceae *Leptolaena* sp.	OF	OF	OF	OF	O			O						
Sarcolaenaceae *Sarcolaena multiflora*	OTF	OT	OT	OT	OT			O	OT		F			
Sarcolaenaceae *Schizolaena elongata*	OF	O						O						
Smilaceae *Smilax anceps*	F													
Sphaerosepalaceae *Rhopalocarpus coriaceus*	F													
Strelitziaceae *Ravenala madagascariensis*									O					
Taccaceae *Tacca leontopetaloides*	OTF											T		
Theaceae *Asteropeia multiflora*	O				T									
Ulmaceae *Trema orientalis*						O	O			O				
Verbenaceae *Vitex chrysomallum*	OF													
? (*fanotabe*)	F													
? (*sarikafe*)	O													
? (*vahifotsy be*)	O													
? (*x205*)												T		
? (*x209*)	OF													

GF	FT	PT	Col	Od	FSP	SP	NS	FW	FL	SL	W	CP	EP	Fat	Sugar	NDF	ADF	Tann
2	1	1	3	2	2	-	-	4.6	24.3	-	-	-	-	-	-	-	-	-
1	1	1	5	1	2	1	1	0.6	10.2	9.3	73	4.4	4.4	7.1	31.9	32.2	17.9	0.2
1	1	1	5	2	2	1	1	0.5	9.6	6.6	86	4.9	2.8	3.4	43.4	24.1	19.1	1.1
2	2	1	3	1	2	1	1	0.3	18.6	-	50	6.1	4.7	38.9	8.0	31.2	22.7	0.5
3	1	1	5	1	2	1	1	0.2	6.5	4.1	-	3.6	1.8	4.0	18.3	49.5	38.0	0.7
2	2	1	5	2	2	2	4	0.2	7.1	3.4	-	-	-	-	-	-	-	-
1	2	2	4	1	3	2	1	1.8	20.5	18.3	-	-	-	-	-	-	-	-
2	2	1	5	1	2	2	1	0.8	14.3	12.8	80	-	-	-	-	-	-	-
1	2	1	5	2	2	2	1	0.9	17.0	15.8	48	3.8	0.6	1.7	38.5	30.6	22.4	0.1
1	2	2	4	2	3	-	-	45.9	52.4	26.2	63	3.0	1.3	1.6	14.0	74.2	60.6	0.0
1	2	2	4	2	3	-	-	-	104.8	-	-	3.9	1.9	1.7	35.7	49.6	38.5	0.1
1	2	2	4	2	3	-	-	-	60.0	35.2	-	2.6	0.9	1.7	4.0	90.1	74.9	0.2
2	2	1	4	2	2	2	2	0.6	13.4	8.6	-	-	-	-	-	-	-	-
1	2	1	4	1	2	2	2	0.3	7.8	6.3	-	5.6	4.3	4.9	18.2	27.8	20.1	0.2
2	1	1	5	2	2	2	1	0.3	7.4	4.7	83	3.5	3.3	2.5	47.9	29.9	24.9	0.8
2	1	1	3	1	1	2	2	0.2	6.3	4.5	-	6.3	4.4	9.9	33.4	-	-	1.2
2	1	1	3	1	1	2	2	5.1	7.1	6.3	91	9.4	3.0	3.0	11.7	23.6	19.1	1.0
3	1	1	2	2	2	2	20	1.7	11.9	5.3	-	-	-	-	-	-	-	-
1	1	1	1	1	2	2	114	9.3	27.0	7.2	-	4.8	0.5	2.4	25.5	-	-	0.0
1	1	1	1	1	2	2	3	3.6	16.7	11.0	74	7.3	4.2	0.2	10.8	25.7	17.2	0.3
