WEEDY AND SECONDARY PALM SPECIES IN CENTRAL AMAZONIAN FOREST FRAGMENTS

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RESUMO – (Palmeiras invasoras e sucessoras secundárias em fragmentos amazônicos) A fragmentação das florestas pode afetar a abundância e distribuição dos organismos. Populações de algumas espécies diminuem e eventualmente são extintas localmente enquanto populações de outras espécies podem aumentar. Em um estudo da composição e abundância de palmeiras secundárias e invasoras em oito fragmentos de florestas (três de 1-, três de 10- e dois de 100-ha), em três sítios (Dimona, Porto Alegre e Esteio) na Amazônia Central, cinco espécies nativas de palmeiras que não ocorreram nas áreas planas de floresta contínua de terra firme foram identificadas. Três espécies eram secundárias (*Astrocaryum acaule* Mart., *Bactris maraja* Mart. var. *maraja* e *Bactris* sp), uma invasora (*Lepidocaryum tenue* Mart.), e uma cujo habitat original era desconhecido (*B. oligocarpa* Barb. Rodr. & Trail). A maior abundância ocorreu nos fragmentos de 1-ha que tiveram 172 das 206 palmeiras encontradas comparado com 33 na de 10-ha e uma no fragmento de 100-ha. A maioria dessas palmeiras ocorreu em Dimona que tinha 195 das 206 palmeiras, comparado com sete em Esteio e quatro em Porto Alegre. A invasora *L. tenue*, que forma populações clonais, embora tenha ocorrido somente em Dimona, representou 91% do total de indivíduos encontrados. É possível que com o aumento da degradação interna dos fragmentos pequenos as populações de espécies secundárias e invasoras também aumentem, o que pode ser prejudicial às populações de espécies de plantas de floresta fechada que ocorrem nos fragmentos florestais.

Palavras-chave – biodiversidade, *Lepidocaryum tenue*, espécie clonal, invasão biológica.

ABSTRACT – (Weedy and secondary palms in amazonian fragments) Forest fragmentation may affect the abundance and distribution of organisms. Some species populations decrease being eventually driven to local extinction while other species may experience population increase. In a survey of the composition and abundance of secondary and weedy palms in eight forest fragments (three of 1-, three of 10- and two of 100-ha), in three sites (Dimona, Porto Alegre and Esteio) in central Amazonia, five native palm species which do not occur in the continuous forest were identified. Three were secondary species (*Astrocaryum acaule* Mart., *Bactris maraja* Mart. var. *maraja* and *Bactris* sp), one weedy (*Lepidocaryum tenue* Mart.), and one of unknown status (*B. oligocarpa* Barb. Rodr. & Trail). The highest abundance was found in the 1-ha fragments which had 172 of the 206 palms found compared with 33 in the 10-ha and one in the 100-ha fragments. However, most of these palms occur in the Dimona site, which accounted for 195 of the 206 of the individuals, compared with seven in Esteio and four in Porto Alegre. The weedy *L. tenue*, which forms clonal populations, although occurring only in Dimona, accounted for 91% of the individuals recorded. It is possible that with increased habitat degradation of small fragments, some populations of secondary and weedy species will also increase, what may be detrimental to the closed forest plant species populations occurring in forest fragments.

Key words – biodiversity, *Lepidocaryum tenue*, clonal species, biological invasion.

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Introduction

Over 15 x 10^4 km^2 yr^{-1} of tropical forests is being deforested each year (Whitmore 1997), and an additional 1% of the total area is being degraded (Myers 1988). In the Brazilian Amazonia, the world's largest rainforest region, the rate of deforestation between 1978 and 1988 was estimated to be 15 - 20 x 10^3 km^2 yr^{-1} (Skole *et al.* 1994) and as 17 x 10^3 km^2 yr^{-1} for the 1997-1998 period (INPE 2000). Deforestation leaves a fragmented habitat, which represents breaks in the continuity of the distribution of original vegetation, reduces the habitat available to wild plants and animals, and adds edges into a formerly continuous landscape.

Most of the Amazonia is going to be subject to development, leaving a mosaic of forest fragments whose areas may range over several orders of magnitude (Bierregaard *et al.* 1992). This development can lead to losses in biological diversity and changes in the distribution and abundance of organisms within and among fragments. The population response of a given species to fragmentation depends on the relative size of habitat fragments, the spatial scale on which the fragments are arrayed, and how fragments mediate dispersal success across the landscape (Doak *et al.* 1992, Fahrig & Merrian 1994).

