Identifying keystone plant resources in tropical forests: the case of gums from *Parkia* pods

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ABSTRACT. Keystone plants that produce seasonally critical trophic resources comprise one of the main classes of keystone species, yet no studies have attempted to examine the ecological attributes that might help us recognize them and evaluate their importance in species-rich plant assemblages. In this paper the concept of keystone plant resources is reviewed using potential candidates proposed in the literature for neotropical forest sites. A poorly known example of a potential keystone resource—the gums produced by mature pods of two emergent tree species (*Parkia nitida* and *P. pendula*, Leguminosae: Mimosoideae)—is described for primates and other arboreal vertebrates in Amazonian forests. In particular, the fruiting phenology, tree density, patterns of vertebrate consumption, and nutritional quality of *Parkia* gums in Amazonian *terra firme* forests are considered. Putative neotropical keystone resources are then divided into four intersecting ecological attributes defining their community-wide importance to vertebrate frugivores: (1) temporal redundancy, (2) degree of consumer specificity, (3) reliability, and (4) abundance. From a vertebrate perspective, keystone plants are here defined as those producing reliable, low-redundancy resources that are consumed by a large proportion of the bird and mammal assemblage with which they coexist. Plant populations proposed to date as keystone species range widely across two of these four variables, which may disqualify most putative taxa (including *Parkia* spp.) from a more formal definition of keystone resources. Other importance attributes, the context-dependent role, the taxonomic refinement, and removal effects of the keystone plant resource concept as applied to tropical forests are also discussed.

KEY WORDS: Amazonia, consumer specificity, fruiting seasonality, gums, keystone resources, keystone species, *Parkia nitida*, *Parkia pendula*, redundancy

INTRODUCTION

Tropical forest keystone plant resources include the fruits, seeds, flowers, floral nectar, and bark produced by a small set of species in a local flora which serve a disproportionately large trophic importance to a loosely defined group of

consumers (Terborgh 1986a, b). The tree, woody liana, or epiphyte taxa providing such resources are thus often described as 'pivotal species' (Howe 1977) or 'keystone mutualists' (Gilbert 1980) in that they may exert a major influence on vertebrate community organization in these ecosystems. It has, therefore, become widely accepted that selective removal of keystone resources may drastically reduce forest carrying capacity for frugivores and seed predators (Howe & Westley 1988, Whitmore 1990), which comprise the bulk of the vertebrate biomass in both paleotropical (Gautier-Hion *et al.* 1985) and neotropical forests (Peres 1999, Terborgh 1983). This, in turn, could lead to a cascade of population declines, if not local extinctions, at both lower and higher trophic levels, including plant mutualists (i.e. seed dispersers and pollinators) and top predators depending directly or indirectly on keystone resources (Howe 1984, Leighton & Leighton 1983, Terborgh 1992).

Keystone plants comprise one of the most frequently discussed classes of keystone species, which in the last decade has become a popular paradigm in conservation ecology among environmental managers and policy makers (Bond 1993, Menge *et al.* 1994, Mills *et al.* 1993, Paine 1995, Power & Mills 1995, Power *et al.* 1996). Yet there have been few detailed studies of the population ecology of potential keystone species, and how to recognize them in species-rich plant assemblages (Howe 1993, Simberloff 1998). Beyond the textbook doctrine, the concept of keystone plant resources (hereafter, KPRs) continues to evade a more formal definition with respect to their community-wide implications to tropical forest dynamics. Although most reports agree that keystone resources have a pervasive influence on community composition, the presumed ecological consequences of subtracting different types of KPRs from tropical forests have at best been ambiguous since the earliest applications of this concept (Gilbert 1980, Howe 1977, Terborgh 1986a). There is little agreement as to how many consumer species in a faunal assemblage a plant part must serve during critical times of the year before it can be characterized as a keystone resource. For instance, the 'keystone-ness' property of a resource has been detected in studies focused on as few as one or two consumer species (e.g. Overdorff 1992, van Roosmalen 1985a). There is also little agreement as to how important a plant resource must be for a consumer assemblage before it can be defined as a KPR. Indeed, KPRs have been described from as absolutely indispensable to apparently rather superfluous, illustrating the prevailing difficulties in evaluating the strength of interactions that might help to assess the substitution value of these resources in species-rich plant communities. For example, potential keystone resources may range from epiphytic and arborescent figs (*Ficus* spp.), which once removed could lead to generalized 'ecosystem collapse' (Terborgh 1986a, p. 339), to fruits of various non-fig trees and vines, which may not be considered as 'true keystone resources because they are eaten by only a few species, are potentially substitutable' (Terborgh 1986b, p. 379), and 'in their absence, the community would probably survive intact'

(Terborgh 1986a, p. 339). Removal or extinction of keystone plants may or may not, therefore, 'profoundly change the competitive relationships, and consequently the relative abundances, of other species in a community' (Howe & Westley 1988, p. 218). Indeed, it remains unclear whether any single plant species in a high-redundancy system such as a species-rich tropical forest can in fact produce a critical keystone resource without which a significant component of the frugivore diversity or biomass would collapse. Such systems have been described as 'species-deletion stable' (*sensu* Pimm 1980) because their patterns of web connectance in the absence of a critical resource may usually allow alternative pathways through which energy from producers can continue to flow to primary consumers, even during seasons of resource scarcity. Moreover, this notion is further confounded because different KPRs have been proposed in a wide range of contexts regarding their degree of taxonomic refinement, specificity of consumer interactions, concurrent availability of alternative resources, long-term reliability to consumers, and *per capita* importance in relation to their patch density, thus weakening the heuristic value of this concept.

In this paper I provide a review of putative KPR candidates proposed to date for neotropical forests, and discuss the empirical evidence for their importance to vertebrate consumers. In order to illustrate the concept, I begin by describing a poorly known example of a potential keystone resource in Amazonian forests: the gums produced by mature pods of two legume congeners—*Parkia pendula* (Willd.) Benth. ex Walp. and *Parkia nitida* Miq. Keystone plants are then divided primarily into four major intersecting ecological gradients defining their relative importance to consumers: temporal redundancy, degree of consumer specificity, reliability, and abundance. Gums from *Parkia* pods and other neotropical KPR candidates are then discussed in terms of how they fit this more formal definition.

NATURAL HISTORY OF *PARKIA PENDULA* AND *P. NITIDA*

Parkia (Leguminosae: Mimosoideae) is a pantropical genus of mostly large canopy or emergent trees with centres of distribution in South American, African and Southeast Asian forests (Hopkins & Hopkins 1983). Most species are easily distinguished by their highly attractive, double inflorescences and imbricate calyx-lobes. In most of the 18 species of neotropical *Parkia* (Hopkins 1986), the fruit is a two-valved leathery or woody pod with a short stipe, which may or may not produce sticky gums. The pod may be dehiscent or indehiscent along one or both of the sutures, and contain up to 35 seeds. As many as five species of *Parkia* may occur within a single square-kilometre of non-flooded (= terra firme) forest of central-western Amazonia (Hopkins 1986, C. Peres, *pers. obs.*). This discussion focuses on two widespread and relatively common *Parkia* species—*Parkia pendula* (section *Platyparkia*) and *Parkia nitida* (section *Parkia*)— that produce pods associated with copious amounts of highly viscous gums.

Parkia pendula and *P. nitida* are bat-pollinated canopy or emergent trees of
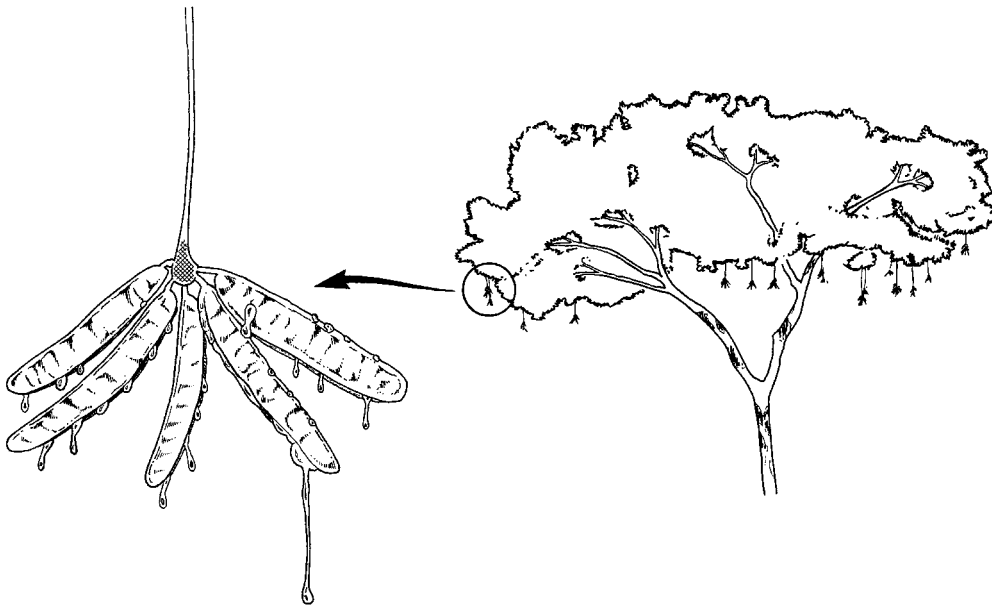
Figure 1. *Parkia pendula* tree showing mature pods hanging well below the flattened crown by their receptacles and long, pendent peduncles. Pods of this species are dehiscent, and produce copious amounts of a highly viscous, externally presented hydrosoluble gum in which the seeds become immersed and available to arboreal vertebrates.

up to 50 m of widespread distribution in Amazonian terra firme forests. In *P. pendula*, the compound inflorescence develops from a bud on a horizontal branch resulting in long, pendent peduncles securing pods that hang well below the large, umbrella-shaped or flattened crowns (Figure 1). In *P. nitida*, mature pods tend to hang in clusters near the edge of the somewhat flattened crown. Mature pods of both species produce large quantities of translucid gums during an extended fruiting period that includes most of the dry season, although the fruiting events of each species may not always synchronize from year to year (C. Peres, *pers. obs.*).

