CHAPTER 3.

POTENTIAL KEYSTONE PLANT SPECIES FOR THE FRUGIVORE COMMUNITY AT TINIGUA PARK, COLOMBIA

PABLO STEVENSON

Abstract
Different practical problems restrict the possibility of rigorously testing the role of plants as keystone species in tropical forests, and therefore we do not yet know the impacts that could result from their removal. Currently, the criteria used to suggest keystone plant species in tropical forests include an assessment of their importance in supporting frugivore communities during periods of fruit scarcity, their reliability during these periods, their abundance, and the number of species that feed on their fruits. However, even for resources that match these criteria it has been shown that the density of these plant species is not necessarily correlated with the abundance of frugivores, so their relevance is still an open question. In this study I use information on feeding behavior and phenological data collected over three years in Tinigua National Park, Colombia, to identify potential plant keystone resources for the fruit-eating animals. Among 29 plant species that produced fruit or were consumed in periods of fruit scarcity, I found virtually no case of a species that could maintain a large proportion of the frugivore community. Plant species previously suggested playing keystone roles, such as palms and figs, were included in the list. But palms did not support a very large coterie of frugivores and figs were reliable only at the genus level. The fact that only 3 of the 29 species suggested to play keystone roles at Tinigua were present in a recent review of the potential keystone resources in Neotropical forests (Peres, 2000), suggests that species playing important roles in one community may be unimportant in other localities. I conclude that postulating keystone resources in tropical forests might lead to strategies to protect local animal guilds, but it is difficult to find species that could support the majority of frugivores in complex communities and it is naïve to generalize about their roles across localities. I suggest that the bulk of frugivores in Tinigua (i.e. primates) may use fat reserves accumulated during periods of fruit abundance to survive the lean period, and therefore keystone resources might not be restricted to particular seasons.

Key words: Frugivory, keystone resources, phenology, primates, tropical forests

J. Lawrence Dew and Jean Philippe Boubli (eds.), Tropical Fruits and Frugivores: The Search for Strong Interactors 37–57.

INTRODUCTION

The concept of keystone resources has changed through time, so several definitions have been used for keystone species in different efforts to identify them. The keystone species term was used for the first time to describe a predator that controlled a rocky intertidal community (Paine, 1969). The most common definitions of keystone species or resources are based on the occurrence of drastic changes at the community level caused by their removal (Mills et al., 1993). Authors disagree in how dramatic the change has to be to merit keystone status for the species: the term has been used for species whose removal causes changes in the density of only a few other species (Fincke et al., 1997), up to the complete loss of integrity of the community (Power et al., 1985; Terborgh et al., 2001). Therefore, the definition of keystone species has changed to make the concept useful for conservation purposes. A common feature of the earliest works trying to identify keystone species was that they proposed organisms (species or guilds) whose removal was expected to result in the disappearance of at least half of the assemblage under study (Mills et al., 1993). Although any definition based on a particular percentage may be greatly affected by the size of the assemblage under consideration, the protection of a keystone species may benefit the stability and integrity of a community more than the conservation of other species without such strong interactions. This is the potential use of keystone species in conservation biology.

Mills et al. (1993) suggested using community importance values that measure interaction strength to quantitatively infer keystone species. These values could be calculated for each species as the percentage of other species lost from the community following its removal. Keystone species might be useful for conservation programs only if there are large asymmetries in the community importance values among the species of that particular community. The methodology for calculating these values should be based on the results of perturbation experiments, in which one species is removed, and the responses of other species are measured over appropriate time scales and compared to controls. However, when the interest is maintaining biodiversity (i.e. in tropical forests), it would be difficult and unethical to monitor long-term effects of removal of one species. In this case, pulse experiments (similar to Bender et al., 1984) looking at short term effects on fitness components (e.g. growth rates) might be an option. A common alternative method is a comparative approach, in which a community that has lost one species (usually by human intervention) is compared to a similar community with the complete original set of species. Two main problems occur in this kind of analysis. First is the difficulty of having appropriate replicates, because spatial heterogeneity may obscure the impact of species removal, and a related problem is that without knowledge of the natural variation in the study communities and without controls, it is difficult to ascertain whether the changes observed in the altered community are caused by the removal.

A recent consensus definition states that “a keystone species is a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance” (Power & Mills, 1995). This definition is also based on the presence of strong interactions, but it incorporates the restriction of dominance within the community. According to this view, dominant elements in the community should be distinguished from keystone species even though both groups participate in strong interactions. Although this distinction seems ecologically appropriate, the purpose should not only be preserving keystone species without considering dominants. In fact, the dominance criterion was not part of the original formulation of keystone plant resources (Howe, 1977; Terborgh, 1986).

Gilbert (1980) used the term “mobile links” to refer to animals that play crucial roles in the persistence of various plant species, which in turn may produce the primary food to sustain the community. Gilbert discussed two groups including pollinators and seed dispersers. There are also examples in tropical rain forest ecology literature of several plant resources such as figs and palm species which have been postulated to be keystone species because they produce fruits during periods of fruit scarcity. Terborgh (1986) reached this conclusion based on an analysis of the energy provided by the fruits in the plant community of Cocha Cashu, Peru. Based on previous studies of fruit availability and frugivore abundance (Janson, 1984; Janson & Emmons, 1990), Terborgh showed that in periods of fruit scarcity the energy provided by the plant community is below the amount required to support the resident guild of frugivores. Patterns of fruiting seasonality seem to be common in many Neotropical forests (van Schaik et al., 1993; van Schaik & Pfannes, 2002), as is the consistent use of a few plant sources by frugivores during periods of fruit shortage (Peres, 2000).

If resources such as figs and palms are supporting the community of frugivores, then one would expect to find higher frugivore biomass in places where these resources are more abundant. However, a recent study suggested the abundance of the proposed plant keystone resources such as palms and figs is not correlated with the biomass of primates (Stevenson, 2001), which constitute one the most important frugivore groups in the New World (Terborgh & van Schaik, 1987). These findings run contrary to expectations if the plants are really keystone resources for the frugivore community. However, methodological issues complicate the picture because it is difficult to quantify fig abundance. For example, the basal area and the density of figs in plots including plants larger than 10 cm DBH. may under represent fig abundance, because some fig species are hemi-epiphytes with only thin roots reaching the ground. Therefore, it is not clear if the postulated keystone role of these resources really exists, and in any case it appears risky to take conservation actions based on the abundance of these apparently critical resources.