Within fragments structural (Laurance *et al.* 1997, 1998a) and microclimatic (Kapos 1989, Murcia 1995) conditions also change, resulting in increased tree mortality (Ferreira & Laurance 1997, Laurance *et al.* 1998a, b) and decreased recruitment (Laurance *et al.* 1998b). This may decrease the size of some plant species populations (Scariot 1999, Benitez-Malvido 1998, Laurance *et al.* 1998b) and favor others (Scariot 1999, Laurance *et al.* 1997, Viana *et al.* 1997), resulting in a decline of old-growth species and an increase of secondary and pioneer vegetation (Laurance *et al.* 1998a, b).

All species studied here are native to the Amazonia (Henderson 1995). In this paper secondary species are defined as those occurring in disturbed patches such as gaps and streamsides, within continuous forests. Weedy species occur naturally in hyper-disturbed sites outside the continuous forest. These species generally are rapidly growth herbs with early reproduction, seeds that are widely dispersed by wind and animals, and the ability to self-fertilize or reproduce asexually (Baker 1974).

Here I present the data of composition and abundance of secondary and weedy palms derived from a larger survey carried out in a set of eight forest fragments of three different sizes in central Amazonia. The questions addressed in this study are: (1) What are the species composition and density of secondary and weedy palm species in forest fragments of different sizes? (2) Is there any significant effect of reserve size on the abundance of these palm species across life stages? (3) What are the traits of these species that would favor them in disturbed habitats? The results are discussed in terms of the conservation of the palm family in this region.

Methods

Study area - I conducted this study on the reserves held by INPA (The Brazilian Institute of Amazonian Research) and the Smithsonian Institution, located in central Amazon, approximately 90 km (2º 18' - 2º 25' S, 59º 44' - 60º 45' W) north of the city of Manaus, Brazil. These reserves are sites of the Biological Dynamics of Forest Fragments Project (BDFFP). In this region, a series of ranches were created in the late 1970's and early 1980's in previously uncut lowland rain forest, leaving a variety of protected reserves (as forest fragments and continuous forest). The fragments are distributed in an east-west orientation across a 40 km swath of what was previously an intact, unbroken forest (Rankin-de-Merona *et al.* 1992). Figures showing the distribution and shape of fragments are presented elsewhere (Laurance *et al.* 1998a, b, Benitez-Malvido 1998).

The eight forest fragments used for this study are isolated by 100 - 350 m of cleared land from the continuous forest, and are located in the Dimona, Porto Alegre and Esteio ranches (hereafter called sites). Fragments were isolated from continuous forest between 1980 and 1984, except for the 100-ha fragment in Dimona, which had its fourth side isolated only in 1990. In both, Dimona and Porto Alegre, three fragments were studied, one each of 1, 10, and 100-ha and in Esteio only two, of 1 and 10-ha, as no 100-ha fragment was available. In Dimona I used one (Reserve #2108) of two 1-ha fragments available. When the forest is cut and left unburned, the remaining forest fragments are surrounded by secondary growth forest dominated by *Cecropia* spp. (Moraceae). When the cut forest is burned, the emerging vegetation is made up of a mixture of woody species dominated by *Vismia* spp. (Clusiaceae). The disturbance and management history of the fragments is presented in Benitez-Malvido (1998).

Annual rainfall measured in Manaus is approximately 2200 mm. Rainfall is strongly seasonal with a dry season extending from June through October, during which the mean monthly rainfall drops near 100 mm. The rainy season reaches its peak in February and March, with monthly rainfall of about 300 mm (Radambrasil 1978). Soils are yellow latosols, nutrient-poor, with high saturation of aluminum and with a high clay content (Chauvel 1983). The soils of upland habitats are dominated by clay, while those of low wet areas have a high percentage of sand (Rankin-de-Merona *et al.* 1992). The uncut forest in this region has a closed canopy averaging 35 m in height; with occasional emergents reaching 50 m while the shaded understory is dominated by stemless palms.

Experimental design, field sampling, and data analysis - In each of the eight fragments, ten 20 m x 20 m plots (each 400 m^2) were randomly positioned, resulting in a total of 80 plots (total of 3.2 hectares). Both low-lying and steep areas, which contain palm communities distinct from that on plateau, were excluded from the study.

In each plot, I recorded and identified palm individuals following Henderson (1995), classifying each in life stages as seedling, juvenile or adult (Scariot 1996, 1999).