The subligneous pods of *P. pendula* (18–30 cm long) are dehiscent at maturity, producing large amounts of a clear, gelatinous gum which becomes available externally after the adaxial suture of the pod partially opens (Hopkins 1986). In contrast, the amber-coloured sticky gum of *P. nitida* is produced internally filling the pod cavity around the seeds, which remain protected by the tough, coriaceous pod walls (30–40 cm long) that do not dehisce upon maturity. Seeds of *P. pendula* (17–25 seeds/pod) are gradually released into the gum that remains adhered to the semi-dehisced pod walls (Figure 1), while those of *P. nitida* (15–24 seeds/pod) are retained within the sealed seed cavities filled with gum. Pods in both species do not fall to the ground at maturity, and remain attached for several months to the tree crown by their elongated peduncles. However, pods of *P. pendula* still containing a fair amount of gum

eventually become available to terrestrial vertebrates after falling to the ground while still attached to the receptacle and peduncle. Because of differences in pod structure, gums of *P. pendula* may be initially harvested by arboreal vertebrates capable of either reaching or reeling in the suspended pods, but those of *P. nitida* become accessible only to larger frugivores capable of tearing the tough pod walls. This correlates with the small seeds of *P. pendula* (seed size = 7–11 × 4–6 mm; seed weight = 0.06–0.11 g), which are ten fold lighter than those of *P. nitida* (20–28 × 8–11 mm; 0.6–1.0 g) (Hopkins 1986). Mature seeds in both species are covered by a thick, hard testa showing a conspicuous horseshoe line, which can be easily distinguished on seeds that have been ingested and defecated by arboreal seed dispersers, such as primates (C. Peres, unpubl. data).

Parkia gums as keystone resources in Amazonian forests

Because of their geographic distribution, the importance of *Parkia* pod gums to frugivores is potentially widespread (15°N–12°S) throughout neotropical forests. *P. pendula* is the most widely distributed *Parkia* species, occurring in lowland terra firme forests from Honduras southwards to Colombia, Venezuela, the Guianas, Amazonian Brazil, Peru and Bolivia, and southeast coastal Brazil up to elevations of 500 m (Hopkins 1986). *P. nitida* occurs from southern Panama, and throughout Amazonia and eastern Venezuela up to elevations of 1200 m. These two species are also the most common *Parkia* species found in Amazonian forests, and exhibit the lowest degree of habitat specificity. Although both species are found primarily in terra firme forests, which account for over 95% of Amazonia, *P. nitida* also occurs in forests seasonally flooded by white-water (*várzea*) (Hopkins 1986), and *P. pendula* is surprisingly flood-tolerant (Scarano & Crawford 1992).

The importance of these *Parkia* species to arboreal vertebrates is illustrated by observations over a continuous 2-y field study at a typical undisturbed terra firme forest of central-western Brazilian Amazonia, the Urucu Forest (Peres 1993a, b, 1994a, b). A total of 21 fruiting *P. pendula* (diameter at breast height, DBH = 61–101 cm) and 19 *P. nitida* trees (DBH = 58–123 cm) were known to occur within a forest area of 200 ha, overlapping an extensive 100-m × 100-m trail grid that was intensively monitored by three independent observers over 21 consecutive months. This amounts to an overall density of 10.5 fertile trees km^{-2} for *P. pendula* and 9.5 trees km^{-2} for *P. nitida*. The pod gums of both *Parkia* species at this site comprised 11.0% (n = 3481 feeding records) and 10.3% (n = 4477 feeding records) of the year-round time spent feeding on plant material by small-bodied primates such as saddle-back (*Saguinus fuscicollis avilapiresi*; mean adult body mass = 0.39 kg) and moustached tamarins (*Saguinus mystax pileatus*; body mass = 0.52 kg), respectively (Peres 1993a), In these terms, *P. pendula* and *P. nitida* were by far the most important of the 174 plant species recorded in the diet of these species, particularly during the 4 mo of lowest fruit availability in this forest, which largely coincided with the dry season
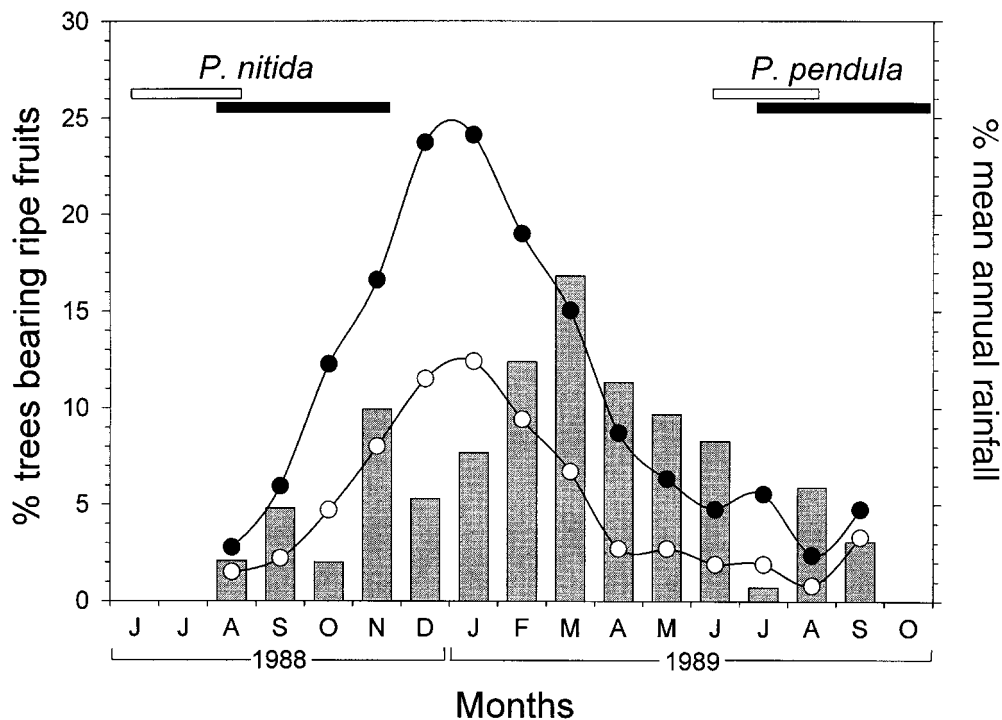
Figure 2. Community-wide fruit phenology at the Urucu forest based on a random set of trees monitored during 14 consecutive months. Solid and open circles indicate the percentage of tree species (n = 253 species) and tree crowns (n = 996 trees ≥ 10 cm in DBH) bearing ripe fruits, respectively (data are unavailable for June–July 1988 and October 1989). Shaded bars represent the proportion of mean annual rainfall during each month of study. Horizontal bars show the availability periods of young seeds (open bars) and gums (solid bars) from mature pods of *Parkia nitida* and *P. pendula*, which largely corresponded to the dry season when few non-*Parkia* fruits were available.

(Figure 2). During those months, *Parkia* gums clearly dominated the diet of the two tamarin species (16–56 and 19–58% of the feeding time of *S. fuscicollis* and *S. mystax*, respectively) and on complete days of observation were often the only plant material ingested by either species, in contrast to their relatively diverse plant diet at other times of the year (as many as 24 fruit species per day during the late wet season). Gums of *P. pendula* were exploited in the canopy while tamarins clung by their hindlimbs to the elongated peduncles, whereas those of *P. nitida* were usually exploited near the ground from pods hanging in the understorey vegetation and still containing some gum, but only after they had been torn open and discarded by larger primates feeding in the tree crown.

Consuming the gums of *Parkia nitida* also comprised 5.9% (n = 3298 feeding records) of the time spent feeding by woolly monkeys (*Lagothrix lagotricha cana*; mean body mass = 8.7 kg) over an 11-mo study at the same site (Peres 1994b). In contrast to tamarins, this large-bodied species fed in the upper crowns by licking the suspended pods after they had been reeled in and torn open. This

was by far the most important of a total of 225 plant species recorded in the diet of woolly monkeys at this site, which included fruits from at least 193 species. *P. nitida* accounted for 39% of the time spent feeding by woolly monkeys during the early dry season when few alternative animal-dispersed fruits were available (Figure 2); the remainder of their diet consisted almost entirely of young leaves and unripe seeds (Peres 1994b). *P. nitida* trees often served as predictable convergence points for the otherwise uncohesive large groups of woolly monkeys, suggesting a high *per capita* value for large trees as sources of gums. Indeed, the distribution of large *P. nitida* trees was congruent with much of the dry season foraging activity of woolly monkeys, which largely determined their ranging patterns at this time of year (Peres 1996a). In contrast, the dietary importance of *P. pendula* gums to woolly monkeys was substantially lower; they allocated only 4–6% of their feeding time to these resources, which comprised less than 1% of their year-round feeding time.

It could be argued that the 'importance' of *Parkia* gums in the dry-season diet of tamarins and woolly monkeys, as quantified in terms of time spent feeding, might be simply attributed to the fact that these food items were highly palatable (the 'candy' hypothesis) or difficult to extract from the pods (the handling time hypothesis). However, the extremely low availability of alternative fruit species at this time of year (Figure 2; Peres 1994a); the highly positive year-round correlation between fruit availability and dietary diversity for both of these primate genera (Peres 1991, 1993a, 1994b); and the fact that gums were readily available on pods visited by these monkeys (high ingestion rate per unit time) all suggest that their single-minded focus on *Parkia* gums was primarily driven by necessity. Indeed, adults of both tamarins and woolly monkeys are known to lose a significant proportion of their body weight during the 'lean' times of the year in Amazonian forests (Goldizen *et al.* 1988; Peres 1994b, unpubl. data), despite their use of such 'safe net' resources.