The main objectives of this paper are: 1) to describe the patterns of fruit production in the lowland tropical forest of Tinigua National Park, Colombia; 2) to present a list of the potential keystone plant species that produce fruit during periods of general scarcity; 3) to compare these resources with the food items ingested by a variety of frugivores in this community; 4) to evaluate using the available evidence (in the absence of experimental studies) the potential role of these species as keystone resources, and 5) to discuss the potential value of plant keystone resources to community dynamics and conservation programs.

METHODS

Site description

The study site is located in a tropical lowland forest on the Eastern border of Tinigua National Park (201,875 ha), west of La Macarena mountains, Departamento del Meta, Colombia (2° 40' north and 74° 10' west, 350-400 m over sea level). The study site, Centro de Investigaciones Ecológicas La Macarena (CIEM), consists of three research stations on the West margin of Río Duda. Rainfall is seasonal in the region, with a 2-3 month dry period occurring between December and March (Stevenson, 2002). Average annual precipitation at Paujil Station during the study periods (March 1990-February 1991, August 1996-July 1997, and January-December 2000) was 2782 mm. I estimated fruit abundance using a combination of phenological transects and fruit morphological information, using a new methodology to assess fruit production from phenological and morphological data (Stevenson, 2002). For the first two study years when I did not estimate individual fruit crops, I used the average crop size in the final year for each species, unless differences between years were evident. In the former cases I used the maximum or minimum crop estimates from just one year. I defined periods of fruit shortage as those when the production was less than one third of the maximum production during the year cycle. This proportion is similar to the one found by Terborgh in his original analysis of keystone plant resources (1986).

I extracted production data from the months of fruit scarcity (usually between September and January in our study site), to suggest keystone resources. All species producing ripe fruit at those shortage periods were ranked according to their production during lean periods.

Frugivore Consumption

The most complete data on frugivore feeding behavior during the study period was collected on woolly monkeys (*Lagothrix lagothricha*), which were continuously studied during those three years. I described the fruit diet of the woolly monkeys at Tinigua following more than 2000 h of focal observations (Stevenson, 2002), when the number of minutes spent feeding on different plant species was measured. A separate database included information on other primate species (Stevenson, 2000, Link pers. comm.). In these cases the sample time was shorter, but for all species dietary information was collected during at least one complete season of fruit scarcity.

I gathered information on feeding behavior of the general frugivore community from observations of focal trees with ripe fruits from 75 plant species that were observed during periods of high frugivore activity (6:10-10:00), for a total of more than 3400 h.

RESULTS

I have found a consistent pattern of fruit production in the study area for all the years when phenological information has been recorded (Figs. 1 a, b, and c). There is generally a unimodal distribution of ripe fleshy fruits across the year. The period of fruit scarcity occurs at the end of the rainy season. An increase in fruit availability starts during the dry season and reaches a maximum at the end of the dry season or the beginning of the rainy season (between March and May). Finally, fruit production drops at the middle of the rainy season and very few species produce ripe fruits during periods of fruit scarcity (usually between September and January); therefore, those species in fruit during those months could be postulated to play keystone roles in the community.

It is evident, however, that there is variability in the species that produce ripe fruits during periods of fruit scarcity (Table 1). Except for three relatively common species, two palms *Oenocarpus bataua* and *Iriartea deltoidea,* and one tree, *Gustavia hexapetala*, none of the other species was among the most important plants producing ripe fruits during lean periods for all three study years.

In general, high fruit production during scarcity periods was not a good predictor of the species that were consumed by frugivores during those periods. For example, correlation coefficients between production and fruit consumption by woolly monkeys in fruit scarcity periods for all study years was always low (1990: r^2=0.04, F=3.0, p=0.09 n= 80 species; 1996: r^2=0.09, F=10.0, p=0.002, n=102; 2000: r^2=0.03, F=2.3, p=0.13, n=86). Two reasons may explain the lack of correlation. First, there was high incidence of consumption of unripe fruits during periods of fruit scarcity (see below), and the monkeys did not ingest some of the fruits available during scarcity periods. For example, after more than 2000 h of observation, I have not observed the woolly monkeys ingesting fruits of *Oenocarpus bataua*, in spite of its abundance and high energy content. Dew (2001) found the same to be true at another Amazonian site in Ecuador. Probably this rejection is due to high tannin contents in the pulp of the fruit (Stevenson et al., 2000).

Based on the fruit consumption by the woolly monkeys during periods of fruit scarcity a set of potential keystone plants is presented in Table 2. Again there is variability in the importance of different fruiting plant species in the diet of woolly monkeys during scarcity periods. Except for *Gustavia hexapetala,* which was actually the most consumed species in the overall diet in all three years, none of the remaining fruit species was important in all study years. This variability could be related to several factors, such as: 1) fortuitous production of species with unpredictable fruiting patterns (i.e. *Ficus* spp.). 2) Small changes in the timing of production of the species (i.e. *Inga alba* producing fruits in January instead of February or *Spondias venulosa* and *Henriettella fissanthera* delaying production

