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FRUIT RICHNESS AND SEASONALITY IN A FRAGMENTED LANDSCAPE OF FRENCH GUIANA

Muriel LARUE¹, Stéphane RINGUET², Daniel SABATIER³
& Pierre-Michel FORGET¹

RÉSUMÉ

Les écosystèmes forestiers tropicaux se caractérisent non seulement par leur richesse et leur complexité, mais aussi par l'importance des relations interspécifiques dans leur fonctionnement. Ainsi, la disponibilité en fruits est un facteur primordial de la dynamique des populations de vertébrés frugivores. Pour estimer la production de fruits à la station Saint-Eugène et ses variations spatiales et temporelles, nous avons utilisé 200 collecteurs de fruits de 1 m². 50 collecteurs ont été placés sur chacun des 4 sites d'étude, et les échantillons ont été récoltés au cours de 5 missions entre septembre 1994 et décembre 1996. 251 espèces appartenant à 55 familles ont été identifiées, les Légumineuses, les Lécythidacées et les Burséracées étant les familles dominantes. Les sites diffèrent tant par le nombre d'espèces de plantes en fruit observées que par l'ordre des familles les plus riches. Ces différences de composition floristique peuvent être expliquées par les conditions édaphiques, elles-mêmes liées à l'inclinaison de la pente et à la topographie. Outre cette hétérogénéité spatiale, nous avons observé des variations saisonnières du nombre d'espèces en fruit, avec un pic pendant la saison des pluies, en conformité avec les données obtenues sur d'autres sites de Guyane française. L'impact de ces variations spatiales et temporelles de la production de fruits à l'échelle locale est envisagé dans le cadre d'une étude des effets de la fragmentation du milieu sur les communautés animales frugivores.

SUMMARY

Tropical forest ecosystems are characterized not only by their richness and their complexity but also by the importance of interspecific relationships in their functioning. Thus, fruit availability is a basic factor of the frugivore population dynamics. In order to estimate the fruit production at Saint-Eugène station and its temporal and spatial variations, we used 200 fruit traps of one square meter. 50 fruit traps were placed at each of the 4 study sites, and items were collected during 5 missions between September 1994 and December 1996. 221 species from 55 families were identified, with Leguminosae, Lecythydaceae and Burseraceae taxa being the dominant ones. The 4 sites show differences both in fruiting plant species number and in richest family order. These differences in floristic composition may be mostly explained by edaphic conditions, which are related to the slope inclination and topographic

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position. We also observed seasonal variations in fruiting species number, with a regular peak during the rainy season, which was already highlighted in French Guiana by several studies. Effects of spatial and temporal heterogeneity in fruit production on a local scale are discussed in regard to forest fragmentation effects on frugivore animal communities.

INTRODUCTION

Tropical forests are among the richest ecosystems, and are characterized by their extraordinary complexity and biodiversity (Keast, 1985; Terborgh, 1992). The wet and warm climates of the tropical zone favour the growth of a luxuriant vegetation where many animal species live. In their botanical studies, Prévost & Sabatier (1996) found up to 190 species of trees ≥ 10 cm DBH (Diameter at Breast Height) per 1-ha plot in French Guianan forest, and the highest tree species richness for DBH ≥ 10 cm is almost 290 species per 1-ha square plot in Peru (Phillips *et al.*, 1994). When other types of plants, like ferns, lianas and epiphytes are also considered, we find an outstanding species diversity of tropical vegetation that may allow a great variety of habitats and micro-habitats. Niche separation is often held as a factor that enhances animal species richness (Klopfer & MacArthur, 1961). Resulting from a long evolutionary history, a lot of complex and frail relationships exist between many forest species.

Because of the relationship between seedling recruitment probability and distance to parental plant, and also to allow the colonization of new areas, seed dispersal is almost an obligation for all plant species (Janzen, 1971). Zoochory is the major mode of dispersion in tropical forest (Smythe, 1970; Herrera, 1981; Howe & Smallwood, 1982; Sabatier, 1983, 1985) and is one of the basic functional relationships of tropical forest dynamics. For example, it concerns up to 86 % of understory plant species on Barro Colorado Island (Leigh & Windsor, 1982).

This strong plant-animal interdependence has for consequence that fluctuations of fruit availability have important effects on frugivore community. Many studies show how global tropical forest phenology is linked to seasonal variations of rainfall and determines the annual biological cycle of many animal species (Snow & Snow, 1971; Fogden, 1972; Snow, 1976; Worthington, 1982; Van Schaik *et al.*, 1993; Henry, 1999). Inter-annual climatic variations and anthropogenic perturbations of the habitat may also have an impact on fruit availability and then on frugivore populations (Adler, 1998; Foster, 1977; Wright, 1999).

Among major causes of species extinction, forest destruction and fragmentation in all tropical areas are often pointed out (Laurence & Bierregaard, 1997), and many researchers study the effects of these perturbations on plant and animal communities. Fruit availability in forest fragments is a basic point to explain the maintenance of frugivore populations, and this availability depends on the fruiting species present in each fragment. Because of high species richness, low density of many plant species (Rankin-de Merona *et al.*, 1992; Prévost & Sabatier, 1996) and spatial heterogeneity (Poncy *et al.*, 1998; Sabatier, 1994; Sabatier *et al.*, 1997; Condit *et al.*, 1996) in tropical forests, floristic composition varies between fragments. In the course of a study on the effects of forest fragmentation on fruit availability for vertebrate frugivore communities, we developed a standardized protocol to measure fruit production on several *terra firme* and island sites in the fragmented area. That allowed us to know which fruiting species did exist before the fragmentation and to make between- and within-site comparisons of fruit richness during five successive seasons.