Parkia pod gums also comprised an important component of the dry-season diet of several other arboreal and terrestrial vertebrate species at Urucu observed less intensively than tamarins and woolly monkeys (Table 1). Young seeds and gums from *Parkia* pods were one of the most important dry-season food items for midsized primates, such as buffy saki monkeys (*Pithecia albicans*: Peres 1993b) and brown capuchin monkeys (*Cebus apella*: Peres 1994a, unpubl. data). While pods still attached to the crown were often exploited primarily by primates and large parrots (e.g. *Amazona* spp., *Ara* spp.), those fallen to the ground or lodged in understorey vegetation were used by ungulates (brocket deer, *Mazama* spp., peccaries, *Tayassu* spp.) and caviomorph rodents (agoutis, *Dasyprocta fuliginosa*) (C. Peres, *pers. obs.*; R. Nonato, *pers. comm.*).

At least one other *Parkia* species—*P. multijuga*—also occurred in the Urucu forest, but the tough pods of this species did not produce gums, dropped to the ground upon maturity, and were often opened by scatter-hoarding terrestrial mammals (e.g. agoutis) or larger seed predators such as collared peccaries,

Tayassu tajacu (C. Peres, *pers. obs.*). Indeed immature *P. multijuga* pods still attached to the tree were handled primarily by canopy granivores, including large parrots, saki monkeys, and woolly monkeys (Table 1), which preyed upon the large unripe seeds contained within developing pods.

The importance of Parkia at other sites

The widespread importance of *Parkia* fruit resources to Amazonian primates has been confirmed by extensive supplemental observations during multiple primate censuses conducted elsewhere in western Amazonia over the last 12 y (Peres 1997), as well as several independent reports on the use of *Parkia* gums by forest frugivores. That *Parkia* pod gums appear to be primarily exploited by primates probably reflects handling and access constraints resulting from the tough pod structure and presentation well below the crown, a sampling bias towards primate field studies, and the ease with which diurnal primate diets can be documented in detail during dawn to dusk observations on habituated groups.

The reports summarized in Table 1 clearly show the enormous seasonal importance of *P. pendula* and *P. nitida* pods to a relatively small set of vertebrate frugivores in Amazonian forests. Large psittacids (parrots and macaws) and primates appear to be the major groups of consumers harvesting *Parkia* seeds or gums either because they are capable of reaching the pods presented away from the foliage, or overcoming the tough pod walls in the case of *P. nitida*. As a consequence, viable seeds (tested by germination trials: C. A. Peres, unpubl. data) of *P. pendula* and *P. nitida* are passed through and dispersed by mostly small and large primates, respectively. This is confirmed by observations in central Surinam where golden-handed tamarins (*Saguinus midas midas*) and spider monkeys (*Ateles paniscus*) consume gums and disperse seeds of *P. pendula* and *P. nitida*, respectively, although the small seeds of the former are also dispersed by spider monkeys (M. van Roosmalen 1985a, *pers. comm.*). The seasonal importance of *Parkia* gums to this relatively small set of vertebrate species can be seen from the degree to which they single-mindedly concentrate on those resources during the dry season. However, this may simply reflect the scarcity of alternative resources rather than a preference for *Parkia* gums *per se*, as a more balanced, mixed diet would probably confer greater fitness benefits either in terms of nutritional complementarity or dilution of secondary metabolites (Bernays *et al.* 1994, Freeland & Janzen 1974). Moreover, *Parkia* trees at Urucu comprised some of the largest and least depletable food patches exploited by tamarins and woolly monkeys, and hosted feeding bouts which were on average longer than those at other times of the year (Peres 1996a, b). Unlike most other dry season food sources, *Parkia* trees accommodated the largest feeding group sizes and were exploited in the apparent absence of intra-group interference competition, which was relatively common within smaller food patches. Moreover, *P. pendula* and *P. nitida* trees are relatively common

Table 1. Documented use of *Parkia* fruit resources by neotropical forest vertebrates.

Parkia species	Item[1] taken	Period[2] taken	Vertebrate consumers	Forest site, country	Source
P. nitida	PG	Jun–Nov	*Saguinus fuscicollis avilapiresi* *Saguinus mystax pileatus* *Cebus apella, Pithecia albicans* *Lagothrix lagotricha, Nasua nasua* *Dasyprocta fuliginosa* *Tapirus terrestris*	Urucu, Brazil	Peres (1993a, b; 1994a, b; *pers. obs.*)
P. nitida	YS	Jun–Aug	*Ara* spp., *Amazona* spp. *Deroptyus accipitrinus* Cebus apella, Pithecia albicans Lagothrix lagotricha	Urucu, Brazil	Peres (1993a, b; 1994a, b; *pers. obs.*)
P. nitida	PG	Nov	*Saguinus m. mystax* *Lagothrix lagotricha*	Seringal Altamira, Brazil	C. Peres, *pers. obs.*
P. nitida	PG	Nov	*Saguinus m. mystax*	Barro Vermelho, Brazil	C. Peres, *pers. obs.*
P. nitida	PG	Dec	*Cebus apella*	Riozinho, Brazil	C. Peres, *pers. obs.*
P. nitida	PG	Oct–Nov	*Ateles p. paniscus*	Raleighvallen, Surinam	van Roosmalen (1985a)
P. nitida[3]	PG	Jul–Dec	*Saguinus fuscicollis illigeri* *Cebuella pygmaea*	Cahuana Island, Peru	Soini (1987), P. Soini, *pers. comm.*
P. nitida[3]	PG	Jul–Sep	*Saguinus nigricollis*	Rio Caquetá, Colombia	Izawa (1978)
P. nitida[3]	YS	Jul–Sep	*Pithecia monachus* *Alouatta seniculus* *Lagothrix lagotricha*	Rio Caquetá, Colombia	Izawa (1975)
P. nitida[3]	PG	Jun–Jul	*Saguinus fuscicollis nigrifrons* *Saguinus m. mystax*	Rio Blanco, Peru	Garber (1993)
P. nitida[3]	PG	May–Sep	*Saguinus fuscicollis nigrifrons* *Saguinus m. mystax* *Cacajao calvus ucayalii*	Quebrada Blanco, Peru	Monge (1987), Castro (1991), Heymann (1990)
P. nitida[3]	PG	Jul–Oct	*Cebuella pygmaea*	Manití, Peru	Soini (1988)
P. pendula	PG	Jul–Oct	*Saguinus fuscicollis avilapiresi* *Saguinus mystax pileatus* *Cebus apella, Pithecia albicans* *Lagothrix lagotricha, Nasua nasua* *Dasyprocta fuliginosa, Mazama* spp.	Urucu, Brazil	Peres (1993a, b; 1994a, b; *pers. obs.*)
P. pendula	PG	Aug–Sep	*Saguinus fuscicollis avilapiresi* *Saguinus mystax pileatus*	Lago Uauaçú, Brazil	M. van Roosmalen & C. Peres, unpubl. data
P. pendula	YS	Jun–July	*Amazona* spp., *Ara* spp. *Pionites leucogaster, Pionus menstruus* *Cebus apella, Lagothrix lagotricha*	Urucu, Brazil	Peres (1994a), *pers. obs.*
P. pendula	PG	Sep–Nov	*Callithrix humeralifer*	Dardanelos, Brazil	Rylands (1981)
P. pendula	PG	Sep–Nov	*Callithrix kuhlii* *Leontopithecus chrysomelas*	Lemos Maia, Brazil	Rylands (1983)
P. pendula	PG	?	*Saguinus m. midas* *Ateles p. paniscus*	Raleighvallen, Surinam	M. van Roosmalen (1985b), *pers. comm.*
P. pendula	PG	Jul–Aug	*Saguinus fuscicollis weddelli* *Callithrix emiliae*	Samuel, Brazil	Lopes & Ferrari (1994)
P. pendula	PG	Jul–Sep	*Saguinus fuscicollis weddelli* *Saguinus labiatus labiatus*	Cocamita, Bolivia	Buchanan-Smith (1991)
P. pendula	PG	Aug	*Saguinus fuscicollis melanoleucus*	Penedo, Brazil	C. Peres, *pers. obs.*
P. pendula	PG	Oct–Nov	*Callithrix jacchus, Alouatta belzebul*	Pacatuba, Brazil	Bonvicino (1989)
Parkia sp.		Mar–Oct	*Saguinus fuscicollis nigrifrons* *Saguinus m. mystax*	Quebrada Blanco, Peru	Monge (1987), Castro (1991)
P. multijuga	PG	Dec	*Saguinus b. bicolor*	Manaus, Brazil	Egler (1992)

Table 1. (*cont*.)

Parkia species	Item[1] taken	Period[2] taken	Vertebrate consumers	Forest site, country	Source
P. multijuga	PG	Feb	*Lagothrix lagotricha*	Caparú, Colombia	Defler & Defler (1996)
P. multijuga	PG	Feb	*Ara ararauna, Lagothrix lagotricha*	Urucu, Brazil	C. Peres, *pers. obs.*
P. auriculata	PG	Jul–Aug	*Saguinus b. bicolor*	Manaus, Brazil	Egler (1992)
P. ulei	YS	Feb–Mar	*Chiropotes satanas*	Raleighvallen, Surinam	van Roosmalen *et al.* (1988)
P. panurensis	MS	?	*Pionus fuscus*	INPA Reserve, Brazil	Hopkins & Hopkins (1983)

1. Fruit part consumed: PG: gums from mature pods; YS: young seeds; MS: mature seeds.
2. This may have been underestimated in several cases as the fruiting period may be longer than the duration of observations.
3. Although these upper Amazonian populations of *P. nitida* have been listed as a distinct species ('*P. oppositifolia*'), following an older taxonomic arrangement, these two taxa are treated as synonymous because no differentiating characters can be found (Hopkins 1986).

and widely distributed in Amazonian terra firme forests (Hopkins 1986), where fruit seasonality is likely to be well demarcated (Peres 1994a).

