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Demography of palm species in Brazil's Atlantic forest: a comparison of harvested and unharvested species using matrix models

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Abstract Surprisingly little is known about the effect of alternative harvesting methods and different means of reproduction on the population dynamics of plant species. Here, we test the hypothesis that habitat fragmentation leads to negative population growth rates for three palm species in Brazil's biodiversity-rich and highly fragmented Atlantic forest. We compared the demography (λ and elasticities) of *Astrocaryum aculeatissimum*, *Euterpe edulis* and *Geonoma schottiana* in five fragments ranging in size from 19 to 3500 ha. A total of 4.05 ha were censused throughout the landscape studied. All individuals of the three palms were tagged in 2005 and their survival was monitored in 2006 and 2007. All new plants were also recorded. Summary matrices were constructed for each transition years by pooling data from all plots of all fragments together for each species. Based on summary matrices, *A. aculeatissimum* and *G. schottiana* asymptotic population growth rates were not significantly different from 1, suggesting that populations of these palms were stable. The projection of *E. edulis* populations was to decrease in size, with 95% confidence intervals of λ for these estimates failing to exceed one in the second transition year. *A. aculeatissimum*, *E. edulis* and *G. schottiana* survivorship was high for all stage classes and exceeded 85% for postseedling stages. We found that the more important vital

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rates were the survival rates in larger stages for all three species. Our results show that the maintenance of high levels of reproductive survivorship should be a focus of conservation strategies for these species, especially in the case of large *E. edulis* individuals.

Introduction

Deforestation and fragmentation are pervasive environmental changes affecting old-growth forest throughout the tropics (Myers et al. 2000). High deforestation rates have converted formerly continuous tropical forest into anthropogenic landscapes, where forest habitats are reduced to scattered forest fragments of varying sizes and quality (Ranta et al. 1998; Fischer and Lindenmayer 2007). In addition to microclimatic and other changes in fragments, remnants are also often degraded by timber harvesting, the extraction of non-timber forest products such as leaves, fruits and palm heart, and the invasion of exotic and weedy plants (Tabarelli et al. 2004; Ewers and Didham 2006).

In species whose leaves are harvested defoliation can actually stimulate leaf production (Anten et al. 2003; Zuidema et al. 2007). However, in species whose fruits are exploited recruitment may be insufficient to maintain populations over the long term (Peres et al. 2003). Similarly, intensive exploitation also appears incompatible with population persistence in species whose stems are harvested for their edible pith (e.g., palm heart) (Nodari et al. 2000; Zuidema 2000). In concert with the detrimental effects of fragmentation, the harvesting of non-timber forest products may mean many harvested species are at especially severe risk of population decline.

Population projection matrices have become the model of choice in plant demographic studies because they are well suited to the range of complex life cycles typical of plants (Silvertown et al. 1996). Matrix-based demographic models also provide an excellent means by which to assess the consequences of altered recruitment for plant population dynamics (Bruna 2003), and the analysis of these matrices provides a range of measures of population structure and behavior that afford comparison between species (Caswell 2001). Finally, matrix models constitute an excellent tool for elaborating management plans in a context of sustainability (Silvertown et al. 1996; Escalante et al. 2004; Zuidema et al. 2007). They are commonly used to project what the asymptotic growth rate of a population, or λ (Caswell 2001), which can also be used as a measure of fitness for organisms possessing a particular set of traits in a particular environment (Caswell 2001).

One of the most fragmented tropical forests is the Atlantic forest of Brazil. This ecosystem, which once stretched for about 4000 km along the coast of Brazil and covered over 1 million km^2, has one of the highest recorded levels of endemism in the world (Myers et al. 2000). Today less than 8% of the Atlantic forest remains (SOS Mata Atlântica 2008), most of which is in fragments of <100 ha (Ranta et al. 1998).