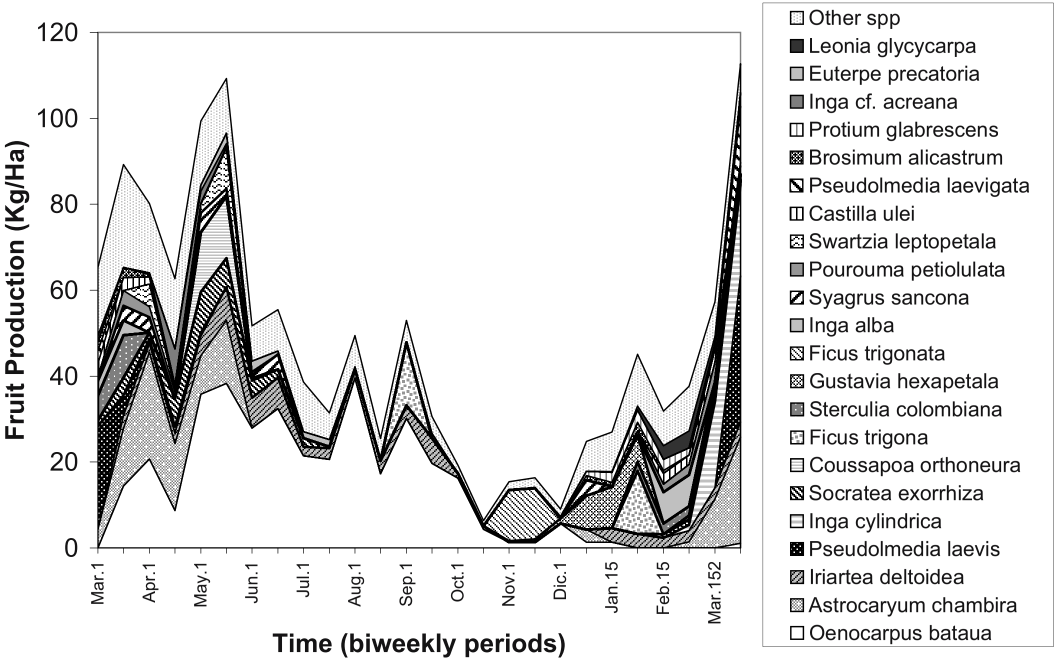

Figure 1a. *Temporal variation in the production of ripe fleshy fruits in Tinigua National Park over an annual cycle: 1990. The production of the main species are shown in different patterns, and the upper line indicates the overall pattern of production. Fruit production was estimated according to a new methodology (Stevenson 2002), and crop size was not measured but inferred from other years (See text for methodological details).*

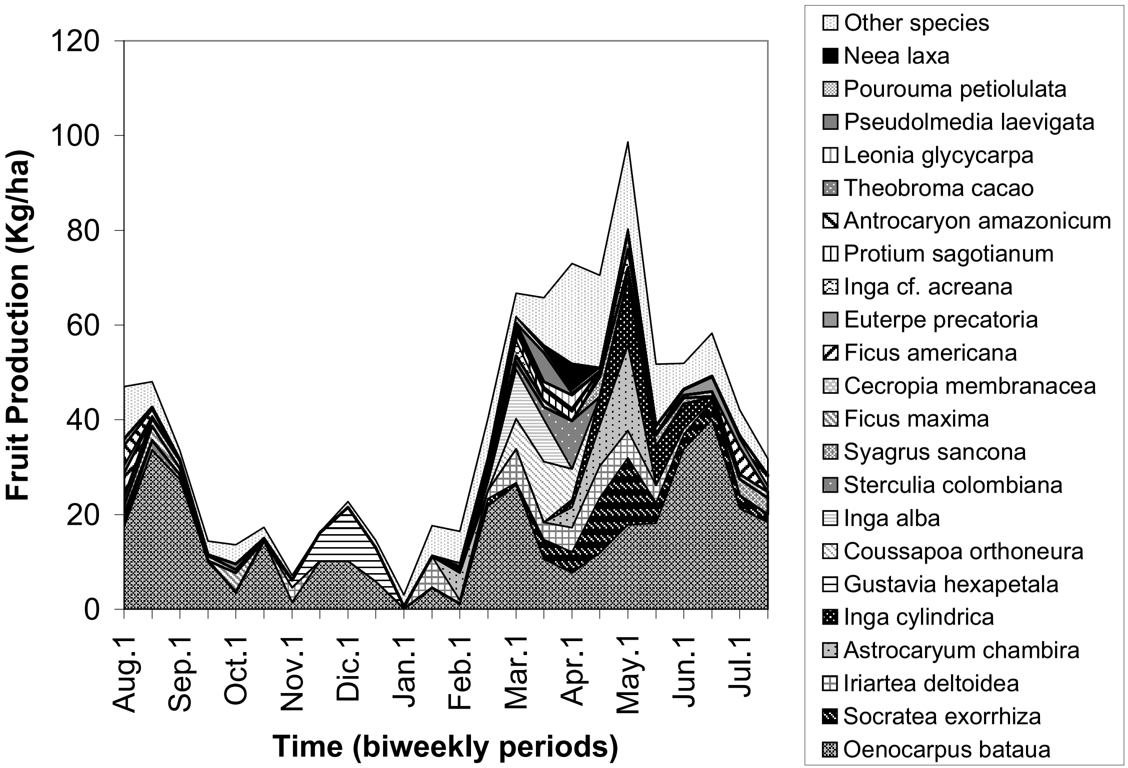

Figure 1b. *Temporal variation in the production of ripe fleshy fruits in Tinigua National Park over an annual cycle: 1996. The production of the main species are shown in different patterns, and the upper line indicates the overall pattern of production.*

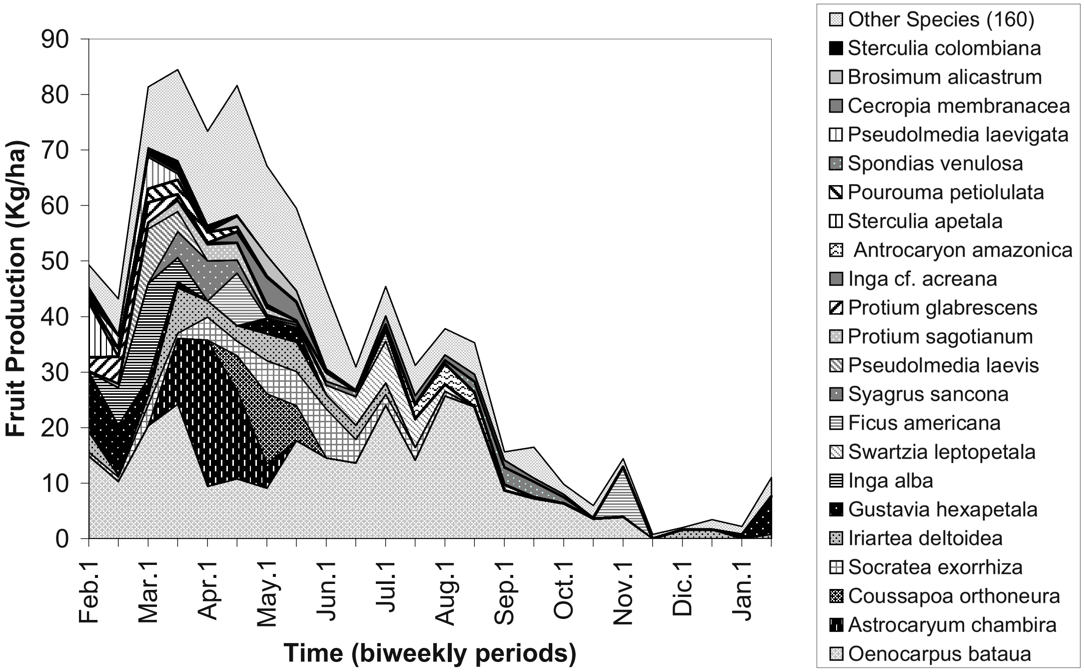

Figure 1c. *Temporal variation in the production of ripe fleshy fruits in Tinigua National Park over an annual cycle:2000. The production of the main species are shown in different patterns, and the upper line indicates the overall pattern of production.*