Although the importance of *Parkia* to paleotropical forest vertebrates remains poorly documented, copious amounts of floral nectar of *Parkia bicolor* at Korup Forest Reserve, southwestern Cameroon, are intensively used by three bat species (Megachiroptera), two species of nocturnal prosimians (*Perodicticus potto* and *Galago* sp.), and several species of sunbirds (Grünmeier 1990). In Madagascar, black lemurs, two species of fruit bats, a bulbul, and a sunbird rely heavily on nectar of *Parkia madagascariensis* flowers (Birkinshaw & Colquhoun 1998). Pteropodid bats (*Eonycteris spelaea*) are also known to feed on, and defend, the flowers of *Parkia speciosa* in Malaya (Gould 1978), just as phyllostomid bats consistently feed on nectar of at least eight chiropterophilous New World *Parkia* species (Hopkins 1984). Although Old World *Parkia* species diverge from *P. nitida* and *P. pendula* because they lack gum production within their pods (Hopkins 1983, 1994), they may contain variable amounts of a mealy pulp that can be highly attractive to primates, thus serving a similar ecological role. Nissen (1931) describes the pulpy endocarp of *P. biglobosa* as the most important single food for chimpanzees (*Pan troglodytes*) at a savanna site in Guinea, West Africa. Although little additional information is available on vertebrate–*Parkia* interactions in the paleotropics, several primate species have been reported consuming pods of different *Parkia* species in Africa and the Indo-Pacific region of Asia, including baboons (*Papio anubis*), long-tailed macaques (*Macaca fascicularis*), dusky leaf monkeys (*Trachypithecus pileatus*), and banded leaf monkeys (*Presbytes femoralis*) (see Hopkins 1983, 1994 and references therein).

Information on interactions between neotropical *Parkia* fruits and vertebrates was largely unavailable at the time of M. Hopkins' detailed review of *Parkia* 'relationships with animals' (in H. Hopkins 1986, pp. 53–56). The

invertebrate bias of this review may reflect the selective depletion of large-bodied vertebrates from the mostly overhunted forests where *Parkia* populations have been studied, and the rare frequency at which vertebrate interactions are observed, particularly in studies approached from the perspective of botanical collections. However, this report confirms previous speculations on the function of *Parkia* pod gums which were thought to be 'unclear, but its presence within the pod probably has some significance in dispersal' (Hopkins & Hopkins 1983). H. Hopkins (1986, p. 45) also correctly alluded to 'some function in dispersal, perhaps as a food source for dispersal agents', although her speculations on the 'uncertain significance' of *Parkia* gums as possible deterrents of invertebrate seed predators cannot yet be confirmed.

Nutritional value of Parkia gums

The chemical composition of fresh gums collected from mature pods of *P. pendula* and *P. nitida* was analysed at the Institute of Food Research, Norwich, UK. Samples were obtained at three Amazonian forest sites during the late dry seasons of 1994 and 1996, frozen in the field within liquid-nitrogen, and later transported for analyses. One of these sites is located in southeast Brazilian Amazonia (Pinkaití, Rio Riozinho, Kayapó Indian Reserve, 7°46′S; 51°57′W), whereas the other two are located in the central-western (Urucu Forest, Rio Urucu, Amazonas, 4°50′S, 65°16′W) and western parts of the region (Condor, Rio Juruá, Amazonas, 6°45′S, 70°51′W). Although samples were not purified in the field, most particles were later removed by centrifugation (1000 g, 40 s) after dispersal by vortexing 0.8 g in 10 ml of water at 50 °C, and recovery of the supernatant by freeze-drying. A brief description of the nutritional analysis of gum samples and their polysaccharide, nitrogen, calcium and phosphate content is shown in Table 2.

The values observed for non-structural carbohydrates, nitrogen and natural inorganic content suggest that gums from *Parkia* pods are important sources of reducing sugars, protein, and calcium, which is often one of the major inorganic components of gums and exudates revealed by ash determinations (Anderson & Pinto 1985, Garber 1993). Parkia gums consisted primarily of non-structural carbohydrates, which ranged from 773 mg g^{-1} of dry sample of *P. pendula* gum from Pinkaití, eastern Amazonia, to 811 mg g^{-1} in a *P. nitida* sample from Condor, western Brazilian Amazonia. Estimates of protein content based on the Kjeldahl procedure (in which the total recovered nitrogen is multiplied by a conversion factor of 6.25 to estimate total protein) and the presence of 0.45–2.22% N were 2.8–3.1% for *P. pendula* and 13.6–13.9% for *P. nitida*. This conversion factor may, however, slightly overestimate protein content if a significant amount of nonprotein nitrogen compounds were present in the gums (cf. Izhaki 1993), although this is unlikely in this case. The value of protein content by the Kjeldahl procedure were somewhat higher than those of 2.2% protein from a sample of *P. pendula* pod gum from Costa Rica, estimated by the same method

Table 2. Carbohydrate, protein and mineral content of gums extracted from mature pods of *Parkia pendula* and *Parkia nitida* trees at three terra firme forest sites of Brazilian Amazonia.

Tree species	P. pendula		P. nitida	
Forest locality	Pinkaití	Rio Juruá	Rio Juruá	Rio Urucu
Dry weight (mg)[1]	26	34	72	73
Yield of dry gum (%)[2]	61.0	47.5	47.3	51.8
% Protein (% N × 6.25)	2.8	3.1	13.6	13.9
Sugar concentrations (mg g^{-1})[3]				
Rhamnose	6.5	6.0	16.0	16.0
Arabinose	619.5	637.5	473.5	516.0
Galactose	105.0	99.5	196.0	173.0
Uronic acid[4]	42.0	57.0	121.5	116.0
Total non-structural carbohydrates (mg g^{-1})	773	800	807	821
Calcium (nmol mg^{-1})[5]	7.2	14.2	25.2	26.1
Phosphate (nmol mg^{-1})[6]	l0.56	1.96	0.0	0.0

1. Dry weight in a 1 ml sample of wet gums from mature pods.
2. From wet weight of material.
3. Neutral sugar analysis (mean of two measurements) based on the Saeman hydrolysis (mg anhydrosugar per g of dry weight of gum).
4. Uronic acid analysis based on the *m*-phenyl phenol method.
5. Calcium assay based on atomic absorption.
6. Phosphate analysis based on the molybdate assay.

(Anderson & Pinto 1985), but considerably lower than those found by Garber (1993) for a northern Peruvian population of *P. oppositifolia* (= *nitida*), which ranged from 13.7 to as much as 39.7%. These analyses of *Parkia* gums thus generally confirm a high nutritional reward to vertebrate consumers—especially in terms of non-structural carbohydrate, protein and mineral elements—which becomes all the more important because these coincide with the annual dearth of alternative fruit resources.

IDENTIFYING KEYSTONE PLANT RESOURCES

The empirical evidence summarized above suggests that gum-producing *Parkia* species appears to be very important to some arboreal vertebrate species in several Amazonian terra firme forests, largely because their nutrient-rich gums and prolonged fruiting seasons coincide with periods of overall fruit scarcity (Figure 2). However, the community-wide importance of *Parkia* gums is substantially reduced because they are consumed only by a small subset of the frugivorous vertebrate assemblage occurring at any given forest (see Peres & Whittaker 1991, Peres 1999 for checklists of bird and mammal species at the Urucu forest). Whether or not *Parkia* and other plant taxa can be defined as a KPR thus depends on several independent but intersecting variables defining the relative importance of a resource to a coexisting consumer assemblage. I have therefore identified four parameters, scaled from 1 to 10, describing the value of a KPR candidate.

1. *Temporal redundancy (TR)*: defined in terms of the degree to which the availability of a potential KPR synchronizes with that of the combined pool of

alternative food resources used by a consumer assemblage. In these terms, a resource may range from entirely indispensable (TR = 1), if it becomes available during periods of maximum overall fruit scarcity, to completely substitutable (TR = 10), if it becomes available only during months of peak availability of all alternative plant resources consumed. Low redundancy values (TR ≤ 5) were assigned to resources becoming available wholly or partially during months of low fleshy fruit availability, whereas values > 5 were assigned to resources whose monthly fruiting pulses synchronized with an increasingly larger number of species bearing fleshy fruits.

2. *Consumer specificity (CS)*: defined as an inverse function of the percentage of frugivorous species in a local vertebrate assemblage (i.e. all bird and mammal species occurring at any one site including at least 50% of fruit in their diet) that were reported to exploit a putative KPR. In these terms, resources could range from being extremely generalized (CS = 1), if they were known or suspected to be consumed by at least one half of the species in a frugivorous vertebrate assemblage ($S_f \geq 50\%$), to extremely specialized (CS = 10), if they were consumed by only 5% or less of the species in a frugivorous assemblage ($S_f \leq 5\%$). Intermediate CS values were then calculated according to the following linear relationship: $CS = -(S_f - 54.7)/4.9$. The definition of this parameter is thus conceptually similar to that of consumer-resource connectance in foodweb theory (Pimm 1980), although it ignores the variation in strength of interactions because these data are largely unavailable.

3. *Resource reliability (RR)*: defined in terms of the degree to which a potential KPR at a given site will predictably become available every year to sustain vertebrate consumers, and in the case of low-redundancy resources, through annual periods of scarcity. In these terms, the year-to-year phenological variation of a plant food-item may range from an extremely unreliable supra-annual resource (RR = 1), if it fails to become available in more than 50% of years, to extremely reliable (RR = 10), if it never fails to become available at least once per year (see Newstrom *et al.* 1994 for a review of tropical plant phenology).

4. *Resource abundance (RA)*: defined in terms of the crude abundance of a potential KPR at a given site, on the basis of the approximate patch density of a given resource and, when available, some indication of patch size (e.g. crown volume). In these terms, a medium-sized plant resource may range from extremely rare (RA = 1), if it occurred at densities equal to or less than 0.01 patch ha^{-1} ($\leq$ 1 patch km^{-2}), to superabundant (RA = 10) if it occurred at densities of 2.5 or more patches ha^{-1} ($\geq$ 250 patches km^{-2}). Intermediate RA values were then roughly estimated using the logarithmic function $RA = 8.25 + (4.06 * \log_{10}D)$, where D is the approximate resource patch density (per hectare) obtained from information provided in each study (see below). This abundance index is simply intended to provide a coarse measure of the total amount of a given resource that becomes seasonally available to vertebrates at a given forest.