Statistical analyses were conducted using bootstrap (2000 resamples) available in the MULTTEST procedure of SAS (1996, 1997). Main site effect comparisons were conducted between pairs of sites with fragment size nested within site. For this analysis, I used only fragment sizes common to both sites being compared. Within sites, fragment sizes were individually analyzed for every life stage and for all life stages pooled (hereafter called total). For all analyses, all individuals of the secondary weedy species were pooled in each plot.

Due to the limitation on the number of forest fragments available for large-scale experiments such as this one, the magnitude of field work necessary to sample several widely distributed forest fragments and locations, and the potentially important implications for the conservation of the Amazonian forest, I relaxed the level of acceptable significance to 0.10 as the threshold for accepting as significant the results of the pairwise comparison of the MULTTEST (SAS 1996, 1997).

Results

Five palm species occur exclusively in the forest fragments, not being found in the 1.2 ha sampled in three areas of continuous forest (Scariot 1996, 1999): *Astrocaryum acaule* Mart., *Bactris maraja* Mart. var. *maraja, Bactris* sp, *B. oligocarpa* Mart., and *Lepidocaryum tenue* Barb. Rodr. & Trail (Tab. 1). *Astrocaryum acaule*, *B. maraja* var. *maraja* and *L. tenue* show habitat specificity, occurring in patches with high light incidence. All species occur in the understory and share similar life history characteristics (Tab. 1) such as low seed production and small plant size, and are distributed in large areas of the Amazonia (see Henderson 1995 for maps of distribution). I excluded *Bactris oligocarpa* from the analysis, as its sucessional status is not clear, although it has been classified as adapted to low light intensity (Granville, 1992). There were 206 individuals of the five species in the eight sampled fragments (3.2 ha), averaging 64.3 individuals/ha, with 7.8 adults, 26.8 juveniles, and 29.7 seedlings/ha. Most (187) of the sampled individuals were *Lepidocaryum tenue*, which occurred only in the 1- and 10-ha reserves of Dimona (Tab. 2), where it formed extensive clones.

Of the 202 individuals of secondary and weedy species (excluding the four plants of *Bactris oligocarpa* from the dataset), the highest number of individuals/ha occurred in Dimona (161.7 ± 92.2; mean and SE) with 19.2 ± 10.4 adults, 67.5 ± 38.2 juveniles and 75.0 ± 45.5 seedlings. In Esteio there were fewer individuals/ha (7.5 ± 7.5; mean and SE) represented by 5.0 ± 5.0 juveniles/ha, and 2.5 ± 2.5 seedlings/ha, without any adults. In Porto Alegre, the site with the lowest number of individuals/ha (1.6 ± 1.1/ha, mean and SE), there were no adults, and only 0.8 ± 0.8 juvenile/ha and 0.8 ± 0.8 seedling/ha. Despite these values, pairwise site comparisons presented no statistically significant differences (p=0.16 – 1.0; MULTTEST procedure).

The smaller the fragment the highest is the number of individuals of the weedy and secondary palm species (excluding the four plants of *B. oligocarpa* found) (Tab. 2). Most of the 143.3 individuals/ha (± 90.8 SE) that occurred in the 1-ha fragments were seedlings (66.7 ± 44.9 SE) and juveniles (57.5 ± 37.3 SE), with 19.2 adults (± 10.4 SE). In the 10-ha fragments there were only 24.2 ± 16.4 individuals/ha with no adults, 14.2 ± 9.0 juveniles/ha, and 10.0 ± 7.6 seedlings/ha. In the 100-ha fragments only seedlings occurred (1.2 ± 1.2 individual/ha). These species represented small fractions (3.4%, 0.6%, and 0.02%) of the 1-ha (4248 ± 510, mean and SE), 10-ha (3983 ± 311) and 100-ha (5901 ± 91) total palm density/ha, respectively.

Density of secondary and weedy species (excluding *B. oligocarpa* from the dataset) among fragment size based on the MULTTEST, differed statistically in the Dimona site only. In this site density of individuals in the 1-ha fragment was significantly higher than in the 100-ha in all life stages (adult, p=0.006; juvenile, p=0.060; seedling, p=0.071; and total, p=0.046) and higher than the adult density (p=0.006) in the 10-ha (Fig. 1).

Discussion

Palm species found exclusively in forest fragments - The secondary and weedy species were important contributors to total species richness, represented by four species of the 36 recorded for the eight fragments and three continuous forest areas studied (Scariot 1999). The disturbance level of the 1- and 10-ha fragments may be contributing to the germination (Robinson *et al.* 1995) and establishment (Burke & Grime 1996) of these species.

Table 1. Life history characteristics of the five palm species occurring in forest fragments north of Manaus.