MATERIALS AND METHODS

STUDY SITE

From January 1994 to August 1995, the completion of a hydroelectric dam (Petit Saut, French Guiana) in a hilly forested area created a total flooded area of 30,000 ha with many islands isolated by water (Granjon *et al.*, 1996; Ringuet *et al.*, 1998; Cosson *et al.*, 1999; Claessens *et al.*, 2002). The National Museum of Natural History of Paris initiated in this area a program of terrestrial vertebrate studies which is now called the Saint-Eugène Fragmentation Project (SEFP). The study area (4° 51' N; 53° 04' W) is on the Courcibo River, a main tributary of the Sinnamary River, and includes all forest fragments and a piece of the mainland in the ca. 10 square km area around the Saint-Eugène field station. The mean annual rainfall is 2,750 mm on the Sinnamary watershed, with a rainy season between December and July (Horeau, 1996). The mean annual temperature is 26 °C, with little variation over the year (see Claessens *et al.*, 2002 for detailed climatic data).

DATA COLLECTION

To assess the species diversity of fruiting trees, palms and lianas, 1 m²-fruit traps were used (Blake *et al.*, 1990; Zhang & Wang, 1995; Stevenson *et al.*, 1998). All the items that fall to the ground were captured, including small ones (≥ 5 mm in diameter). Traps were hung up at about 1 m 30 high in order to preclude consumption of fruit sample by ground frugivores. Indeed, other methods such as picking up fruits on tracks may underestimate total fruit and seed production because of this ground predation (Zhang & Wang, 1995; Chapman *et al.*, 1992), especially in a fragmented zone (Burkey, 1993; Tabarelli & Mantavoni, 1997; Benitez-Malvido, 1998).

To estimate forest spatial heterogeneity, we compared fruit richness at four relatively close sites in the Saint-Eugène study zone, i.e. a *terra firme* site (TF), a small peninsula in the north of the *terra firme* (PEN) and two isolated sites. Island n° 2 (I2) with a small temporarily split part (island n° 21) is about 30 ha in area and island n° 3 (I3) almost 70 ha (see Claessens *et al.*, 2002).

To study short-term effects of fragmentation on resource availability for the frugivore guild, we set traps at the four study sites during the filling of the reservoir. Given that final limit of the flooded zone was unpredictable (Ringuet, 1998; Huynh *et al.*, 1996), traps were placed along three parallel ridges, separated by more than 200 m, on the smallest island (i.e. I2) to prevent them from being flooded. One of the ridges became isolated from the rest of the island when water level reached its maximal height and was called island n° 21. Fifty locations were randomly sorted out of the 120 locations 10 m apart from each other along a 1,200 m transect. Mean distance between successive traps varied between 18.7 and 31.2 m according to ridges. Fifty traps were thus monitored following this pattern at each of the other sites.

Traps were emptied every two weeks during five successive field trips: September-December 1994, February-July 1995, September-December 1995, February-May 1996 and September-December 1996. Trap contents were gathered and sorted, and fruits and seeds were collected. Samples were identified on site whenever possible with identification guides (Sabatier, 1983; Roosmalen, 1985) or

were preserved in formaldehyde (10 %) for later identification at the laboratory by D. Sabatier. Twenty eight collections were made at TF and PEN, thirty and twenty nine at I2 and I3 respectively.

All fruit items (fruits, seeds, pods...) collected at each site were counted. Item determination led to an estimation of fruiting plant species richness at both global and family levels. To compare fruit richness at the four sites, we used Sorenson coefficient $C_s = 2j/a+b$ where a and b are the number of fruit species found respectively at sites A and B, and j the number of fruit species common to A and B (Magurran, 1988). We also made simple factorial analysis to test seasonal variations in species richness.

RESULTS

SPECIES RICHNESS AND INTER-SITE COMPARISONS

Altogether, we found 251 plant species belonging to 55 families (see list in Appendix). The most diverse fruiting plants families at Saint-Eugène were Bignoniaceae and Lecythidaceae (each accounting for 8.4 % of all species), Burceraceae (6.4 %), Mimosaceae (5.6 %), and Sapotaceae and Lauraceae (4.4 %) (Fig. 1). With Caesalpiniaceae and Chrysobalanaceae (about 4 % each), these eight dominant families represented just over 45 % of all the species found at Saint-Eugène. Indeed, Leguminosae (Caesalpiniaceae, Fabaceae, Mimosaceae) represented the major group of fruiting tree species, with a total of 30 species (12 %). The ten richest families (18 % of total number) accounted for about 50 % of the species. About 20 % of species fell into only eight genera that are represented by at least five species each: *Arrabidaea*, *Clusia*, *Inga*, *Pouteria* (5 spp), *Lecythis* (6 spp), *Licania* (7 spp), *Eschweilera* (8 spp), *Protium* (12 spp).

Table I presents the fruiting plant species richness at family level for each site. The three richest families at Saint-Eugène (i.e. Bignoniaceae, Lecythidaceae and Burceraceae) are always among the five richest ones at each site. However, important differences in family characteristics, e. g. order and species numbers, exist among sites.

We found 131 species from 43 families fruiting on TF during this study. Though fruiting plants at TF were mainly Burseraceae, Bignoniaceae and Lecythidaceae, with ten species or more from each family, 52.7 % of identified fruiting plant species fell into ten families. Fruiting plant species richness at TF was distinguishable from that at other sites by fewer Caesalpiniaceae and more Lauraceae and Moraceae. In addition, three families (four species) were found only at this site.

At PEN, only 82 fruiting plant species of 36 families were found. Caesalpiniaceae, Lecythidaceae and Mimosaceae were the richest families (6 species in each family). Bignoniaceae, Burseraceae and Cecropiaceae were also important, each accounting for more than 4 % of the total number of fruiting species. The ten first families (i.e. 28 % of the families) represented 52.4 % of fruiting plant species. As at TF, there were many heliophilous plant species but lianas were less frequent (22 % of species). With 3 *Pourouma* species and 4 *Inga* species, which are gap-species, this forest appeared characterized by intensive dynamics. PEN was notable for lacking Chrysobalanaceae and Quiniaceae, but having the only fruiting species of Connaraceae in its fruit samples.