From a vertebrate perspective, keystone plants are then defined as those producing highly reliable (RR > 5), low-redundancy (TR < 5) resources that are consumed by a large proportion of the bird and mammal assemblage with which they coexist (CS < 5). Resource abundance could also be used to further narrow the definition of a KPR, but in any case this attribute is seen as secondary to the redundancy, reliability, and specificity of a given resource (see below).

Using information compiled from published and unpublished studies, I attempted to verify the keystone role of Central and South American plants by assigning values to the above parameters for 37 populations of 35 tree, epiphyte and liana species that have been explicitly proposed as KPRs in neotropical forests (Table 3). In most cases, values assigned to this crude ten-point scale were only approximate because available information on the composition of the overall frugivore assemblage, consumer-resource matrix, and patterns of fruiting phenology for the entire plant community was incomplete and not strictly comparable for every forest site considered. In every case, scoring RR values required inferences from studies spanning no more than 3 y because longer-term phenological data are unavailable for all KPRs proposed to date. However, most neotropical KPRs have been described from sites with relatively well documented vertebrate and plant communities (e.g. Cocha Cashu, Peru; La Selva, Costa Rica; Urucu, Brazil), so that supplementary information from subsidiary studies conducted at the same sites could be used to boost the accuracy of these scoring procedures (Galetti 1996, Gentry 1990, Janzen 1983, McDade *et al.* 1994, Peres 1991, and references therein). Moreover, ecological studies on neotropical keystone plants tend to share a community-wide emphasis, rather than a focus on any given consumer species, thus providing reasonably detailed information on the importance of a given resource to its consumer assemblage. Although this comparative analysis is admittedly hindered by the quality of information derived from several studies, it does provide a coarse indication of the variation in resource importance attributes at different forest sites.

Several additional variables could be considered in refining how important is a putative KPR to a consumer assemblage, including its nutritional value, availability period (e.g. length of fruiting season), the frequency at which it is consumed, physical accessibility, harvesting effort (e.g. handling time), and spatial distribution in the forest. However, these characteristics are not entirely independent of the temporal redundancy, consumer specificity, reliability, or abundance of a given resource. I have thus attempted to simplify the theoretical properties defining the 'keystone-ness' of a given resource to a minimum number of largely independent variables.

Plant resources potentially serving a keystone role in neotropical forests show a high degree of variability in terms of their importance to vertebrate consumers as defined by the above parameters (Table 3). In general, putative KPRs tend to share low scores in relation to their redundancy and reliability,

Table 3. Proposed keystone plant resource populations in neotropical forests, their vertebrate consumers, and 'keystoness' attributes.

Plant species	Plant[1] family	Life[2] form	Part[3] eaten	Period available	Consumers[4] recorded	TR[5]	CS[5]	RR[5]	RA[5]	Forest site, country	Sources[6]
Figs											
Ficus perforata	Mora	CT	WF	May–Oct	Most frugivores	VL	VL	H	L	Cocha Cashu, Peru	1
F. killipii	Mora	SCT	WF	Jul–Mar	Most frugivores	VL	VL	H	VL	Cocha Cashu, Peru	1
F. erythrosticta	Mora	SCT	WF	All year	Most frugivores	VL	VL	H	VL	Cocha Cashu, Peru	1
F. trigona	Mora	HE	WF	All year	Most frugivores	VL	VL	H	L	Urucu, Brazil	2
F. gomelleira	Mora	CT	WF	May–Nov	Most frugivores	VL	L	VH	VL	Urucu, Brazil	2
F. guianensis	Mora	HE	WF	Aug–Nov	Most frugivores	VL	VL	VH	L	Urucu, Brazil	2
F. mathewsi	Mora	HE	WF	Oct–Jun	Most frugivores	VL	VL	H	VL	Urucu, Brazil	2
Palms											
Iriartea ventricosa	Arec	ArP	Me,YS	May–Jul	SqM, MP, LP, Pec	VL	H	VH	VH	Cocha Cashu, Peru	1,3
Scheelea (= Attalea) cephalotes	Arec	UnP	YS,Se	All year	Ceb, SqM, Sci	VL	VH	VH	VH	Cocha Cashu, Peru	1,3
Astrocaryum murumuru	Arec	UnP	YS,Se	All year	Ceb, Sci	VL	H	VH	VH	Cocha Cashu, Peru	1
Euterpe edulis	Arec	ArP	Me	May–Sep	15 bird spp.	H	M	VH	H	Saibadela, Brazil	4
E. edulis	Arec	ArP	Me	Oct–Feb	LR, Ung, PhB, Ram, Cra, Psi, Tur,Cot,Tro	L	M	VH	H	Serra do Mar, Brazil	5
Oenocarpus bataua	Arec	ArP	Me,YS	All year	Ceb, LP, Cra, Tin	L	H	VH	H	Urucu, Brazil	2
Mauritia flexuosa	Arec	ArP	Me	All year	MP, LP, LR, Ung, Psi	L	M	VH	VL	Urucu, Brazil	2
Attalea maripa	Arec	ArP	Me,Se	Jan–Mar	Ceb, LR, Ung, Psi	L	L	VH	H	Pinkaiti, Brazil	6
Other sources of fruits											
M. hypoleuca	Mela	SCT	WF	Dry season	Ceb, 34 bird spp.	VL	VL	VH	VH	Linhares, Brazil	7
M. centrodesma	Mela	SCT	WF	All year	12 spp. passerines	VL	L	VH	H	La Selva, Costa Rica	8
Casearia corymbosa	Flac	CT	Me	Dec–Feb	22 bird spp.	VL	M	VH	VL	La Selva, Costa Rica	9
Virola sebifera	Myri	CT	Ar	Sep–Feb	6 bird spp.	L	H	VH	M	Barro Colorado Island, Panama	10
Celtis iguanea	Ulma	HCL	Fr	Mar–Aug	SP, MP, LP, Psi	M	M	VH	VH	Cocha Cashu, Peru	1
Allophyllus scrobiculatus	Sapi	CT	Fr	May–Jun	SqM, Ceb, LP, Tru	M	H	VH	H	Cocha Cashu, Peru	1,3
Calatola sp.	Icac	CT	Fr	May–Jun	Tit, Tru	M	VH	VH	H	Cocha Cashu, Peru	1
Souroubea guianensis	Marc	HCL	Fr	Sep–Jun	Tam, Tit, SqM, Ceb, Ram, Cra, 15 spp. passerines	VL	M	VH	H	Urucu, Brazil	2

Table 3. (cont.)

Plant species	Plant family[1]	Life form[2]	Part eaten[3]	Period available	Consumer recorded[4]	TR[5]	CS[5]	RR[5]	RA[5]	Forest site, country	Sources[6]
Quararibea ochrocalyx	Bomb	UT	Me	Sep–Oct	Tam, Tit, Ceb	L	VH	VH	H	Urucu, Brazil	2
Apeiba echinata	Tili	CT	Fr	Jun–Sep	MP, LP, LR, Pec, Tap, Tin	VL	VH	VH	VL	Urucu, Brazil	2
Inga alba	Mimo	SCT	Me	May–Sep	SP, MP, LP, Psi	L	VH	VH	L	Urucu, Brazil	2
Parkia nitida	Mimo	ET	G,YS	Jun–Aug	SP, MP, LP, LR, Ung, Psi	VL	VH	M	VL	Urucu, Brazil	11
P. pendula	Mimo	ET	G,YS	Jun–Aug	SP, MP, LP, LR, Ung, Psi	VL	VH	M	VL	Urucu, Brazil	11
Other sources of seeds											
Cariniana micrantha	Lecy	ET	Se	Jul–Sep	Ceb, SkM	VL	VH	VH	VL	Urucu, Brazil	2
Bertholletia excelsa	Lecy	ET	Se	Nov–May	LR, Ceb	L	VH	VH	VL	Pinkaití, Brazil	12
Sources of nectar											
Quararibea cordata	Bomb	UT	Nc	Aug–Sep	Tam, SqM, Tit, NiM, Ceb, DiM, Pro, 14 bird spp.	L	M	VH	L	Cocha Cashu, Peru	1,13
Erythrina ulei	Papi	CT	Nc	Jul–Aug	SqM, Ceb, SpM, Psi, other bird spp.	L	M	VH	H	Cocha Cashu, Peru	1
Combretum assimile	Comb	HCL	Nc	Jul–Aug	PyM, Tam, Cap, SqM, SpM	VL	M	VH	H	Cocha Cashu, Peru	1,13
C. fruticosum	Comb	HCL	LNc	Jul–Sep	LiT, Ceb, 12 spp. passerines	VL	M	VH	L	Poço d'Antas, Brazil	14
Mabea cf. eximia	Euph	HCL	Nc	Jul–Sep	PyM, Tam, SqM, Ceb	VL	H	VH	L	Urucu, Brazil	2
S. globulifera	Gutt	SCT	Nc	May–Aug	LiT, Hum, Tan	VL	H	VH	L	Poço d'Antas, Brazil	14
S. globulifera	Gutt	SCT	Nc	Jul–Oct	Tam, DiM, Hum, Tan	L	H	VH	L	Urucu, Brazil	2

1. Families: Mora, Moraceae; Arec, Arecaceae; Mela, Melastomataceae; Flac, Flacortiaceae; Myri, Myristicaceae; Ulma, Ulmaceae; Sapi, Sapindaceae; Icac, Icacinaceae; Marc, Marcgraviaceae; Bomb, Bombacaceae; Tili, Tiliaceae; Mimo, Leguminosae Mimosoideae; Lecy, Lecythidaceae; Papi, Leguminosae Papilionoideae; Comb, Combretaceae; Euph, Euphorbiaceae; Gutt, Guttiferae.