Palms are considered a "keystone" family in the Neotropics—their fruits and seeds are consumed by a wide variety of animal species and they are often the main food source for many taxa in periods of fruit scarcity (Terborgh 1986). In Brazil's Atlantic Forest, there are ten genera and ca. 45 species of palms, of which most are endemic to this ecosystem (Henderson et al. 1995). The leaves of many of these palms, such as *Geonoma schottiana* and *Chamaedorea* species, are used for basketry, thatching, or in the floral industry (Zuidema et al. 2007; Martínez-Ramos et al. 2009). Others, such as *Euterpe edulis*, are

exploited for their edible palm heart (Silva-Matos et al. 1999; Galetti and Aleixo 1998; Fantini and Guries 2007). The effect of this exploitation by humans on population viability and plant demography is for the most part unknown, as is the potential for synergistic effects of fragmentation and harvesting.

Here we present the result of a study in which we compared the dynamics of three palm species found in Atlantic forest fragments, with the goal of both quantifying the population growth rates of these species and proposing potential management interventions. Our study focused on one palm species with clonal growth that is not harvested by humans (*Astrocaryum aculeatissimum*), one single-stemmed species that is harvesting by felling for palm heart (*E. edulis*), and one single-stemmed species whose leaves are harvested (*G. schottiana*). We used stage-classified (Lefkovitch 1965) matrix population models to address the following questions: (1) What are the projected values of λ for *A. aculeatissimum*, *G. schottiana* and *E. edulis* populations in our fragmented study landscape? (2) What lower-level vital rates have large influences of λ, suggesting they would make suitable targets or management interventions?

Methods

Study site and species

The study was carried out in southeastern Brazil in five fragments of lowland Atlantic rain forest ("floresta pluvial baixo montana", Rizzini 1979). These fragments were part of a large forest expanse until a century ago (Carvalho 2005), when coffee plantations and other forms of agriculture led to extensive deforestation and fragmentation. Two of these sites were protected areas: the National Biological Reserve of Poço das Antas ($\sim$3500 ha) and National Biological Reserve of União ($\sim$2400 ha). The other three sites—Santa Helena (57 ha), Estreito (21 ha) and Afetiva-Jorge (19 ha)—were forest fragments located on private property in the municipalities of Silva Jardim, Casimiro de Abreu and Rio das Ostras (Rio de Janeiro state). These municipalities still have 33% (31466 ha), 30% (14031 ha) and 15% (3429 ha) forest cover, respectively (SOS Mata Atlântica 2008).

The climate in the region is classified as Walter and Lieth's Equatorial type (Walter 1971), with mean annual rainfall of ca. 2100 mm (1987–1997 data, Souza and Martins 2004). There is no distinct dry season and, despite large variation between years, a drier period occurs normally from May to August. Details on the vegetation structure of the fragments can be found in Carvalho (2005). All fragments and both reserves are surrounded by pasture, agricultural fields and secondary forest.

Astrocaryum aculeatissimum (Schott) Burret is a monoecious, slow-growing, palm that is found in both single-stemmed (hereafter "solitary") or multi-stemmed forms. It is typically 4–8 m in height and 11–15 cm in diameter (Henderson et al. 1995; Lorenzi et al. 2004). This species is endemic to the Atlantic Forest and occurs from Bahia to Santa Catarina (Henderson et al. 1995; Lorenzi et al. 2004). It is found primarily in the understory of lowland forest, though it is occasionally found in flooded sites and in the matrix surrounding the forest fragments.

Euterpe edulis Mart. (i.e., "*palmito Juçara*") is a monoecious, solitary, shade-tolerant palm. It is a slow-growing subcanopy palm that can reach 20 m in height and 10–15 cm in diameter. It occurs primarily in forests along the Atlantic coast of Brazil, though it can be found inland as far as Argentina and Paraguay (Henderson et al. 1995). It occupied the crests or slopes of hills and flooded sites up to 1000 m elevation (Henderson et al. 1995;

Silva-Matos and Watkinson 1998). This species is harvested for palm heart and it is one of the most abundant and valuable non-timber forest products in the Atlantic forest (Fantini and Guries 2007). The palm must be 8 years old before it is large enough to be harvested (Gaiotto et al. 2003). Intensive harvesting has led to the decline of the palm over much of the region, many of the surviving populations are small and fragmented (Silva-Matos et al. 1999; Galetti and Aleixo 1998). Because *E. edulis* has a single apical meristem, the removal of the heart of palm results in the death of the plant.