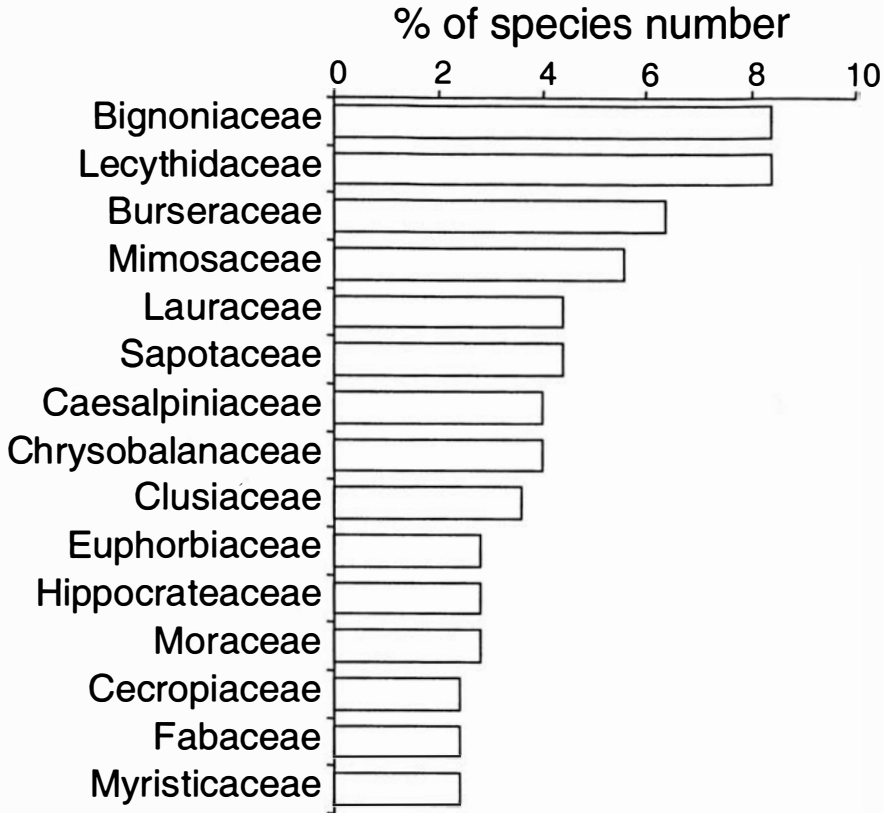


Figure 1. — Relative proportion of the 15 most species-rich fruiting plant families at the Saint-Eugène station.

With 135 fruiting plant species of 46 families, I2 was the richest site in spite of being the smallest one. Lecythidaceae were a major family there, representing almost 12 % of all fruiting plant species whereas secondary families such as Clusiaceae, Bignoniaceae and Mimosaceae included between 5.2 to 6.7 % of fruiting plant species. Sapotaceae and Myristicaceae were also rich families, each with six fruiting species. There were more Olacaceae species at I2 than at all other sites and we found there five families (6 species) that were not found elsewhere. The nine richest families represented 51.8 % of fruiting plant species.

I3 was the poorest site with only 70 fruiting plant species from 32 families. It was well characterized too by a high fruiting species richness of Lecythidaceae with nearly 13 % of identified species. The three families Bignoniaceae, Mimosaceae and Sapotaceae represented each 7-8.6 % of fruiting plants species. Several families present at the three other sites were lacking at I3 (e. g. Malpighiaceae, Sapindaceae, Flacourtiaceae) but one family (Verbenaceae) was recorded only there. The seven richest families grouped exactly 50 % of all the fruiting plant species found at this site.

TABLE I

The ten most species-rich fruiting plant families at each of the four sampled sites ordered according to number of species recorded in fruit-traps (species number in parenthesis).

TF	PEN	I2	I3
Burseraceae (12)	Lecythidaceae (6)	Lecythidaceae (16)	Lecythidaceae (9)
Bignoniaceae (11)	Caesalpiniaceae (6)	Clusiaceae (9)	Bignoniaceae (6)
Lecythidaceae (10)	Mimosaceae (6)	Bignoniaceae (8)	Mimosaceae (5)
Lauraceae (7)	Bignoniaceae (5)	Mimosaceae (7)	Sapotaceae (5)
Moraceae (6)	Burseraceae (4)	Burseraceae (6)	Burseraceae (4)
Fabaceae (5)	Cecropiaceae (4)	Caesalpiniaceae (6)	Caesalpiniaceae (3)
Mimosaceae (5)	Annonaceae (3)	Chrysobalanaceae (6)	Chrysobalanaceae (3)
Sapotaceae (5)	Clusiaceae (3)	Myristicaceae (6)	Myristicaceae (3)
Cecropiaceae (4)	Lauraceae (3)	Sapotaceae (6)	Clusiaceae (2)
Chrysobalanaceae (4)	Sapotaceae (3)	Fabaceae (5)	Lauraceae (2)

TF = *terra firme* site, PEN = peninsula of the *terra firme*, I2 = Island n° 2 and I3 = Island n° 3. The three most species-rich families at the Saint-Eugène station are in bold type.

We used Sorenson similarity index to compare fruiting plant species richness among the four sites (Fig. 2). There were only 14 fruit species common to the four sites. According to Sorenson coefficient, the most similar sites were TF and I2 with 95 species in common ($C_s = 0.56$) and the most different sites were TF and I3 with only 26 species in common and $C_s = 0.20$. At family level, only 24 families out of the 55 recorded were common to the four sites. Once again, TF and I2 were the most similar sites ($C_s = 0.8$) whereas I3 was the most dissimilar site ($C_s < 0.77$).