2. Life form: ET, emergent tree; CT, canopy tree; SCT, sub-canopy tree; UT, understorey tree; ArP, arborescent palm; UnP, understorey palm; HE, hemi-epiphyte; HCL, high-climbing liana.

3. Part eaten: WF, whole fruits; Fr, fruit pulp; Ar, arils; Me, mesocarp; YS, young seeds; Se, mature seeds; G, gums from mature pods; Nc, floral nectar.

4. Consumers: SP, small primates; MP, midsized primates; LP, large primates; Ung, ungulates; Tap, tapirs; Pec, peccaries; LR, large caviomorph rodents; Sci, squirrels; DiM, didelphid marsupials; PyM, pygmy marmosets; Tam, tamarins; LiT, lion tamarins; (Tit) titi monkeys; NiM, night monkeys; SqM, squirrel monkeys; Ceb, *Cebus* monkeys; SkM, saki monkeys; SpM, spider monkeys; PhB, phyllostomid bats; Ram, ramphastids; Tru, trumpeters; Cra, cracids; Tin, tinamids; Psi, most psittacids; (Ara) macaws; Tur, thrushes; Cot, cotingas; Tro, trogons; Tan, tanagers; Hum, hummingbirds.

5. Population-specific resource importance parameters: TR, temporal redundancy; CS, consumer specificity; RR, resource reliability; and RA, resource abundance, assigned to one of five categories: VL, very low: 1–2; L, low: 3–4; M, medium: 5–6; H, high: 7–8, and VH, very high: 9–10.

6. Sources: (1) Terborgh 1986a, b, *pers. comm.*; (2) Peres 1991, 1994a; (3) Mitchell 1990; (4) Galetti & Aleixo 1998; (5) Laps 1996; (6) R. Salm & C. Peres, unpubl. dat; (7) Galetti & Stoltz 1996; (8) Levey 1990; (9) Howe 1977; (10) Howe 1981; (11) this study; (12) Peres *et al.* 1997, C. Baider & C. Peres, unpubl. data; (13) Janson *et al.* 1981; (14) Peres 1986, unpubl. data.

but are widely variable with respect to their consumer specificity and abundance. For example, gums of both *Parkia* species at Urucu had low scores in terms of their redundancy and abundance, intermediate scores in terms of reliability, and high scores in terms of consumer specificity. According to these criteria, *Parkia nitida* gums could only be described as a keystone resource in Amazonian terra firme forests if its consumer specificity and resource reliability axes are ignored because (i) only largely frugivorous primates—ranging in body size from tamarins to woolly monkeys—are significant beneficiaries; and (ii) pod gums may not become available during every season of overall food scarcity.

Only a handful of other proposed candidates for neotropical KPRs would adequately fit a quantitative definition of keystone resources, as described by a three-dimensional mesh fitted to 50% of the range of resource importance values (Figure 3). In these terms, very few neotropical plant species reliably produce resources that are both non-redundant and 'popular' with a wide suite of consumer species. These include several species of fig trees and epiphytes (*Ficus* spp.) occurring at terra firme (Peres 1994a) or floodplain forests of western Amazonia (Terborgh 1983, 1986a), and *Miconia* shrubs and treelets in sites ranging from Mesoamerica (Greenberg 1981, Levey 1990) to the Atlantic forest of southeastern Brazil (Galetti & Stoltz 1996). On the other hand, if we were to take into account the *per capita* value of KPR patches to comply with some definitions of keystone species (Bond 1993, Paine 1966, Power & Mills 1995, Power *et al.* 1996, Simberloff 1998), then only relatively rare resources (RA < 5) could be considered as KPRs (Figure 4). In these terms, the relatively common patches of *Miconia* berries would not fit the abundance criteria of the KPR definition, although they are widely consumed and become predictably available during every lean season (Figure 4). However, I later attempt to argue that resource abundance should be relegated to a secondary consideration in identifying KPRs in tropical forests.

DISCUSSION

This review emphasizes the multiple dimensions of consumer-resource interactions during the 'food crunch' of neotropical forests, and provides a more elaborate quantitative framework for identifying keystone plants. The narrower definition of KPRs applied here is not meant to undermine the importance of minor resources produced by single plant species outside the fruiting peak of most of the plant community, which *in aggregate* may sustain entire tropical frugivore assemblages through periods of scarcity (Leighton & Leighton 1983, Peres 1994a, Terborgh 1986a, White 1994). These low-redundancy species will often amount to a tiny, but disproportionately important, fraction of the entire flora found in a tropical forest because few non-anemochorous species consistently bear ripe fruits during the dry season (van Schaik *et al.* 1993). This definition is also not meant to erode the value of high consumer-specificity resources
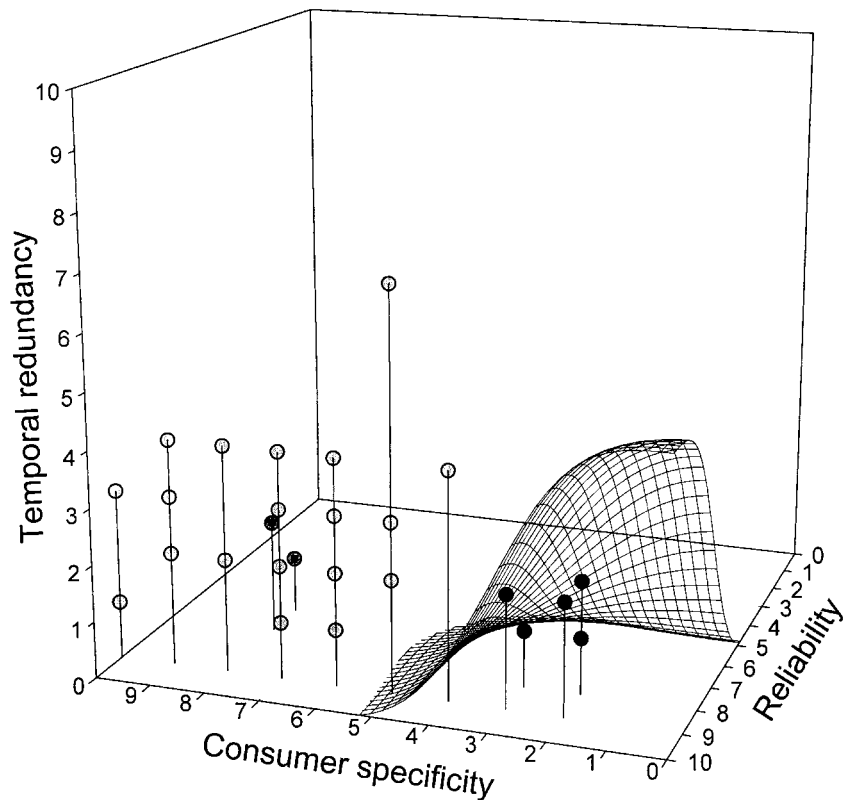
Figure 3. Community-wide importance of putative keystone plant resources (KPRs) in neotropical forests (see Table 3) as defined by their consumer specificity, temporal redundancy, and reliability. Solid circles falling underneath the 50% mesh, here representing several species of *Ficus* spp. and *Miconia* spp., are most likely to fulfil the ecological conditions that could distinguish them as KPRs. Shaded circles with a solid dot indicate the two *Parkia* species discussed in the text. Circles may indicate more than one resource population.

becoming available during (or previously cached for) critical times of the year, without which their small set of consumer species might succumb to steep population declines (e.g. Brazilnut seeds, *Bertholletia excelsa*: Peres *et al.* 1997). However, implicit or explicit definitions of keystone plants have ranged from those emphasizing resource redundancy only (e.g. Leighton & Leighton 1983, White 1994), to those emphasizing both redundancy and reliability (Terborgh 1986a, b), those that also consider resource abundance (Paine 1966, Power & Mills 1995, Power *et al.* 1996), and finally those primarily concerned with post-removal effects (Bond 1993, Howe & Westley 1988, Lawton 1993, Mills *et al.* 1993). In the ensuing discussion, I consider these and other aspects of the keystone resource paradigm.

The role of keystone plants as food sources

Keystone plants as described in the literature are seen to be important primarily because of their trophic role as producers in sustaining vertebrate assemblages, and this paper is no exception. However, a number of plant species
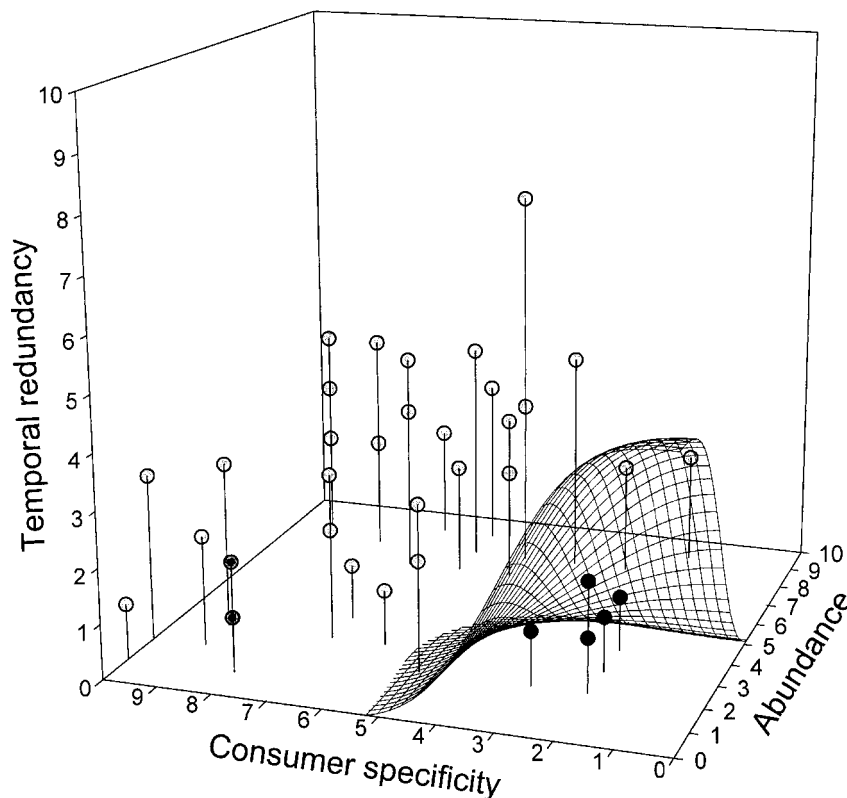
Figure 4. Putative neotropical forest KPRs according to their consumer specificity, temporal redundancy and resource abundance. Solid circles falling underneath the 50% mesh represent several *Ficus* species; shaded circles with a solid dot indicate the two *Parkia* species discussed in the text. Circles may indicate more than one resource population.