Geonoma schottiana Mart. (Ouricana) is a monoecious, solitary or rarely multi-stemmed species, shade-tolerant and slow-growing palm. It is typically 1–4 m in height and occupies the forest understory of lowland forest (Henderson et al. 1995; Lorenzi et al. 2004). This species occurs in Atlantic rain forest and the *Cerrado* (Henderson et al. 1995; Lorenzi et al. 2004). In our sites the leaves of *G. schottiana* are harvested for floral arrangements; leaves are harvested by either removing the leaves or cutting the stem of the plant. Cutting the stem of the plant leads to its death.

Demographic plots and annual censuses

In each fragment we censused palms in nine 30 × 30 m plots that were distributed systematically in three blocks. Each block had three plots that were 50 m apart, and each block was 100 m apart. A total of 0.81 ha was censused in each fragment, for a total of 4.05 ha across the landscape. This sampling method was adopted because we hoped to sample the same possible environmental heterogeneity in the five fragments studied. This layout and intensity was also decided upon on previously casual field observation and on data of palms distribution collected by Pires (2006). One block was established in the middle of each fragment and the other two blocks were established on opposite sides of the first block. In the two National Biological Reserves we used a previously-established trail close to the center of the fragment; all other methods were the same. All individuals of the three palms species were tagged with a numbered aluminum label from June to September of 2005. The survivals of the plants were subsequently monitored between June and September of 2006 and 2007. All new plants were also tagged. Each individual was assigned to one of five ontogenetic stages based on morphological and morphometrical analysis (Table 1, for additional details see Portela 2008). From June to September of 2007 we also counted the number of *E. edulis* and *G. schottiana* individuals inside the plots that had been harvested (Portela 2008).

Matrix construction

We distinguished five ontogenetic stages for each palm species based on morphological and morphometrical analysis (Table 1). We construct life cycle graphs for the three palm species (Figs. 1a, 2a, 3a), which we then summarized in Lefkovitch matrices based on these five ontogenetic stages (Figs. 1b, 2b, 3b). The construction of Lefkovitch matrices and their analysis is described in detail elsewhere (Caswell 2001); all matrices used in our analyses are summary matrices made by pooling data from all populations and then estimating the transition probabilities and fecundity using pooled data (Horvitz and Schemske 1995; Bruna 2003). A summary matrix is the best means of synthesizing the demography of multiple populations, as opposed to a matrix composed of the average of multiple projection matrices, because it accounts for the disproportionate weight that low plant numbers in some size classes in some locations can give to transition probabilities (Horvitz and Schemske 1995; Bruna 2003). In our study using pooled matrices is also advantageous

Table 1 Characteristics of the five ontogenetic stages for the three species studied (*A. aculeatissimum*, *E. edulis* and *G. schottiana*) in the five forest fragments of Atlantic rain forest based on morphological and morphometrical analysis

	A. aculeatissimum	*E. edulis*	*G. schottiana*
Seedling	Bifid leaves	Palmate leaves	Bifid leaves
Infant (*sensu* Piñero et al. 1984)	Bifid leaves, incompletely segmented ones or only incompletely segmented ones	Completely segmented leaves, but palmate ones can still be present	Bifid leaves or incompletely segmented ones or completely segmented ones, with diameter but stemless
Juvenile	First completely segmented leaf blades, but bifid leaves and incompletely segmented ones can be also present	Only completely segmented leaf blades and maximum diameter of 52 mm but stemless	Bifid leaves or incompletely segmented ones or completely segmented ones, with apparent stem and diameter up to 30 mm
Immature	Completely segmented leaf blades and apparent stem but no signals of reproductive event	Completely segmented leaf blades, apparent stem with diameter bigger than 52 mm but no signals of reproductive event	Bifid leaves or incompletely segmented ones or completely segmented ones, with apparent stem and diameter bigger than 30 mm but no signals of reproductive event
Reproductive	Recognized by the production of flowers and fruits		

because it allows the estimation of several vital rates not observed in some of the forest fragments due to low plant density. It is important to emphasize, however, that summary matrices represent a comprehensive perspective on the demography of a species across a landscape, rather than of populations in any particular fragment.