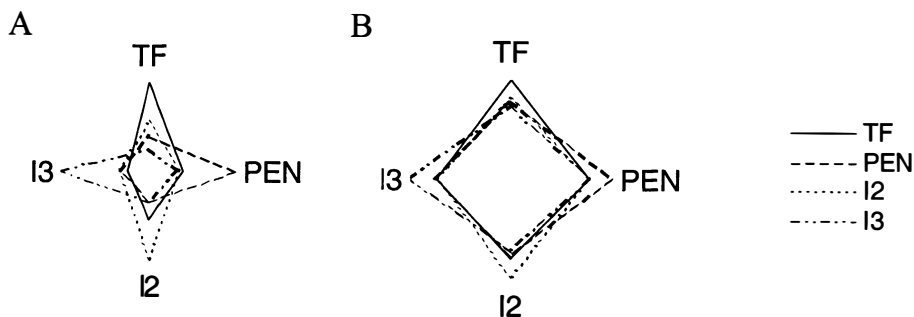


Figure 2. — Sorenson similarity indices between the four sites at the species (A) and the family (B) level.

SEASONAL VARIATIONS

Variations of species richness at each site peaked in March-April, during the rainy season (Fig. 3). Mean number of fruiting plant species per collection (i.e. in fifty traps at one date) was about 20 during the wet season against 10 during the

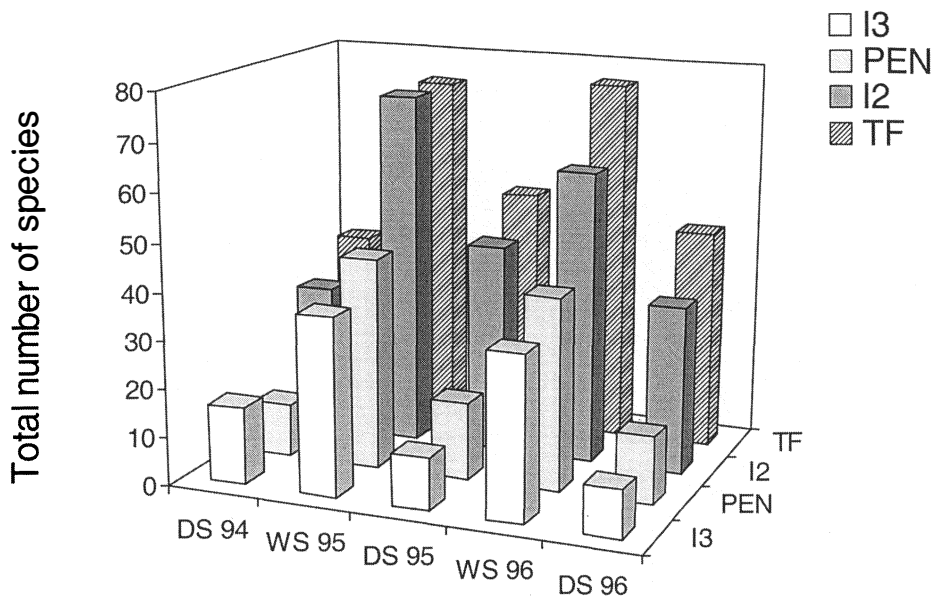


Figure 3. — Seasonal variation of the fruiting species number at each of the four sites. (TF = *terra firme* site, PEN = peninsula of the *terra firme*, I2 = Island n° 2 and I3 = Island n° 3; DS 94 = Dry Season 1994, WS 95 = Wet season 1995, DS 95 = Dry Season 1995, WS 96 = Wet season 1996, DS 96 = Dry Season 1996).

dry season. Whatever the site or the year, there were always more fruiting plant species during the wet season than during the dry season ($p < 0.0001$). There was also a great difference in fruit richness between the four sites ($p < 0.001$). Thus, we found significantly more fruiting plant species at TF than at the three other sites, and I2 was significantly different from PEN and I3. There was no year effect, neither in the dry season ($p = 0.435$) nor in the wet season ($p = 0.709$).

DISCUSSION

FRUIT RICHNESS AND FLORISTIC COMPOSITION

The 251 fruiting plant species identified at Saint-Eugène station represent a large proportion of the plant families known in French Guiana (Sabatier & Prévost, 1989) and the greatest part of this fruit richness is composed of a few species-rich families which are also among the richest families in the Neotropics (Boggan *et al.*, 1997).

Because of phenological biases, relative proportions of fruit families are obviously different from those obtained by floristic inventory (J.-F. Villiers, com. pers.). Thus, Annonaceae are among the five most frequent tree families on a 1-ha plot at I2 (6.4 % of trees with DBH ≥ 10 cm) whereas they account for only 2 % in our sample of fruiting plant species.

On the contrary, some families such as Lauraceae and Sapotaceae are known to be rich but rarely dominant families in the forest (Sabatier & Prévost, 1989). Actually, these two families account for 2.1 % of trees and 4.4 % of fruiting plant species. This high species richness (4.4 % = 11 species) was found at Saint-Eugène despite difficulties resulting from species identifications based only on fruits and seeds. It shows that some families may have a basic role in fruit production though not being globally dominant in forest composition. Bignoniaceae, a major family in terms of fruiting plant species richness at Saint-Eugène, are in this case. Many species of this family are lianas producing winged seeds (*Arrabidaea*, *Distictella*, *Martinella*, etc.). The importance of lianas and also the presence of many heliophilous species (*Cecropia obtusa*, *Laetia procera*, *Inga spp.*, *Pourouma spp.*, *Sclerobium sp.*, *Couratari guianensis*), particularly at TF, can be related to the topographic features of the study site. Actually, to escape from flooding, fruit traps were especially placed on top of main ridges. Lianas are favoured in dry open habitats, and frequency of anemochorous species increases with elevation (Killeen *et al.*, 1998). Therefore this unusual richness might be explained by a sampling bias on ridges related to site peculiarities, i.e. habitat simplification after forest fragmentation.