Table 1. *Potential keystone plant species producing fruit in periods of fruit scarcity during three different years at Tinigua Park. Estimates of fruit production are in kg/ha.*

Species (1990)	*Prod.*	*Species (1996)*	*Prod.*	*Species (2000)*	*Prod.*
Oenocarpus bataua	87.2	Oenocarpus bataua	60.3	Oenocarpus bataua	29.7
Ficus trigonata	23.8	*Gustavia hexapetala*	26.5	*Ficus americana*	8.9
Gustavia hexapetala	22.4	*Iriartea deltoidea*	9.5	*Gustavia hexapetala*	7.5
Ficus trigona	14.7	*Ficus maxima*	4.0	*Spondias venulosa*	6.9
Iriartea deltoidea	14.1	*Ficus pertusa*	3.2	*Cecropia membranacea*	5.4
Bursera inversa	6.6	*Cecropia membranacea*	2.5	*Iriartea deltoidea*	4.0
Sterculia apetala	5.2	*Cecropia engleriana*	1.5	*Henriettella fissanthera*	2.8
Ficus andicola	4.6	*Ficus obtusifolia*	1.5	*Apeiba aspera*	2.7
Spondias venulosa	4.6	*Pourouma bicolor*	1.5	*Ficus sphenophylla*	1.9
Protium glabrescens	4.6	*Euterpe precatoria*	1.4	*Protium robustum*	1.4
Genus (1990)		*Genus (1996)*		*Genus (2000)*	
Oenocarpus	87.2	*Oenocarpus*	60.3	*Oenocarpus*	29.7
Ficus	43.1	*Gustavia*	26.6	*Ficus*	11.8
Gustavia	22.5	*Ficus*	10.8	*Gustavia*	7.5
Iriartea	14.1	*Iriartea*	9.5	*Spondias*	7.1
Bursera	6.6	*Cecropia*	8.1	*Cecropia*	5.4
Sterculia	5.2	Virola	2.1	*Iriartea*	4.0
Protium	5.1	*Pourouma*	1.7	*Apeiba*	2.9
Spondias	4.6	*Apeiba*	1.6	*Henriettella*	2.8
Syagrus	3.6	*Euterpe*	1.4	*Protium*	1.9
Virola	3.5	*Protium*	1.3	*Virola*	1.7

until September). 3) Changes in fruit production patterns (i.e. poor fruit production in *Pourouma bicolor* at the end of 2000 or the death of a large *Doliocarpus multiflorus* vine after 1990). 4) Supra-annual patterns of fruit production (cf. *Enterolobium schomburgkii*); and/or 5) fruit preference for species eaten only when few alternative resources were present (cf. *Bursera inversa*).

Table 2. *Plant resources used by woolly monkeys in periods of fruit scarcity during three different years in Tinigua Park. Plant species in three different diet categories are organized by consumption time (min). Bold plant names indicate unripe consumption.*

1990	Time	**1996**	Time	**2000**	Time
FRUITS					
Gustavia hexapetala	686	*Gustavia hexapetala*	1382	*Gustavia hexapetala*	459
Brosimum alicastrum	166	***Pseudolmedia obliqua***	766	*Henriettella fissanthera*	457
Brosimum guianensis	102	*Pourouma bicolor*	403	*Ficus andicola*	167
Doliocarpus multiflorus	99	***Brosimum lactescens***	244	*Inga alba*	140
Enterolobium schomburgkii	98	***Hymenaea courbaril***	115	*Spondias venulosa*	138
Ficus trigonata	97	*Ocotea tomentosa*	110	***Pseudolmedia obliqua***	113
Ficus sphenophylla	80	*Ficus guianensis*	88	*Bursera inversa*	111
Apeiba aspera	66	***Brosimum alicastrum***	82	***Hymenaea courbaril***	66
Dialium guianensis	65	***Brosimum utile***	79	*Ficus sphenophylla*	65
Pourouma bicolor	63	*Apeiba aspera*	76	*Ficus nymphaeifolia*	65
YOUNG LEAVES					
Brosimum alicastrum	230	*Derris pterocarpus*	129	*Brosimum alicastrum*	334
		Brosimum alicastrum	81	*Derris pterocarpus*	66
		Xylophragma seemannianum	67	*Dialium guianensis*	58
		Dialium guianensis	63	*Adenocalymna purpurascens*	52
		Cestrum racemosum	34	*Clarisia biflora*	31
		Clarisia biflora	27	*Xylophragma seemannianum*	18
FLOWERS					
Astrocaryum chambira	25	*Astrocaryum chambira*	151	*Astrocaryum chambira*	118
		Brosimum	72	*Dalbergia sp.*	107

alicastrum			
Dalbergia sp.	42	*Pseudolmedia obliqua*	38
Apeiba aspera	40	*Pseudolmedia laevis*	29
Phryganocydia corymbosa	20	*Brosimum guianensis*	28
Pisonia aculeata	11	*Pseudolmedia laevigata*	22

In contrast, the leaf resources ingested during periods of fruit scarcity seemed to be more regularly recorded in the diet of the woolly monkeys (Table 2). In this case, the most important species seem to reoccur in the diet at different years (although a direct comparison among the three study years was precluded because I was unable to recognize all vine species ingested during the first year). The most important flower species consumed by woolly monkeys during periods of fruit scarcity seemed to be fairly constant among years (e.g. *Astrocaryum chambira*).