have been defined as 'keystones' or 'key species' (sensu Lawton 1993) because of their structural function in creating and maintaining habitats for a host of other species, thus having major non-trophic impacts on energy flow, nutrient cycling, and other ecological processes. In these terms, for example, kapok trees (*Ceiba pentandra*, Bombacaceae) of Amazonian várzea forests could be considered as a keystone plant because the enormous 'cauliflower' crowns of these majestic emergents provide much needed structural support well above the várzea canopy for a variety of other organisms, including nesting sites for harpy eagles (*Harpia harpyja*) which in turn may regulate populations of large arboreal mammals. In other regions, several tall arborescent species of arid ecosystems have been identified as 'habitat modifiers' (*sensu* Mills *et al.* 1993) because they create a favourable microhabitat for the dispersal, germination, seedling establishment and survival of other plants. As an example, several legume tree species of the Sonoran Desert of northern Mexico/southern Arizona, including the ironwood (*Olneya tesota*), mesquite (*Prosopis* spp.), and palo verde (*Cercidium* spp.), serve as key 'nurse plants' for giant columnar cacti such as saguaros (*Carnegiea gigantea*) and other perennials, which require a moist seed bed and

a shaded environment for successful recruitment (Tewksbury & Petrovich 1994). By the same token, one could argue that the dense stands of *Euterpe oleracea* and *Mauritia flexuosa* palms serve a key structural role in Amazonian estuarine riparian forests and backwater palm swamps, respectively, creating a favourable environment for a host of other species, independent of their importance as a source of fruits consumed by a wide range of vertebrates (Kahn 1991; Peres 1994a, c; Zona & Henderson 1989). Here, however, I refer to tropical keystone plants primarily as producers of flowers and fruits rather than as structural components of the habitat. I am unaware of any formal reference to neotropical KPRs consisting of non-reproductive plant structures, although the vegetative and structural parts of several plant species apparently serve as seasonally important resources for capuchin monkeys (*Cebus* spp.), including the pith of *Attalea* (= *Scheelea*) *cephalotes* (Terborgh 1983) and *Astrocaryum jauari* palms (C. Peres, *pers. obs.*) in Amazonian forests, and the base of bromeliad leaves in the Atlantic forest (P. Izar, *pers. comm.*). Spider monkeys in central Surinam also resort to a number of reliable non-reproductive plant parts on a seasonal basis including the barks softened by rainwater on trunks and boughs of *Licania micrantha*, the debris accumulated at the base of *Attalea* (= *Maximiliana*) *maripa* palm leaves, and the aerial root tips and young leaves of various epiphytic Araceae (*Philodendron scandens* and *Heteropsis flexuosa*) and Piperaceae (*Peperomia glabella*) (M. van Roosmalen 1985a, *pers. comm.*). One could make a similar case for bark (e.g. Rogers *et al.* 1994) and the foliage of a number of coarse herbs in favourable light environments of both neotropical and paleotropical forests, which can sustain populations of large facultative frugivores foraging on the ground during periods of fruit scarcity (e.g. White *et al.* 1995, C. Peres, unpubl. data).

Per capita *value of keystone plants*

Definitions of keystone species often revolve around the notion that some species have a disproportionately large impact on many others from what might be expected from their relatively low abundance or biomass (Bond 1993, Paine 1966, Power & Mills 1995, Power *et al.* 1996, Simberloff 1998). This is probably the main reason why the keystone species concept was initially developed around the surprisingly pervasive role of keystone predators (Paine 1966, 1969), which by definition are relatively rare, and only later expanded to include more abundant species near the bottom of foodwebs (Terborgh 1986a, Bond 1993, Menge *et al.* 1994). A failure to consider population abundance could therefore blur the definition of keystone plants, adding to the difficulties in identifying KPRs. A recent review of the keystone species concept has attempted to deal with this issue by simply excluding 'ecologically dominant' species, the large abundance and biomass of which make them indispensable for the whole community (Power *et al.* 1996). Accordingly, the extremely abundant *Sphagnum* mosses in blanket bogs, and *Phragmites* reed grasses in reedbeds, could not be considered as

keystone species, even though they create, maintain and form quintessential structural components of these ecosystems. This is intuitively reasonable because the relative abundance of a keystone resource is likely to correlate with its importance to all potential consumers. From this perspective, it may be tautological to describe *Mauritia flexuosa* palm fruits as a keystone resource in a monodominant *Mauritia* palm swamp (termed *aguajale* in Peru and *buritizal* in Brazil) because these large arborescent palms spell the very structure and composition of this ecosystem, which by definition has selected for consumers of *M. flexuosa* fruits. Yet one would be tempted to consider *M. flexuosa* fruits as a keystone resource not least because of their undeniable (and apparently irreplaceable) value to both people (Vasquez & Gentry 1989) and wildlife (Bodmer *et al.* 1999, Peres 1994c) in upper Amazonia. Moreover, tropical forest plants are usually not sufficiently dominant, rendering the resource abundance attribute less relevant to the KPR definition. Finally, the importance of rare resources may be so low that their abrupt removal may not result in significant perturbations in consumer community structure.

Considering the abundance of a putative KPR would, however, be most relevant from a conservation standpoint because the depletion probability of a potential keystone plant—which might be caused by selective loggers, fruit and seed extractors, or latex tappers—should be inversely related to the plant's population density. Hence, the *per capita* removal of a KPR by any given harvest intensity is likely to have greater effects with decreasing levels of resource density. Explicitly incorporating resource abundance into the KPR definition would thus be more appropriate in conservation than in ecological terms, even though the value of a rare KPR patch is expected to be greater than that of a common KPR. For example, a selective logging operation targeting large *Parkia* trees, whose hardwood are of high quality and great commercial value in some parts of Brazil (Paula *et al.* 1980), could rapidly reduce gum availability to primates because of the typically low densities of fertile *Parkia* trees. The same would not be expected for seasonally super-abundant resource patches such as *Miconia* berries because of the typically high local densities of these melastomes (Galetti & Stoltz 1996, Greenberg 1981, Levey 1980).

Taxonomic refinement of keystone resources

One of the problems in the current use of the KPR concept relates to the degree of taxonomic refinement of the relevant plant taxa. As reported in the literature, keystone resources may be supplied by as few as one (e.g. *Casearia corymbosa*: Howe 1977) and as many as dozens of species grouped under a single or a few categories (e.g. figs, palm nuts, nectar: Terborgh 1986a, b; herbaceous plants in the families Marantaceae and Zingiberaceae: White *et al.* 1995). Likewise, all epiphytes in a given forest have been considered as an aggregate keystone resource because they add to the forest

structural complexity and contribute to ecosystem processes such as nutrient cycling (Nadkarni 1994). The so-called 'cornucopia' species of the spring floras of the Mediterranean region have also been collectively described as keystones because they subsidize pollinators interacting with other species offering smaller or no nectar and pollen rewards (Bond 1993, Dafni 1983). This general disregard for a common taxonomic denominator obviously adds to the imprecision in identifying a keystone resource, and renders comparisons of the importance of single plant species to consumers inconsistent. Figs, for example, are often described as a major keystone resource (Kalko *et al.* 1996; Terborgh 1983, 1986a), although they can be supplied by almost the entire *Ficus* community of hemi-epiphytes, stranglers, and self-standing trees in a given forest (e.g. 35 species at Cocha Cashu, Peru: Foster 1990, J. Terborgh, *pers. comm.*; 29 species at Kuala Lompat, Malaysia: Lambert & Marshall 1991; eight species in the Western Ghats, southern India: Patel 1997). It is hardly surprising that one of the largest and most ubiquitous pantropical genera of woody plants should in aggregate provide a relatively constant fruit supply to generalist frugivores at a given forest, particularly because of its intra-population fruiting asynchrony. At the other extreme, several nectar and fruit resources viewed as seasonally crucial staple foods to forest vertebrates in both the paleotropics (e.g. *Polyalthia suaveolens* fruits in Gabon: Gautier-Hion & Michaloud 1989; *Daniella pynaertii* nectar in Zaire: Gautier-Hion & Maisels 1994) and neotropics (*Combretum assimile* nectar in Peru: Terborgh & Stern 1987; *Mabea fistulifera* nectar and *Syagrus romanzoffiana* palm fruits in the semi-deciduous Atlantic forest of southeastern Brazil: Ferrari & Strier 1992, Passos 1998) are produced by a single plant species. In fact, it is entirely possible that seasonal staples provided by many lesser known non-fig plant species at some sites (e.g. Leighton & Leighton 1983, Tutin *et al.* 1997), can be more important to the wider vertebrate community than any single fig species. For instance, none of at least 18 *Ficus* species occurring at the Urucu forest, which were usually small-crowned hemi-epiphytes accommodating only small frugivore feeding parties, were more important to some primate species than were *Parkia nitida* gums (Peres 1994a). Yet only four fig species at Urucu could be defined as a KPR if resource abundance and other importance criteria are taken into account (Table 3).