On the other hand, the first eight families in terms of tree number on a 1-ha plot are among the fifteen most species-rich families at the Saint-Eugène station. Therefore, floristic composition seems to be dominated by a few rich families, and at first by those (Leguminosae and Lecythidaceae) which are numerous both in term of species and tree numbers.

It is generally agreed that French Guiana is mainly covered by a lowland rain forest dominated by Lecythidaceae, Leguminosae, Chrysobalanaceae and Burseraceae (Granville in *Atlas de Guyane*, 1979; Sabatier & Prévost, 1989). As in other sites in French Guiana (Sabatier & Prévost, 1989; Poncy *et al.*, 1998), Lauraceae and Sapotaceae are among the most diverse families. Thus, the fruiting plant species richness resulting from present study is congruent with the classical floristic composition of the tropical forest of French Guiana and even of the Amazonian Basin (Milliken, 1998).

SPATIAL VARIATION OF THE FRUITING PLANT SPECIES RICHNESS

On the one hand, the predominance of Lecythidaceae is clearly marked at three, out of the four sites, and the three richest families at Saint-Eugène (Bignoniaceae, Lecythidaceae and Burseraceae) are among the first five most diverse families at each site. That confirms their basic place in the flora of this region, whatever the spatial scale.

On the other hand, there are some clear differences between the four sites when family richnesses are compared in detail. For example, families such as Caesalpiniaceae (3 to 6 species per site) and Lauraceae (2 to 7 species per site) rank very differently among sites. At the family level, Sorenson similarity indices are high but whereas TF and I2 are very similar, I3 seems to be the most particular site. Its fruiting plant species richness is more similar to that of PEN than to that at the three other sites. It is also the closest site to PEN in distance and their topographies are quite comparable. TF and I2 are similar mainly because both harbour a high species richness; differences can be explained by lack of steep slopes, and hence of some liana species at I2, as discussed above.

The 23 families common to the four sites are more or less the most species-rich ones, with the notable exception of Chrysobalanaceae which were not found at PEN during this study whereas up to six species were found at one of the sites (I2). On the opposite, ten families were just found at a single site. It may be argued that these families are species-poor ones, represented by only one species, except Humiriaceae (two species at I2) and Menispermaceae (two species at TF). This relative scarcity may be related to a heterogeneous spatial distribution. Thus these families are not important in forest structure, but can play a basic role in fruit richness available to frugivorous vertebrates. The floristic spatial variation at a local scale, due to a few rare taxa, was already known in tropical forest (Rankin-de Merona *et al.*, 1992), and especially in French Guiana (Prévost & Sabatier, 1996; Poncy *et al.*, 1998). It results in a heterogeneous spatial distribution of fruit which is also a well known attribute of tropical forests (Denslow & Moermond, 1985).

Differences between sites are more important at species than family level. However, TF and I2 are still the most similar sites, and I3 seems very particular, especially because of its poor fruiting plant species richness. Yet, and despite relatively strong similarity between the four sites at family level, there is a spatial heterogeneity at species level, even at this local scale, due to the dominance of few very diverse genera (*Protium*, *Eschweilera* and *Inga*).

This great spatial heterogeneity of fruiting plant species richness at station level may be related to differences in the floristic composition on each site. This floristic heterogeneity, already revealed by a number of studies (e.g. Prance *et al.*, 1992; Rankin-de Merona, 1992; Sabatier *et al.*, 1997; Milliken, 1998; Poncy *et al.*, 1998), is one of the characteristics of the tropical rain forest and can be wholly explained by topographic and edaphic features (Sabatier *et al.*, 1997). At family level, site differences are of little importance. Actually, even if diversity always increases when surveyed area grows (Condit *et al.*, 1996), new reported taxa belong to scarce families, thus not influencing forest types.

However, differences in floristic composition and fruit richness between close sites may be of great importance, especially when forest fragmentation effects are studied. For instance, a type of fruit resource can be isolated or become extinct at a site, decreasing chances of viability for frugivore populations. On the contrary, the presence of a typical resource may allow the persistence of its consumers, even on small islands. This may be the case of the persistence of a *Pithecia pithecia* population at a high density on I2, even though this species has disappeared from other small islands (Dalecky *et al.*, 2002). In fact, the most species-rich plant families of the Saki's diet in French Guiana are Euphorbiaceae, Moraceae, Melastomataceae, Sapotaceae, Mimosaceae, Lecythidaceae and Chrysobalanaceae (Vié, 1998) which are well represented at our sites, especially at I2.

Because of the importance of the relationship between fruit availability and maintenance of frugivore populations, our data will be of basic interest to future studies aimed at analysing fragmentation effects on many animal species at Saint-Eugène.

SEASONAL VARIATION OF THE FRUITING RICHNESS

As already done at various other tropical sites (e.g. Smythe, 1970 and Foster, 1985 in Panama; Frankie *et al.*, 1974 and Denslow *et al.*, 1986 in Costa Rica; Hilty, 1980 in Colombia; Sabatier, 1983 in French Guiana), we stress out here the importance of fruit production seasonality at Saint-Eugène station. A similar

phenological pattern, with an increase of fruiting plant species richness during the rainy season, was already known in French Guiana where slight variations appear depending on the sites (Sabatier, 1983, 1985; Julien-Laferrière, 1989; Henry, 1994) or the sampling method used (Zhang & Wang, 1995). Both abiotic and biotic factors were considered in order to explain this phenological rhythm in tropical areas despite a relatively steady climate (Augspurger, 1985; Primack, 1987; Van Schaik *et al.*, 1993; Wright, 1996; Leigh, 1999). In fact, observed cycles of fructification are global tendencies summing varied phenological rhythms, and there is a continuous (though seasonally variable in quantity of fruit and number of fruiting plant species) production of fruit in tropical forest which allow the maintenance of an important frugivore community (Herrera, 1981; Poulin *et al.*, 1999). However, at the end of each dry season there is a period of fruit scarcity which involves adaptations in frugivorous animal populations: e.g. changes in behaviour (Van Schaik *et al.*, 1993), diet (Pack *et al.*, 1999) or home range (Judas, 1998) and seasonality of reproduction (Adler, 1998; Henry, 1999; Worthington, 1982). Inter-annual climatic variations and habitat modifications may amplify this scarcity and then cause drastic fluctuations in vertebrate frugivorous populations (Adler, 1998; Foster, 1977, 1982b; Leigh, 1999; Wright, 1999). Local extinctions may take place, when migrations and re-colonization are limited by forest destruction and fragmentation. The entire forest ecosystem is then threatened.