Species	Stem habit	Seed set [a]	Fruit size [b] cm.	Vegetative Reproduction	Habitat	Stratum	Distribution in Amazonia [b]
Astrocaryum acaule	subterranean	low	2-3.0	no	secondary	understory	Amazonian region and peripheral areas in Brazil, Colombia, Venezuela, and the Guianas.
Bactris maraja var. *maraja*	aerial	low	1-1.7	yes	secondary [c]	understory	Brazil, Colombia, Venezuela, the Guianas, Bolivia, Peru, and Ecuador.
Bactris sp	subterranean	low	?	?	secondary?	understory	?
Bactris oligocarpa	subterranean	low	1-2.0	yes	closed forest	understory	Central and eastern Amazonian regions of Brazil and the Guianas.
Lepidocaryum tenue	aerial	low	?	yes	disturbed	understory	Brazil, Colombia, and Peru.

[a] personal observations

[b] Henderson 1995.

[c] occurs near streams and water bodies, seasonally flooded areas, in all cases where the canopy is more open than in the closed forest.

Table 2. Density individuals/ha. of secondary and weedy palm species and the species of unknown status (*B. oligocarpa*) found in the experimental forest fragments north of Manaus. The number of fragments sampled is denoted by the letter n.

Species	Life Stage	Reserve Size			Site		
		1-ha n=3	10-ha n=3	100-ha n=2	Dimona n=3	P. Alegre n=3	Esteio n=2
Astrocaryum acaule	Adult	—-	—-	—-	—-	—-	—-
	Juvenile	—-	0.83	—-	—-	0.83	—-
	Seedling	—-	—-	—-	—-	—-	—-
	Total	—-	0.83	—-	—-	0.83	—-
Bactris sp	Adult	—-	—-	—-	—-	—-	—-
	Juvenile	—-	—-	—-	—-	—-	—-
	Seedling	2.50	—-	1.25	2.50	0.83	—-
	Total	2.50	—-	1.25	2.50	0.83	—-
Bactris maraja var. *maraja*	Adult	—-	—-	—-	—-	—-	—-
	Juvenile	0.83	5.00	—-	2.50	—-	5.00
	Seedling	—-	1.67	—-	—-	—-	2.50
	Total	0.83	6.67	—-	2.50	—-	7.50
Bactris oligocarpa	Adult	—-	1.67	—-	0.83	—-	1.25
	Juvenile	—-	—-	—-	—-	—-	—-
	Seedling	—-	1.67	—-	—-	1.67	—-
	Total	—-	3.34	—-	0.83	1.67	1.25
Lepidocaryum tenue	Adult	19.17	—-	—-	19.17	—-	—-
	Juvenile	56.70	8.33	—-	65.00	—-	—-
	Seedling	64.17	8.33	—-	72.50	—-	—-
	Total	140.00	16.66	—-	156.67	—-	—-
TOTAL		143.35	27.50	1.25	162.50	3.33	8.75

The weedy *Lepidocaryum tenue*, which also occurs in lowland forest, commonly in *terra firme* and sometimes in flooded areas (Henderson 1995), and can form large colonies in the understory (Kahn & Mejia 1987, A. Scariot, pers. obs.), found an adequate habitat in the hyper-disturbed small fragments to establish and expand its population. The addition of weedy species to the existing pool of species may potentially increase species richness (Huston 1994) through immigrant seeds (Martinez-Ramos & Soto-Castro 1993). However, in central Amazonia, decreased seedling population and reduced richness in palm species among closed forest species in early life stages (Scariot 1996, 1999) can be a direct consequence of the less integrated biota of the forest fragments, which make them more vulnerable to penetration of weedy plants (Pimm 1984, 1991). Invaders such as *L. tenue* may also be detrimental to the closed forest species, fostering species decay in hyper-disturbed forest fragments.

The secondary species *Astrocaryum acaule, Bactris maraja* var. *maraja,* and *Bactris* sp. grow in open and secondary areas (Henderson 1995) such as gaps and streamsides (A. Scariot pers. obs.). Conversely*, B. oligocarpa* is characteristic of lowland forest on *terra firme* (Henderson 1995), and cannot be classified either as secondary or as weedy. The secondary species were not found in the sampled plots of the flat, continuous forest (Scariot 1996), probably because their microhabitat is not common in flat, continuous, undisturbed forests. As the deforestation increases, both the habitat disturbance characteristic of small forest fragments (e.g. tree gaps) and the edges (Kapos 1989, Murcia 1995, Laurance *et al.* 1998a, b) increase, providing a considerable area of suitable habitat for secondary species to expand their population sizes.