1	1	1	4	2	2	2	2	4.7	17.7	8.3	-	5.4	0.9	1.3	34.0	35.6	26.9	0.0
2	1	1	4	2	2	-	-	0.3	7.8	5.1	86	-	-	-	-	-	-	-
1	1	1	1	1	2	2	1	0.2	6.6	5.8	-	-	-	-	-	-	-	-
1	1	1	4	2	3	2	100	35.3	40.4	4.3	63	4.6	5.2	0.3	8.1	50.5	35.7	0.1
2	1	1	5	2	2	2	1	0.2	5.3	-	94	4.4	0.9	3.6	49.9	23.2	17.0	0.3
2	2	1	6	2	2	1	8	0.7	12.7	3.6	74	3.7	0.7	3.2	36.0	27.3	21.3	0.0
2	1	1	3	2	2	1	6	0.4	10.9	4.9	78	7.9	2.8	2.3	54.0	23.3	17.1	0.3
1	1	1	4	2	2	2	100	2.1	15.2	3.7	-	2.7	12.0	1.2	8.4	38.7	33.9	0.4
1	2	2	1	2	2	1	4	0.8	10.2	7.5	84	8.6	1.5	5.2	5.2	44.2	32.2	0.0
1	2	1	1	2	2	2	3	0.6	9.9	6.8	76	7.9	1.4	14.7	6.4	24.0	17.2	0.0
1	2	1	1	2	2	2	2	8.2	8.5	6.8	71	5.4	5.1	7.4	19.8	23.2	15.4	1.2
1	.	1	1	2	2	1	2	5.9	25.2	15.6	76	-	-	-	-	-	-	-
2	3	1	1	2	1	1	2	5.4	25.5	18.6	70	-	-	-	-	-	-	-
1	7	3	2	2	1	1	1	0.7	17.9	3.8	65	3.5	6.7	3.1	18.1	36.0	23.0	1.9
1	7	3	1	2	1	1	1	1.8	20.0	12.0	72	6.9	8.1	8.3	16.3	32.0	22.5	4.7
1	1	1	4	2	2	1	2	42.5	37.5	19.2	60	2.9	7.1	5.2	21.3	43.7	25.1	3.5
1	1	1	1	1	2	1	18	3.9	28.2	6.6	53	8.0	2.9	0.3	6.5	62.4	46.0	1.0
1	3	1	1	1	2	2	2	0.1	5.6	2.9	71	5.6	6.6	2.2	3.0	42.1	35.6	0.2
1	3	1	1	1	2	2	5	0.7	14.1	2.7	81	4.3	2.5	3.9	15.0	47.5	34.5	0.2
1	3	1	1	2	1	2	2	0.8	8.9	3.1	73	6.2	9.7	2.2	26.6	18.2	13.7	0.0
3	1	1	5	2	2	2	2	0.7	10.1	6.2	82	6.2	3.4	1.6	69.7	19.0	16.3	1.3
1	3	1	6	2	3	2	1	5.9	22.4	16.0	11	-	-	-	-	-	-	-
1	3	3	4	2	1	2	-	-	-	6.9	-	-	-	-	-	-	-	-
3	1	1	1	2	2	1	42	7.6	44.6	5.4	89	54.7	2.2	1.4	48.3	20.3	13.7	0.7
1	3	3	1	1	2	1	1	1.6	16.1	-	-	-	-	-	-	-	-	-
1	2	1	6	1	2	1	1	0.0	3.2	2.2	58	14.0	2.7	44.7	3.4	19.3	16.7	0.2
1	2	2	1	2	2	2	1	0.5	12.2	8.2	-	4.5	1.7	2.7	33.0	46.2	32.8	1.0
3	2	1	2	2	2	2	1	2.3	22.9	16.3	77	7.4	2.2	11.4	36.0	33.3	24.5	0.6
1	-	3	1	-	3	1	2	1.1	15.8	9.9	84	-	-	-	-	-	-	-
3	-	3	4	2	1	1	2	1.1	15.7	8.0	-	7.3	4.6	4.3	14.8	62.5	46.6	0.5
2	1	3	4	1	2	1	1	2.8	13.6	10.3	63	-	-	-	-	-	-	-
1	1	3	3	1	2	2	3	7.7	14.4	4.8	73	-	-	-	-	-	-	-