CONCLUSION

In this study, we point out the spatial and temporal variations of fruiting plant species richness in a French Guiana tropical forest (short-term fragmentation effects on fruit quantity will be presented elsewhere). These variations are of basic importance in a study of the frugivore community because resource availability is an important determinant of animal behaviour and of the maintenance of frugivore populations.

The first results of the Saint-Eugène scientific program demonstrate some fragmentation effects in a few groups of organisms (Cosson *et al.*, 1999), but this presently short-term study underlines above all island particularities. Site characteristics depend not only on isolation features but also on historical events (e.g. timber harvesting, hunting, more or less recent human impact) that influence both flora and fauna compositions. The choice of relevant study sites and the pre-alteration description of these areas are then basic points in this type of work. Indeed, pre-alteration conditions of the isolated fragments are rarely known (Smith, 1997). On one hand, the need of both qualitative and quantitative fruit data is obvious to tackle correctly spatial variability of resource availability on forest fragments. On the other hand, knowledge of fruit richness at the very first stages of habitat fragmentation brings some important information about floristic composition before the perturbation.

Long-term studies are needed to improve our knowledge of intra- and inter-annual climatic variations and phenological rhythms. It will be then possible to distinguish effects of habitat alteration from normal variations in fruit production.

APPENDIX

List of the fruiting plant species found at the Saint-Eugène station with indication of site and year of collection.

	TF			PEN			I2			I3		
	1994	1995	1996	1994	1995	1996	1994	1995	1996	1994	1995	1996
Anacardiaceae												
<i>Tapirira guianensis</i>								*				
Annonaceae												
<i>Anaxagorea</i> sp.		*			*	*				*		
<i>Duguetia</i> sp.					*							
<i>Oxandra asbeckii</i>								*				
<i>Unonopsis stipitata</i>		*			*			*				
<i>Xylopia nitida</i>										*		
Apocynaceae												
<i>Aspidosperma album</i>								*				*
<i>Geissospermum laeve</i>		*						*	*		*	
<i>Odontadenia macrantha</i>		*	*					*	*			
<i>Tabernaemontana undulata</i>					*							
Araceae												
<i>Heteropsis jenmani</i>											*	*
<i>Heteropsis</i> sp.		*	*		*			*	*			
<i>Monstera adansonii</i>						*						
<i>Philodendron acutatum</i>			*					*	*			*
Araliaceae												
<i>Schefflera decaphylla</i>								*	*			*
Arecaceae												
<i>Astrocaryum</i> sp.						*						
<i>Jessenia bataua</i>	*	*	*		*	*		*	*		*	*
<i>Oenocarpus bacaba</i>		*		*		*					*	*
Indétermin+ A50é		*	*					*	*			
Bignoniaceae												
<i>Arrabidaea candicans</i>			*									
<i>Arrabidaea tuberculata</i>												*
<i>Arrabidaea</i> sp. 01						*						*
<i>Arrabidaea</i> sp. 02		*	*					*	*			
<i>Arrabidaea</i> sp. 03										*		
<i>Callichlamys latifolia</i>								*				
<i>Distictella magnoliifolia</i>		*	*						*			
<i>Distictella</i> sp. 01											*	
<i>Distictella</i> sp. 03						*						
<i>Martinella obovata</i>	*						*		*			
<i>Pleonotoma</i> sp.					*							*
indeterminate sp. 01					*							
indeterminate sp. "00b"		*						*	*			
indeterminate sp. "01g"									*			
indeterminate sp. "20"					*						*	
indeterminate sp. "22a"		*	*					*				
indeterminate sp. "50b"			*									
indeterminate sp. "50c"			*									
indeterminate sp. "50d"		*	*									
indeterminate sp. "50e"		*							*			
indeterminate sp. "59f"			*									

	TF			PEN			I2			I3		
	1994	1995	1996	1994	1995	1996	1994	1995	1996	1994	1995	1996
Bombacaceae												
<i>Pachira insignis</i>					*							
<i>Quararibea duckei</i>	*	*	*		*							
Boraginaceae												
<i>Cordia sagotii</i>			*									
<i>Cordia</i> sp. 01								*				
<i>Cordia</i> sp. 04	*											
Burseraceae												
<i>Dacryodes nitens</i>	*		*					*				
<i>Protium apiculatum</i>		*	*		*	*						
<i>Protium decandrum</i>											*	*
<i>Protium giganteum</i>											*	
<i>Protium opacum</i>							*	*				
<i>Protium trifoliolatum</i>												*
<i>Protium</i> sp. 01		*	*		*	*		*	*			
<i>Protium</i> sp. 02		*	*						*			
<i>Protium</i> sp. 03		*										
<i>Protium</i> sp. 04		*	*									
<i>Protium</i> sp. 06	*	*										
<i>Protium</i> sp. "32a"		*	*		*			*	*	*	*	*
<i>Protium</i> sp. "32b"	*	*	*									
<i>Tetragastris altissima</i>		*	*									
<i>Tetragastris panamensis</i>	*	*	*									
<i>Tetragastris</i> sp.	*				*							*
Caesalpiniaceae												
<i>Bauhinia</i> sp.					*	*						
<i>Bocoa prouacensis</i>		*	*	*	*	*	*	*	*			
<i>Dicorynia guianensis</i>		*	*		*	*		*	*	*	*	
<i>Eperua falcata</i>								*				
<i>Eperua grandiflora</i>					*	*						
<i>Sclerobium melinonii</i>									*			
<i>Sclerobium</i> sp.		*										
<i>Swartzia</i> sp.					*			*		*	*	
<i>Tachigali paniculata</i>					*							
<i>Vouacapoua americana</i>									*	*	*	
Cecropiaceae												
<i>Cecropia obtusa</i>	*	*	*									
<i>Coussapoa latifolia</i>	*	*	*		*			*	*	*	*	
<i>Pourouma minor</i>		*	*			*						
<i>Pourouma mollis</i>					*	*						
<i>Pourouma</i> sp. 02								*	*			
<i>Pourouma</i> sp. "03f"	*	*	*		*	*	*	*	*			
Celastraceae												
indeterminate sp.			*									
Chrysobalanaceae												
<i>Couepia</i> sp. 01							*		*			
<i>Couepia</i> sp. "50a"		*							*			
<i>Licania alba</i>							*	*	*			
<i>Licania membranacea</i>		*										
<i>Licania micrantha</i>								*				
<i>Licania parvifructa</i>										*		
<i>Licania</i> sp. 01										*	*	*
<i>Licania</i> sp. "46a"			*									
<i>Licania</i> sp. "51a"			*				*	*	*	*	*	*
<i>Parinari excelsa</i>								*	*			