There was also variability in the fruit species consumed by other primate species during periods of fruit scarcity (Table 3). Spider monkeys used many of the fruit sources used by woolly monkeys, though the latter relied more on palms such as *Oenocarpus bataua* and *Astrocaryum chambira* than the woolly monkeys did. Capuchin monkeys in contrast to large atelines, did not consume *Gustavia hexapetala* fruits in any important amount. The capuchins instead relied heavily on *Astrocaryum chambira* fruits, which were less used by other primate species. Howler monkeys in this community drastically changed their feeding patterns during periods of fruit scarcity, feeding on very few species and consuming mainly unripe fruits (Table 3). There were also differences in the non-fruit foodstuffs eaten by different primate species at fruit scarcity periods. For example, the main plant items consumed by capuchins included the pith of *Phenakospermum guyanense*, flowers of *Astrocaryum chambira*, petioles of *Guadua angustifolia*, young buds of *Carludovica palmata*, and no leaves. In contrast, the most important items for the larger ateline monkeys were always young leaves of vines and trees (i.e. *Brosimum alicastrum*).

In the years when I conducted observations of fruiting trees, most of the activity in the frugivore community during the fruit scarcity period was focused on large fig trees and a few other species (i.e. *Cecropia membranacea, Oenocarpus bataua, Bursera inversa,* and *Apeiba aspera*). Trees of *Ficus* spp., *Cecropia membranacea* and *Bursera inversa* were consistently visited by a large coterie of frugivores including birds and primates. Table 4 shows the complete list of potential fruit sources that could be postulated as keystone resources at Tinigua, given that they produce fruit during the scarcity period or because they are consumed by frugivores in those periods.

Table 3. *Fruit resources used by four primate species during at least one period of fruit scarcity (data from Angulo, 2001; Stevenson et al., 2000; Samper & Pineda unpublished, and results from this study). Fruit species are arranged in decreasing order of feeding time (handling and ingestion). Bold names indicate consumption of unripe fruits.*

Woolly Monkeys (90, 96, 00)		*Spider monkeys (1990)*	
Gustavia hexapetala	2527	*Gustavia hexapetala*	323
Pseudolmedia obliqua	879	*Ficus andicola*	320
Brosimum alicastrum	492	*Ficus yoponensis*	168
Pourouma bicolor	466	*Ficus schultesii*	99
Henriettella fissanthera	457	*Pourouma bicolor*	84
Hymenaea courbaril	181	***Astrocaryum chambira***	82
Ficus andicola	167	Ficus nymphaeifolia	78
Ficus sphenophylla	145	*Iriartea deltoidea*	62
Apeiba aspera	142	*Brosimum utile* (unripe?)	54
Inga alba	140	***Oenocarpus bataua***	52

Howler Monkeys (1990)		*Capuchin Monkeys (1990)*	
Pseudolmedia obliqua	226	***Astrocaryum chambira***	1083
Brosimum alicastrum	150	***Oenocarpus bataua***	379
Brosimum utile	148	*Pourouma bicolor*	167
Gustavia hexapetala	97	*Ficus guianensis*	150
Ficus yoponensis	67	*Pseudolmedia obliqua*	147
Ficus trigona	63	***Socratea exorrhiza***	100
Pseudolmedia laevigata	25	*Apeiba aspera*	92
Dipteryx micrantha	24	*Ficus nymphaeifolia*	60
Ficus membranacea	23	*Perebea xanthochyma*	42
Pourouma bicolor	18	*Protium glabrescens*	35

Squirrel Monkeys (2000)	
	(%)
Ficus andicola	46.5
Piper fresnoense	10.7
Streptochaeta spicata	9.7
Henriettella fissanthera	8.1
Ficus americana	6.1
Cecropia membranacea	4.2

Table 4. *List of plant species postulated as potential keystone resources for frugivores in the Tinigua forests because they produce or are consumed during scarcity periods. Bold names indicate some extent of unripe consumption*

Species	*Consumer Specificity*	*Resource Reliability*	*Resource Production*	*Index*
Oenocarpus bataua	8	3	177.2	7.32
Cecropia membranacea	35	3	9.6	6.36
Bursera inversa	30	3	6.8	5.90
Ficus andicola	38	2	5.4	5.41
Gustavia hexapetala	5	3	56.4	4.80
Brosimum alicastrum	14	3	1.8	4.51
Ficus sphenophylla	41	1	1.9	4.48
Brosimum guianense	12	3	0.2	4.31
Iriartea deltoidea	5	3	27.7	4.26
Astrocaryum chambira	8	3	0	3.98
Apeiba aspera	4	3	6.9	3.79
Pseudolmedia obliqua	19	2	0.1	3.77
Brosimum utile	5	3	1.4	3.77
Ficus americana	30	1	8.9	3.72
Dialium guianense	3	3	0	3.58
Henriettella fissanthera	26	1	2.8	3.28
Ficus trigonata	6	2	24	3.16
Pourouma bicolor	10	2	1.7	3.07
Enterolobium schomburgkii	6	2	0.7	2.72
Ficus trigona	14	1	14.7	2.53
Hymenaea courbaril	2	2	0	2.38
Ficus guianensis	14	1	0.9	2.27
Doliocarpus multiflorus	14	1	0	2.25
Inga alba	11	1	0	2.01
Ocotea tomentosa	10	1	0	1.92
Spondias venulosa	7	1	11.5	1.90
Ficus schultesii	8	1	0	1.76
Ficus yoponensis	7	1	0	1.68
Ficus nymphaeifolia	6	1	1.3	1.62

I estimated their potential as keystone species, looking at the number of species known to feed on the fruits, their reliability during fruit scarcity periods, and their production during these periods. The potential for acting as a keystone species was ranked from 0 to 10 for each of these four parameters (from the values in table 4), so that the closer the value is to ten, the better the chance to play a keystone role (following Peres, 2000). I used the average value for the three parameters (specificity, reliability and production at fruit scarcity) to order the potential species from Tinigua in decreasing order given their potential as keystone species. I discarded parameters such as redundancy and overall abundance, because they were not contemplated in the original definition of plant keystone resources (Terborgh, 1983), and because they might obscure the actual ecological role of fruits on animal populations.