Fragmentation and the establishment of weedy palm species - Fragments differ from continuous forest with respect to their lower quantity of rare microhabitats, increased number and intensity of edge effects, and microclimate. These aspects may affect the dispersal and migration patterns of plant and animal species (Soulé & Kohm 1989), and the distribution, behavior, and survival of organisms (Kapos 1989, Murcia 1995). For example, the density of palms decreases from continuous forest towards fragments of 100, 10, and 1-ha, with lower seedling densities in the smaller fragments (Scariot 1996), which can favor secondary and weedy plant species. Conversely, secondary and weedy palm species present an opposite trend, with higher densities in the smaller fragments. It seems that with fragmentation, resources available or the conditions amenable to forest species decrease, opening windows for weedy palm species to establish themselves and for secondary species to increase their densities. When climatic conditions associated with fragmentation change more inside smaller fragments than in larger ones, some species are disproportionately harmed, and unharmed competitors may increase their densities in compensation (Tilman 1996), as may be occurring with the secondary palm species.

The occurrence of *Lepidocaryum tenue* only in Dimona may be just a chance effect perhaps related to the proximity of this site to a seed source. Although most of the habitat, demography and life history characteristics (Tab. 1) are similar for the five studied species, their low seed production may make them slow to increase in abundance. Vegetative reproduction can be essential for establishment and short-distance dispersal of many terrestrial species (Andersen 1995). It is possible that *L. tenue* invaded *via* seed dispersal and subsequently reproduced through stolon-like rhizomes, which in this species, can reach up to 2 m in length (Kahn

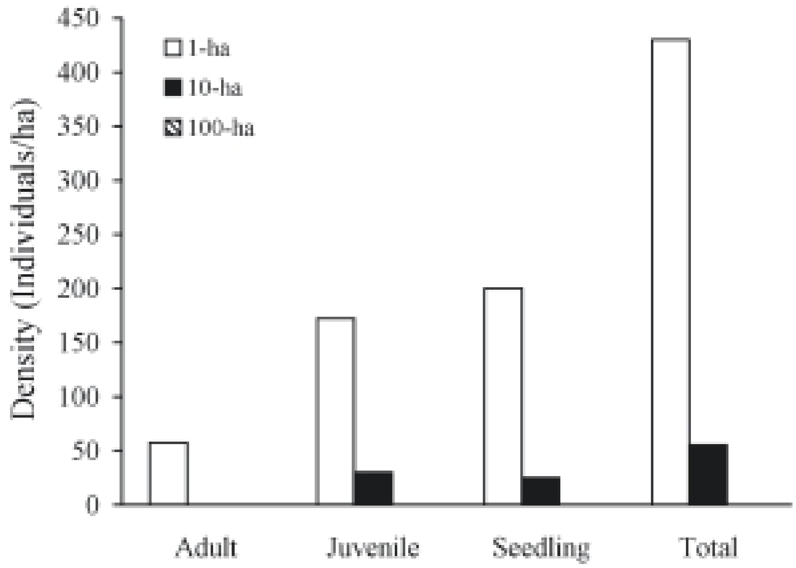

Figure 1. Mean density of individuals/ha for the three secondary and the weedy palm species pooled in the Dimona site. Total represents all life stages pooled. Each category of fragment size has three reserves sampled, except for the 100-ha, which has only two.

& Mejia 1987). Vegetative reproduction may have contributed to increase *L. tenue* population size, which has been favored by environmental conditions found in the hyper-disturbed smaller forest fragment, even though they had been isolated for only 10-15 yrs. Probably, *L. tenue* population size will continue to increase in the 1- and 10-ha fragments and may also colonize other fragments.

The future scenario - In this area of the Amazonia, one-third of the 31 forest palm species occurring in the continuous forest was rare (Scariot 1999), which may make them very susceptible to habitat disturbance. When the diversity of the recipient biota is reduced through extinction or over-exploitation it becomes more vulnerable to invasion by other species (Vermeij 1991, 1996), and hyper-disturbed fragments may be colonized by weedy species.

In the future, in highly fragmented areas of Amazonia, to maintain most of the original diversity native palm species characteristic of closed forest will need large and extensive tracts of continuous forest, exceeding those studied here, where ecological patterns and processes may be preserved (Scariot 1996). Secondary species may be present in naturally disturbed patches of unbroken forest and in forest fragments. However, as the fragmentation increases and the remaining fragments decay, more hyper-disturbed areas will be available for the weedy species, which may eventually foster the decline of closed forest species populations and affect the abundance of low-density palms.

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