	TF			PEN			I2			I3		
	1994	1995	1996	1994	1995	1996	1994	1995	1996	1994	1995	1996
Clusiaceae												
<i>Clusia cuneata</i>								*				
<i>Clusia grandiflora</i>				*	*	*		*	*	*	*	*
<i>Clusia scrobiculata</i>					*		*	*	*			
<i>Clusia</i> sp. "52b"		*				*				*	*	
<i>Clusia</i> sp. "52c"										*	*	
<i>Symphonia globulifera</i>		*	*					*	*			
<i>Symphonia</i> sp. 01		*						*				
<i>Tovomita</i> sp.							*					
<i>Vismia guianensis</i>								*				
Combretaceae												
<i>Combretum laxum</i>								*	*			
Connaraceae												
<i>Connarus</i> sp. 01					*							
Convolvulaceae												
<i>Dicranostyles</i> sp.		*	*									
<i>Maripa glabra</i>								*				
<i>Maripa scandens</i>										*		
Cucurbitaceae												
<i>Cayaponia ophthalmica</i>						*						
<i>Cayaponia</i> sp. 01		*	*							*		
<i>Cayaponia</i> sp. 03			*									
Dilleniaceae												
<i>Doliocarpus</i> sp.	*	*	*					*	*			
<i>Tetracera</i> sp.						*			*			*
Elaeocarpaceae												
<i>Sloanea acutiflora</i>				*								
<i>Sloanea grandiflora</i>	*	*	*									*
<i>Sloanea</i> sp.	*	*	*									*
Ericaceae												
indeterminate sp. 01	*		*			*	*	*	*	*	*	
Euphorbiaceae												
<i>Aparisthium cordatum</i>								*				
<i>Conceveiba guianensis</i>		*	*	*	*	*		*				*
<i>Mabea</i> sp.										*	*	
<i>Pera</i> sp.			*									
<i>Plukenetia abutifolia</i>	*											
<i>Sandwithia</i> sp.								*				
indeterminate sp. 02		*										
Fabaceae												
<i>Dioclea</i> sp.	*	*						*				
<i>Diploptropis purpurea</i>		*	*		*			*				
<i>Hymenolobium flavum</i>			*			*			*			
<i>Machaerium kegelii</i>		*										
<i>Machaerium guinata</i>								*				
<i>Machaerium</i> sp.		*						*		*		
Flacourtiaceae												
<i>Casearia</i> sp.		*										
<i>Laetia procera</i>	*	*	*	*	*	*	*					
Gnetaceae												
<i>Gnetum urens</i>		*										
<i>Gnetum</i> sp.												*
Hippocrateaceae												
<i>Cheiloclinium</i> sp.										*		
<i>Hippocratea volubilis</i>		*	*		*			*	*			
<i>Prionostemma aspera</i>		*										

	TF			PEN			I2			I3		
	1994	1995	1996	1994	1995	1996	1994	1995	1996	1994	1995	1996
<i>Salacia impressifolia</i>							*					
<i>Salacia</i> sp. 01											*	
<i>Salacia</i> sp. 02			*									
<i>Salacia</i> sp. 03					*							
Humiriaceae												
<i>Sacoglottis amazonica</i>								*				
<i>Sacoglottis</i> sp. 01												
Icacinaceae												
<i>Poraqueiba guianensis</i>					*	*				*		
Lauraceae												
<i>Licaria</i> sp. 01					*							
<i>Licaria</i> sp. 02											*	
<i>Ocotea floribunda</i>	*	*	*									
<i>Ocotea rubra</i>	*	*	*									
<i>Ocotea schomburgkiana</i>	*											
indeterminate sp. 08		*	*									
indeterminate sp. "02d"	*		*				*					
indeterminate sp. "08"						*						
indeterminate sp. "16"					*						*	
indeterminate sp. "16e"						*	*	*				
indeterminate sp. "22d"		*										
Lecythidaceae												
<i>Couratari guianensis</i>	*	*	*			*	*	*				
<i>Eschweilera apiculata</i>							*	*			*	
<i>Eschweilera chartacea</i>							*	*				
<i>Eschweilera coriacea</i>							*	*		*		
<i>Eschweilera grandiflora</i>			*			*		*				
<i>Eschweilera micrantha</i>							*	*		*		
<i>Eschweilera parviflora</i>								*			*	
<i>Eschweilera pedicellata</i>		*					*			*		
<i>Eschweilera</i> sp.		*			*		*			*	*	*
<i>Gustavia augusta</i>			*									
<i>Gustavia hexapetala</i>		*	*		*		*			*	*	
<i>Lecythis confertiflora</i>							*	*				
<i>Lecythis corrugata</i>		*										
<i>Lecythis idatimon</i>								*	*	*	*	
<i>Lecythis persistens</i>							*	*				
<i>Lecythis poiteaui</i>			*		*							
<i>Lecythis</i> sp.								*				
indeterminate sp. "05"					*					*		
indeterminate sp. "f03"							*	*				
indeterminate sp. "f06"	*		*				*					
indeterminate sp. "f11"		*	*					*				
Malpighiaceae												
<i>Byrsonima laevigata</i>	*	*	*	*	*	*	*	*	*			
<i>Hiraea</i> sp.			*				*					
<i>Lophopterys</i> sp.		*	*	*	*		*	*	*			
Marcgraviaceae												
<i>Marcgravia coriacea</i>			*									
<i>Norantea guianensis</i>					*							
<i>Souroubea</i> sp.						*						
indeterminate sp. "56b"	*		*				*					
Melastomataceae												
<i>Mouriri crassifolia</i>		*						*				
Meliaceae												
<i>Guarea kunthiana</i>		*	*					*				