Oenocarpus bataua turned out to be the fruit species with highest rank. This palm species produced large amounts of fruit in the community every year, including some time in the scarcity period, and has been observed consumed by a relatively small coterie of consumers (8 species). The second most important species was a pioneer species, *Cecropia membranacea*, which also produced fruits every year at the beginning of the fruit scarcity period. Its production was small compared to palm species, but it is consumed by more frugivore species. The third species in this list, *Bursera inversa*, shared the same keystone traits as the former species. Nine fig species are present in the list, small-fruited figs (e.g. *F. andicola* and *F. sphenophylla*) being the most important, with large number of frugivores feeding on them, and relatively high fruit production. However, no particular fig species appears to be a reliable source producing fruits every year. *Gustavia hexapetala* produced fruits at the end of the fruit scarcity period every year, and its coterie of seed dispersers is restricted to large primates. Two *Brosimum* species were included in the list, and they were consumed mainly for their unripe fruits. Beside *O. bataua*, two other palm species were included in this list of potential keystone fruit resources (*Iriartea deltoidea* and *Astrocaryum chambira*). In spite of their high reliability in periods of fruit scarcity *Apeiba aspera* and *Hymenaea courbaril* did not rank high because they were consumed by a small set of frugivores, and their fruit production was not very high. *Doliocarpus multiflorus* showed a low reliability value probably because the main fruiting vine in the area died after the first study period. Several fruits heavily consumed by primate species such as *Gustavia hexapetala, Spondias venulosa*, and *Pourouma bicolor* produced fruits usually at the beginning or the end of the fruit scarcity period, and were seldom consumed by birds. *Pseudolmedia obliqua* tends to be very variable in its phenology and it does not always produce in scarcity periods. Two species were included in the list (*Henriettella fissanthera* and *Inga alba*) because of an unusual timing of fruit production during just one year. About one third of the species included in the list corresponded to plants that were consumed at least temporally for their unripe fruits, suggesting that these kinds of fruit sources might play important ecological roles during periods of fruit scarcity.

DISCUSSION

The roles of certain plant resources that are suggested to play keystone roles for frugivores in tropical forests have not been tested, mainly because there are practical limitations and ethical considerations in carrying out appropriate experimental designs. Previous studies have suggested that species producing fruits in periods of fruit scarcity can play important roles for the whole frugivore community, given that the energy that the forest is providing them is less than the energy the animals need (Terborgh, 1986). This approach has been used in studies, including this one, but in the absence of a rigorous test, conservation efforts to preserve frugivorous animals and the integrity of lowland tropical forests by means of managing suggested keystone resources could result in failure. This approach assumes that the redundant production during periods of fruit abundance results in a waste of energy that is not used by frugivores. However, there are several frugivores that are known to accumulate fat reserves during periods of fruit abundance [i.e. woolly monkeys (Di Fiore, 1997; Peres, 1994b; and see other contributions in this book)]. So far we do not know the relative importance of these reserves compared to the production of apparent keystone resources producing in fruit scarcity periods. There are also cases of primates that mainly use fruits to store enough fat during good seasons, which allow them to hibernate during the lean season (Fietz & Ganzhorn, 1999). If management policies allow harvest or logging of species producing fruits in periods of fruit abundance, there should be a threshold point at which a low maximum fruit production in the community could not allow fat storage and even these fruiting peak species could limit frugivore populations.

There is recent evidence suggesting that some rodent species are food limited, even during periods of resource abundance in the Neotropics (Adler, 1998). Furthermore, the high correlation between general fruit production and primate biomass in Neotropical forests (Stevenson, 2001), and the lack of a significant correlation between primate abundance and the density of potential keystone resources (such as figs and palms), point to the importance of the overall pattern of fruit production. With regard to primate behavior, it is a common strategy for the largest Atelines to increase movement patterns during periods of fruit abundance (possibly to locate more food) and to save energy in lean periods (e.g. Di Fiore, 1997; Stevenson et al., 2000; Strier, 1992). This strategy is also consistent with the idea that for these animals which constitute a large proportion of the frugivore biomass in undisturbed Neotropical forests, the production of fruit resources in periods of abundance is a limiting factor. Therefore, I suggest that even plant species producing fruits in periods of fruit abundance can be determinant factors for frugivore populations. Some other observations at Tinigua seem to support this argument.

For example, a large *Doliocarpus multiflorus* vine that was frequently visited by frugivores died from unknown causes in 1991. This species was one of the most important fruits in the overall diet of woolly monkeys during the first year of observations (Stevenson et al., 1994) because the monkeys consumed large amounts of fruits from one particular individual during the period of fruit scarcity. However, the disappearance of the vine did not cause any decrease in woolly monkey populations, which has actually increased after that event (Stevenson, 2002). It may seem naïve to expect that an individual could support the population of woolly monkeys. However, the point I wish to make is that in an analysis of potential keystone species based on consumption and timing of fruit production for that year, *D. multiflorus* would have scored high, yet its removal did not alter the population densities of its consumers. Therefore at least two questions should stay in the minds of people trying to use these assessments for conservation purposes: 1.) Does the applicability of a keystone role depend on the sampling year in a particular system? And, 2) Should we really expect changes in the community from the removal of these uncommon resources? Although these cases are non-replicated and uncontrolled events, this case suggests again that other factors could be more important for the maintenance of the frugivore community in periods of fruit scarcity. These factors may include the acquisition of fat reserves from common species at periods of abundance, as well as non-fruit resources producing food at scarcity periods (e.g. Figure 2, Stevenson et al., 2000). Among these resources young leaves of several tree and vine species, as well as flowers of *Astrocaryum chambira* seem to be most important in the Tinigua community.

Several authors have suggested restricting the use of the term keystone species to resources that are not common or abundant (Mills et al., 1993). However, if overall abundance were included in the analysis made in table 4, species such as *Oenocarpus bataua* and *Gustavia hexapetala*, that are dense in the area and heavily consumed by primates during periods of fruit shortage would not rank high in the scores as potential important keystone species. Both species are known to be among the most important fruit sources for the most abundant frugivorous primates, which comprise the largest component of the vertebrate community in terms of biomass. Therefore, it seems logical to imagine that the removal of these resources from the community could have profound negative influences on the primates, perhaps more drastic than other sources with higher scores. In conclusion, I think that in the search of keystone species, low scores should not be given to species just for being abundant, if the main purpose is to protect important resources for frugivore populations.

A recent review identifying keystone plants in Neotropical forests (Peres, 2000) used redundancy and abundance as criteria to rank keystone species. An analysis including such factors turned out to show different results compared to those presented here (data not shown). For example, no palm or fig species would have ranked among the top five species, mainly because the palm species considered here are relatively abundant, and they produce fruits outside the scarcity period as well (Fig. 1). The absence of fig species within the most important species was in part because they also produce fruits at different seasons.