Context-dependent role of keystone resources

The preceding discussion on how taxonomic refinement can affect the importance of keystone plants suggests that further caution must be exerted in identifying KPRs because of our tendency to indiscriminately label certain plant taxa as keystones regardless of its local substitutability, phenology and consumer interactions. Indeed the importance of putative KPRs to tropical forest vertebrates has been repeatedly shown to be clearly context-dependent, thus making no exception to temperate keystone processes, which can be highly

variable across even short spatial scales (e.g. Brown *et al.* 1986). The wide geographic variation in different aspects of the KPR concept can be seen in the pronounced differences in fruit crop size and crown volume of *Ficus* spp. between terra firme and floodplain forests of Amazonia (Terborgh 1986a, Peres 1994a), the greater fruiting redundancy of *Euterpe edulis* palm populations in lowland Atlantic forests (Galetti & Aleixo 1998) compared to those in montane forests (*c.* 800 m asl) of the Serra do Mar (Laps 1996), and differences in the flowering phenology of *Symphonia globulifera* among populations in Atlantic (Peres 1986), Amazonian (Peres 1994a, Garber 1988), and Guianan forests (Gill *et al.* 1998). Several Myrtaceae tree species are often the only fruit sources available to frugivores during the lean season of the lowland Atlantic forest of southeastern Brazil (M. Tabarelli, *pers. comm.*), yet this family is rather unimportant for Amazonian frugivores in general.

The genus *Ficus* is perhaps one of the best examples of the variable role of KPRs in sustaining vertebrate communities through periods of scarcity. Figs in the Urucu Forest and Gabon, for instance, are not considered to be nearly as important to vertebrates as in Cocha Cashu, southern Peru (Terborgh 1986a), or in Peninsular Malaysia (Lambert & Marshall 1991), because they tend to be produced in small patches (Peres 1994a), or are only infrequently eaten by most frugivores, and at that in small amounts (Gautier-Hion & Michaloud 1989). In the Old World tropics, this can also be seen in the considerable differences in the redundancy of ripe figs even within the same geographic region. For example, the fruiting peaks of a fig community of the western Ghats, southern India, coincided with that of all non-fig trees in an evergreen forest, but not in a deciduous forest some 50 km away (Patel 1997). Two Myristicaceae and one Annonaceae tree species are considered to produce KPRs during the long dry season of northeast Gabon (M'Passa: Gautier-Hion & Michaloud 1989), but not in central Gabon (Lopé Reserve: White 1994) where fruit production peaks of the same species do not coincide with the height of the dry season. Likewise, the apparent community-wide importance of palm fruits at different Amazonian forests ranges from being critical to only one or a few vertebrate species (Peres 1994a, Spironello 1991), to sites where they may play a far more substantial role for bird and mammal community assemblages (*Attalea maripa* in the highly seasonal forests of southeastern Amazonia: R. Salm & C. Peres, unpubl. data).

The keystone role of a given resource is therefore more a function of the species associations and patterns of resource seasonality wherever it happens to be inserted, rather than an emergent property of the plant taxon considered. Overall degree of fruiting seasonality in a given forest clearly boosts the importance of a low-redundancy keystone resource, as does the resource predictability and the number of consumer species with which it interacts.

Non-redundancy of keystone resources
Because flowering and fruiting seasonality are affected by a number of abiotic variables in addition to constraints of pollination and seed-dispersal (see

van Schaik *et al.* 1993 for a review), the reproductive phenology of most plant species is expected to cluster at climatically favourable times of the year. Yet the community-wide demand for any given resource should be frequency-dependent and inversely related to the number of alternative resources that are simultaneously available. For instance, while seed germination and seedling growth may be maximized during the early wet season (Garwood 1983), the *per capita* probability of effective seed dispersal may be substantially reduced at this time of year. Herein lies an important trade-off between biotic and abiotic selective pressures controlling the timing of resource production for tropical forest frugivores.

KPRs are heavily demanded by consumers primarily because they tend to be produced at 'unfavourable' times of the year, and are therefore associated with little or no redundancy. All but one of the 37 KPR populations examined here were assigned to low redundancy values ranging between 1 and 4 (Figure 3). This can result from essentially three different mechanisms: (i) year-round intra-population asynchrony in resource production; (ii) very prolonged production peaks that are largely synchronous within a population but partially overlap with the lean season; and (iii) highly synchronous and pulsed peaks coinciding entirely with the lean season. Figs are perhaps the best pan-tropical examples of low intra-population fruiting synchrony. Extended and partly asynchronous fruiting peaks that largely or wholly coincide with months of greatest fruit scarcity can be illustrated by *Parkia nitida* and *P. pendula*, as well as several other poorly known species. For example, the seeds of the large globose fruits of the cannonball tree (*Couroupita peruviana*, Lecythidaceae) become an important seasonal resource for two sympatric species of capuchin monkeys (*Cebus apella* and *C. albifrons*) in the flooded forests of the Pacaya-Samiria Reserve, northern Peru (P. Soini & F. Encarnación, *pers. comm.*) because their somewhat asynchronous production coincides with the dry season. Examples of highly synchronous KPRs consistently coinciding with the dry season include nectar of *Quararibea cordata* at Cocha Cashu (Janson *et al.* 1981, Terborgh 1983) and fruits of *Q. ochrocalyx* at Urucu (Peres 1994a), the dry fruits of *Apeiba* spp. in lowland Amazonia and the Guianan Shields (e.g. Peres 1994a; M. van Roosmalen, *pers. comm.*), and nectar of *Combretum* vines in Amazonia (Janson *et al.* 1981, Terborgh & Stern 1987) and the Atlantic forest of southeastern Brazil (Peres 1986). In contrast, several large-crowned tree species that produce massive fruit crops and attract a huge proportion of any given frugivore assemblage throughout Amazonia, including several Moraceae (e.g. *Pseudolmedia laevis*, *Clarisia racemosa*, *Brosimum* spp.), cannot be described as keystone resources because of their high fruiting redundancy (C. Peres, *pers. obs.*). In all cases, therefore, it is crucial to consider the temporal redundancy of putative KPRs to ascertain their value to consumers.

Specificity of keystone resource use

One central question in identifying critical resources is what proportion of a local vertebrate assemblage must be seasonally sustained by a plant

species before it can be recognized as the source of a KPR. Neotropical forests are characterized by complex networks of plant–animal interactions (e.g. Gilbert 1980, Terborgh 1992), yet the fabric of their vertebrate communities is unlikely to be appreciably dented should a small, random set of plant species be extirpated. Some species may provide extremely important seasonal resources that are nevertheless consumed by only a tiny fraction of the overall faunal assemblage. The systematic removal, for example, of all brightly coloured inflorescences of a *Heliconia* assemblage for a booming ornamental flower market could trigger sharp population declines in *Phaethornis* hummingbirds (Gilbert 1980, Stiles & Wolf 1979). However, few would seriously consider these locally abundant, coarse herbs as good candidates for KPRs, unless those keystone services are restricted to understorey hummingbirds. The main examples of potential KPRs illustrated in this paper also fail to meet this criterion because only a very small fraction of the vertebrate community in Amazonian forests appears to benefit significantly from gum-producing *Parkia* species.

Community-level effects of keystone resource removal

Virtually all studies to date provide only circumstantial evidence on the actual ecological role of potential KPRs, which should be most appropriately evaluated by large-scale removal experiments, such as those proposed by Rosenweig (1987). The question here is not so much the population responses of plants deprived of their mutualist partners by extinctions of pollinators and seed dispersers (e.g. Bond 1994, Chapman & Chapman 1995), but the fate of consumer species deprived of seasonally critical resources. However, classic removal studies on an ecologically meaningful scale are impractical, unfeasible, or questionable from an ethical standpoint and are thus unlikely to elucidate the community role of putative KPRs. Current thinking on keystone species is largely based on rather questionable controlled but small-scale experiments, or on large-scale natural experiments in which the causes of perturbations are seriously confounded (e.g. synergistic effects of selective logging and hunting which often co-occur). What little evidence is available from natural experiments that are not significantly confounded by other perturbations does not suggest detectable community-wide changes on the structure of consumer assemblages deprived of a putative KPR. For instance, selective removal of *Euterpe edulis* palm-hearts, the fruits of which are widely presumed to be a keystone resource to avian frugivores in the lowland Atlantic forest of southeastern Brazil, had no clear observable effects on frugivorous birds at Saibadela, São Paulo; most species simply switched to alternative food resources without any apparent detrimental effects (Galetti & Aleixo 1998). The importance of KPRs has also been questioned in forests characterized by far lower floristic diversities and therefore containing resource populations that on average are less likely to be redundant. For instance, the near extinction of American chestnut

(*Castanea dentata*) from temperate woodlands of eastern North America had little discernible impact on the community (Opler 1978). Indeed, it is unlikely that the loss of a plant species will cause significant further losses in the trophic web of forest communities, particularly those containing a high proportion of generalist herbivores (Redfern & Pimm 1987).

Keystone species have been simply defined as 'animal or plant species with a pervasive influence on community composition' (Howe & Westley 1988). A sharp decline or increase in the abundance of a KPR should therefore lead to noticeable changes in community composition. A more quantitative definition in terms of community importance consistent with the KPR concept proposed here would include only those species whose removal is expected to drive at least 50% of the assemblage considered to extinction (Mills *et al.* 1993). The available evidence for the role of neotropical keystone plants is therefore mostly inconsistent with the way keystone species have been defined, even if the proportion of species affected is substantially relaxed. Indeed it remains to be seen whether the local extinction or observable population declines of even a single vertebrate species in a tropical forest can be directly attributed to the loss of any KPR.

Despite the questionable evidence available, keystone mutualisms remain a highly plausible but largely untested possibility at a time when many potential KPRs are being removed at an alarming rate from neotropical forests. For instance, heavy selective logging of commercially valuable low-density softwoods used as 'floats' for roundlog rafts in Amazonian flooded forests—such as *Hevea spruceana*, *Apeiba* sp., *Xylopia calophyllum* and *Hura crepitans*—has already destroyed an important resource base for fish and arboreal vertebrates feeding on the fruit pulp or seeds of these species (Albernaz & Ayres 1999). Further work on the ecology of harvested and unharvested populations of keystone plant candidates, which should be shaped by a strong dose of enlightened natural history, is therefore urgently needed.

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