	TF			PEN			I2			I3		
	1994	1995	1996	1994	1995	1996	1994	1995	1996	1994	1995	1996
Mendonciaceae												
<i>Mendoncia hoffmannseggiana</i>					*							
<i>Mendoncia</i> sp.		*	*					*	*			
Menispermaceae												
<i>Odontocaria wullschlaegelii</i>												*
<i>Orthomene schomburgkii</i>		*										
Mimosaceae												
<i>Abarema curvicarpa</i>				*	*	*						
<i>Abarema</i> sp.								*	*			*
<i>Balizia pedicellaris</i>		*						*	*			
<i>Enterolobium schomburgkii</i>								*				
<i>Inga fanchoniana</i>												*
<i>Inga lateriflora</i>	*	*			*							
<i>Inga leiocalycina</i>				*	*							
<i>Inga stipularis</i>					*							
<i>Inga</i> sp.	*	*	*		*	*		*	*		*	*
<i>Mimosa micracantha</i>					*			*				
<i>Mimosa</i> sp.	*	*	*					*				
<i>Parkia pendula</i>											*	*
indeterminate sp. "01"										*		
indeterminate sp. "22c"		*	*						*			
Moraceae												
<i>Brosimum guianense</i>						*						
<i>Ficus</i> sp. "35a"		*	*					*				
<i>Ficus</i> sp. "54c"	*	*	*					*	*	*		
<i>Helicostylis pedunculata</i>		*										
<i>Helicostylis tomentosa</i>		*	*					*	*		*	
<i>Perebea guianensis</i>			*		*							
<i>Perebea mollis</i>		*	*									
Myristicaceae												
<i>Iryanthera hostmannii</i>								*	*			
<i>Iryanthera sagotiana</i>	*	*	*					*	*	*		*
<i>Iryanthera</i> sp.	*	*	*		*	*		*	*	*		*
<i>Virola kwatae</i>	*		*			*						
<i>Virola michelii</i>								*				
<i>Virola</i> sp.									*		*	*
Myrtaceae												
indeterminate sp. 01								*	*			
indeterminate sp. 02						*						*
Ochnaceae												
<i>Elvasia</i> sp.	*	*			*							
Olacaceae												
<i>Heisteria scandens</i>		*	*		*	*		*	*			
<i>Minuartia guianensis</i>								*				
<i>Ptychopetalum olacoides</i>									*		*	
Passifloraceae												
<i>Dilkea</i> sp. 01								*	*	*		
Polyganaceae												
<i>Moutabea</i> sp.								*	*			
<i>Securidaca</i> sp.	*	*	*		*			*	*			*
Quiinaceae												
<i>Quiina guianensis</i>		*	*					*	*			
<i>Quiina obovata</i>		*	*					*				*
Rhamnaceae												
<i>Gouania blanchetiana</i>		*	*					*				

	TF			PEN			I2			I3		
	1994	1995	1996	1994	1995	1996	1994	1995	1996	1994	1995	1996
Rubiaceae							*					
<i>Posoqueria latifolia</i>												
Sapindaceae												
<i>Cupania</i> sp. 01		*	*			*		*	*			
<i>Paullinia anodonta</i>		*										
<i>Paullinia</i> sp. 01						*						
<i>Pseudima frutescens</i>	*											
<i>Serjania</i> sp.											*	
Sapotaceae												
<i>Chrysophyllum cuneifolium</i>											*	
<i>Chrysophyllum</i> sp.									*			
<i>Micropholis egensis</i>		*	*		*	*		*	*		*	
<i>Micropholis guyanensis</i>											*	*
<i>Micropholis venulosa</i>								*			*	*
<i>Pouteria brachyandra</i>											*	
<i>Pouteria egregia</i>		*			*							
<i>Pouteria</i> sp. 01												*
<i>Pouteria</i> sp. 02								*				
<i>Pouteria</i> sp. "00t"		*	*			*		*	*			
indeterminate sp. "11h"								*				
Sterculiaceae												
<i>Guazuma ulmifolia</i>					*							
<i>Sterculia excelsa</i>											*	
<i>Theobroma</i> sp.									*			
Tiliaceae												
<i>Apeiba</i> sp.						*						
indeterminate sp. 01								*				
Verbenaceae												
<i>Petrea</i> sp.											*	
Violaceae												
<i>Rinorea amapensis</i>					*	*						
<i>Rinorea flavescens</i>											*	
<i>Rinorea</i> sp.	*	*	*			*	*	*	*			*
indeterminate sp. 01					*							
indeterminate sp. "05b"	*									*		
Vochysiaceae												
<i>Vochysia</i> sp.			*									

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