How Useful is the Keystone Resources Concept in the Conservation of Tropical Forests?

Given the difficulties involved in testing keystone roles, I consider that the concept is of limited use in the conservation of complex tropical forests. An approach looking at fruit production patterns and feeding behavior can certainly provide an idea of the resources that provide energy and nutrients to frugivores.

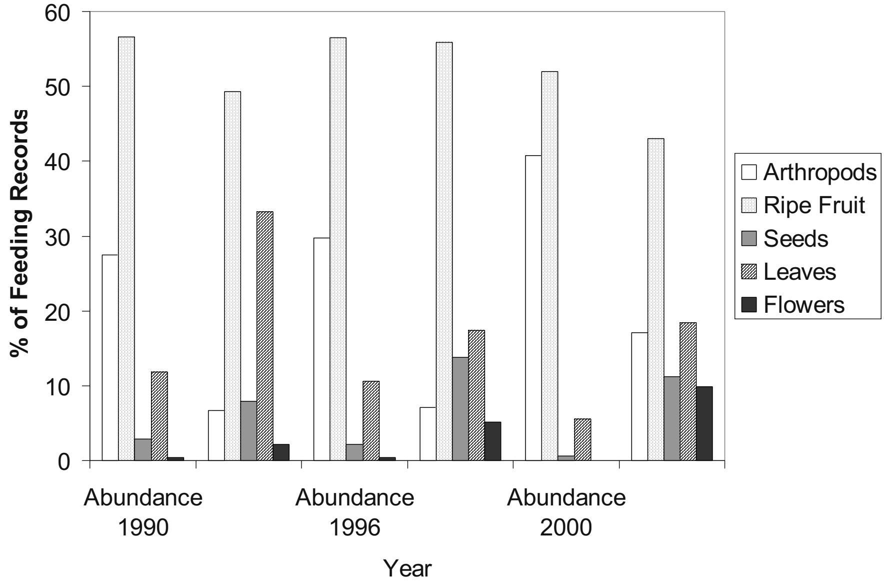

Figure 2. *Comparison in diet composition of woolly monkeys in Tinigua Park between periods of fruit scarcity and fruit abundance at three different study years.*

The preservation of common fruits and resources used during fruit scarcity may be a good approach to increase the chances of survival of the animals that feed on them. However, the persistence of the suggested keystone resources does not guarantee the integrity of the community if other resources are depleted.

Only three of the 29 species producing fruit in periods of scarcity at Tinigua were included in a review of potential keystone plant resources in other Neotropical forests (Peres, 2000). The majority of the plant species present at Tinigua have wide distributions, including Central America and peripheral Amazonia (Stevenson in prep.), so the disparity in keystone roles suggest that potential keystone resources may vary from place to place. For example, *Gustavia hexapetala*, the main fruit source for woolly monkeys at Tinigua, is not very important in the diet of these monkeys at other areas (Defler & Defler, 1996; Dew, 2001; Di Fiore, 1997; Difiore, 2001; Peres, 1994a), even though this plant species is also present at those localities.

Some palm species such as *Oenocarpus bataua,* that have been postulated as keystone species, seem to play important ecological roles in other neotropical forests (Peres, 2000), but the proportion of fruit consumers that these species have is low compared to other resources (8 vs. up to 41 species). The conservation of this palm species would probably not guarantee the survival of a diverse set of frugivores, and even the most abundant frugivore species such as the woolly monkeys will not be particularly benefited by such a management protocol.

Figs, especially small-fruited species, are visited by a large variety of frugivores, and as a group fig species tend to be present during periods of fruit scarcity (Table 2). The fact that different fig species have been postulated as keystone resources in different habitats suggests that the variability in their fruiting patterns is responsible for the keystone label when they produce during fruit scarcity periods. Fig species as a group fit the criteria of keystone plant resources. But it is puzzling why there is no positive correlation between the density of fig species and the abundance of primates in Neotropical forests (Stevenson, 2001). We found that some of the fig species that were heavily consumed during periods of fruit scarcity were completely ignored when there were other fruits available, and this low fruit preference has been found at other tropical sites (Conklin & Wrangham, 1994). This pattern of preference might be associated to low energetic contents compared to other fruits, and also argue against their potential value as keystone resources (Gautier-Hion & Michaloud, 1989). In this sense it would be interesting to know the energetic and nutrient value of figs compared to other plants with low energetic contents that are consumed in scarcity periods, such as young leaves and unripe fruits. In fact, the most consistent pattern of consumption during fruit scarcity periods, at least for primates, was feeding on young leaves and unripe fruits, suggesting that these resources are important components in the strategy to overcome fruit shortage (Stevenson et al., 2000).

There are some inherent characteristics in the life history of figs and the palm species postulated as plant keystone resources that predispose them to be consumed during periods of fruit scarcity. First, the specialized pollination system of fig by fig wasps requires multiple fruiting episodes each year to assure that the wasps will find fruiting trees in the community to lay eggs (Anstett et al., 1997). Thus, pollination system might be the cause of fruit production in periods of scarcity, perhaps independent of animal consumption and seed dispersal processes. On the other hand, most of the palm species postulated as keystone resources have large fruits which usually take longer periods to develop. Part of their importance as keystone resources, at least in Tinigua, was associated with the consumption of unripe fruits during the scarcity period (i.e. *Astrocaryum chambira, Oenocarpus bataua, Socratea exorrhiza*, and *Syagrus sancona*). If the benefit associated with seed dispersal at the start of the rainy period, when seedlings usually find better conditions for development (Garwood, 1982), applies to palm species, then there is a high probability of finding unripe fruits in scarcity periods prior to the rains. It remains to be seen if their consumption depends more on seasonal production than on nutritional factors in a variety of tropical forests.

Some other fruit sources suggested as keystone resources in this study, such as *Henriettella fissanthera* and *Inga alba*, fruited in the scarcity period only as exceptions to what seems to be their common fruiting patterns from more extensive records than those reported here. I do not know the causes for these deviations, but if they were due to unpredictable factors or chance effects, it is expected that opportunistic cases of this kind would be more frequent in diverse plant communities. Therefore we should include a potential stochastic factor in the sustainability of frugivore communities derived from the overall pattern of plant diversity.

REFERENCES

Adler, G. H. (1998). Impacts of resource abundance on populations of a tropical forest rodent. *Ecology,* 79, 242-254.

Angulo, M. A. (2001). Determinación del rango de hogar y patrones de actividad de una manada de monos ardilla (*Saimiri sciureus*) en el Parque Nacional Natural Tinigua. *Departamento de Ciencias Biológicas*. Universidad de Los Andes, Bogotá, Colombia.

Anstett, M. C., HossaertMcKey M. & McKey, D. (1997). Modeling the persistence of small populations of strongly interdependent species: Figs and fig wasps. *Conservation Biology* 11, 204-213.

Bender, E. A., Case T. J. & Gilpin, M. E. (1984). Perturbation Experiments in Community Ecology - Theory and Practice. *Ecology,* 65, 1-13.

Conklin, N. L. & Wrangham, R. W. (1994). The Value of Figs to a Hind-Gut Fermenting Frugivore - a Nutritional Analysis. *Biochem. Syst. Ecol.,* 22, 137-151.

Defler, T. R. & Defler, S. B. (1996). Diet of a group of *Lagothrix lagothricha lagothricha* in Southeastern Colombia. *International Journal of Primatology*, 17, 161-189.

Dew. L. (2001). Synecology and Seed Dispersal in Woolly Monkeys (*Lagothrix lagotricha poeppigii*) and Spider Monkeys (*Ateles belzebuth belzebuth*) in Parque Nacional Yasuni, Ecuador. PhD dissertation, University of California, Davis.

Di Fiore, A. F. (1997). Ecology and behavior of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*, Atelinae) in Eastern Ecuador. PhD dissertation, University of California, Davis.

Di Fiore, A. (2001). Ranging behavior and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha*). *American Journal of Physical Anthropology*, suppl. 32, 59-59.

Fietz, J. & Ganzhorn, J. U. (1999). Feeding ecology of the hibernating primate *Cheirogaleus medius*: how does it get so fat? *Oecologia*, 121, 157-164.

Fincke, O. M., Yanoviak, S. P. & Hanschu, R. D. (1997). Predation by odonates depresses mosquito abundance in water- filled tree holes in Panama. *Oecologia*, 112, 244-253.

Garwood, N. (1982). Seasonal rythm of seed germitation in a semideciduous forest. In E. G. Leigh Jr., A. S. Rand & D. M. Windsor (Eds.), *the Ecology of a Tropical Forest* (pp. 173-185). Washington DC: Smithsonian Institution Press.

Gautier-Hion, A. & Michaloud, G. (1989). Are Figs Always Keystone Resources for Tropical Frugivorous Vertebrates - a Test in Gabon. *Ecology*, 70, 1826-1833.

Howe, H. F. (1977). Bird Activity and Seed Dispersal of a Tropical Wet Forest Tree. *Ecology*, 58, 539-550.

Janson, C. H. (1984). Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). *Journal of Comparative Ethology,* 65, 177-200.

Janson, C. H. & Emmons, L. H. (1990). Ecological Structure of teh nonflying mammal community at Cocha Cashu biological station, Manu National Park, Peru. In A. Gentry (Ed.). *Four neotropical rainforests* (pp. 314-338). New Haven: Yale University Press.

Mills, L. S., Soule M. E. & Doak, D. F. (1993). The Keystone-Species Concept in Ecology and Conservation. *Bioscience*, 43, 219-224.

Paine, R. T. 1969. Pisaster-Tegula Interaction - Prey Patches, Predator Food Preference, and Intertidal Community Structure. *Ecology*, 50, 950-961.

Peres, C. A. (1994a). Diet and Feeding Ecology of Gray Woolly Monkeys (*Lagothrix lagotricha cana*) in Central Amazonia - Comparisons With Other Atelines. *International Journal Primatology*, 15, 799-799.

Peres, C. A. (1994b). Which are the largest New World monkeys? *Journal of Human Evolution*, 26, 245-249.

Peres, C. A. (2000). Identifying keystone plant resources in tropical forests: the case of gums from *Parkia* pods. *Journal of Tropical Ecology*, 16, 287-317.

Power, M. E., Matthews, W. J. & Stewart, A. J. (1985). Grazing minnows, piscivorous baass and stream algae: dynamics of a strong interaction. *Ecology*, 66, 1448-1456.

Power, M. E. & Mills, L. S. (1995). The Keystone Cops Meet in Hilo. *Trends in Ecology and Evolution*, 10, 182-184.

Stevenson, P. R. (2001). The Relationship between fruit production and primate abundance in Neotropical forests. *Biological Journal of the Linnean Society*, 72, 161-178.

Stevenson, P. R., Quiñones, M. J. & Ahumada, J. A. (2000). Influence of fruit availability on ecological overlap among four neotropical primates at Tinigua National Park, Colombia. *Biotropica*, 32, 533-544.

Stevenson, P. R. (2002). Frugivory and Seed Dispersal by Woolly Monkeys at Tinigua Park, Colombia. PhD. dissertation. Dept. of Anthroppology. SUNY at Stony Brook.USA.

Strier, K.B. (1992). Atelinae Adaptations - Behavioral Strategies and Ecological Constraints. *American Journal of Physical.Anthropology*, 88, 515-524.

Terborgh, J. (1986). Keystone plant resources in the tropical forests. In M. E. Soule (Ed.). *Conservation Biology: The Science of Scarcity and Diversity* (pp. 330-344)., Sunderland, MA: Sinauer.

Terborgh, J., Lopez, L., Nunez, P., Rao, M. Shahabuddin,,G., Orihuela, G., Riveros, M., Ascanio, R. Adler, G. H. Lambert, T. D. & Balbas, L. (2001). Ecological meltdown in predator-free forest fragments. *Science*, 294, 1923-1926.

Terborgh, J. & van Schaik, C. P. (1987). Convergence vs. nonconvergence in Primate Communities. In J. H. Gee, & P. S. Giller (Eds.). *Organization of Communities, Past and Present* (pp. 205-226). Oxford: Blackwell Scientific Publications.

van Schaik, C. P. & Pfannes, K. (2002). Tropical Climates and Phenology: a primate perspective (in press).

van Schaik, C. P., Terborgh, J. & Wright, S. J. (1993). The Phenology of Tropical Forests - Adaptive Significance and Consequences for Primary Consumers. *Annual. Review of Ecology and Systematics*, 24, 353-377.

Department of Anthropology. SUNY at Stony Brook. Stony Brook, NY 11794-4364. USA