We constructed summary projection matrices for each palm species for each transition years (2005–2006, 2006–2007, Figs. 1b, 2b, 3b). From 1 year to the next, plants can grow into the next ontogenetic stage (G), remain at the same stage (S), shrink into a smaller stage (R), or die; these are the upper-level vital rates (matrix elements). Each of these rates are a product of lower level vital rates (LLVR) (or underlying vital rates), which represent more concrete biological processes in the life of each individual (Caswell 2001). To estimate these matrix elements, we calculated first the underlying vital rates (Figs. 1c, 2c, 3c). More details of how to calculate underlying vital rates and use them to construct transition matrices can be found elsewhere (Morris and Doak 2002, 2005).

Matrix population model

Each summary matrix was used to calculate the asymptotic population growth rate (λ) and the elasticities of λ to different LLVR (Caswell 2001). We assessed whether estimates of λ for each species were significantly different from 1.0 by comparing the bias-corrected 95% confidence intervals (95% CI), which we estimated by bootstrapping (Kalisz and McPeek 1992). The raw data (individuals) were resampled 2,000 times to obtain 2,000 transitions matrices and calculate the corresponding 95% CI of λ (Caswell 2001; Bruna and Oli 2005). Unlike the elasticities of matrix elements, the elasticities of the underlying vital rates effectively separate the independent influence of the demographic processes on population growth (Franco and Silvertown 2004). Therefore, the vital rate elasticities are preferred because they strictly correspond to the fundamental demographic processes those matrix element elasticities only approximate (Franco and Silvertown 2004). Ideally, demographic
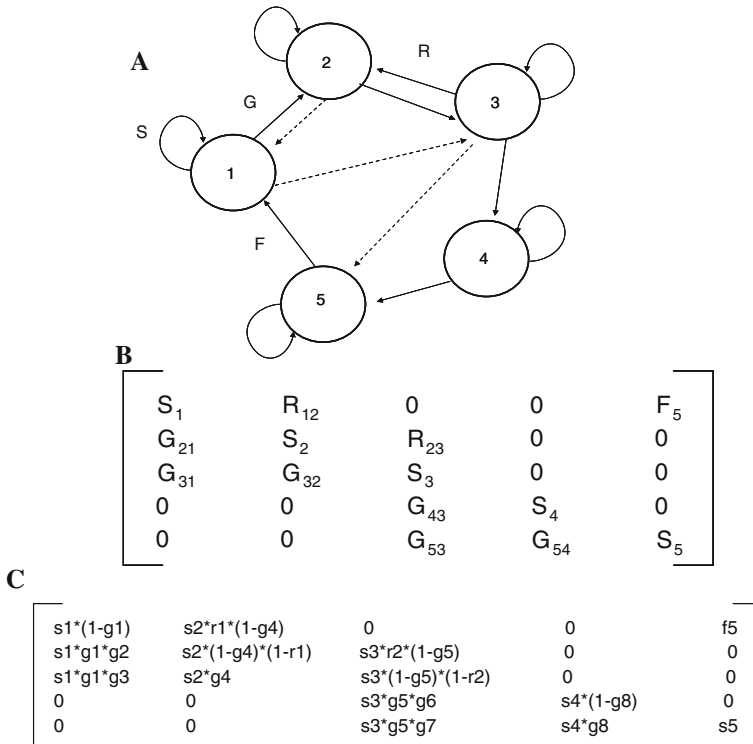
Fig. 1 a Life-cycle graph for *A. aculeatissimum. Arrows* indicate potential transitions between five stage classes, including contribution to seedling (stage class 1) via reproduction. *Dashed lines* indicate transitions that were rarely observed (<1%). Examples of the transitions elements from matrix A that represent fertility (F), stasis (S), regression (R), and growth (G) are included. Ontogenetic stages: *1* seedling, *2* infant, *3* juvenile, *4* immature and *5* reproductive. **b** A population projection matrix corresponding to the life-cycle in **a**. The elements of the matrix represent fecundity per reproductive individual (F_5), the probability of survival and growth from a give stage to a larger one (G_{ij}), the probability of survival and regression to smaller stages (R_{ij}), or the probability of survival and remaining in the same stage from one time interval to the next (stasis S_i). Zero entries represent transitions that are never observed. **c** A population projection matrix corresponding to the life-cycle in **a** based on the lower levels vital rates. *s1* seedling survival, *g1* positive growth of seedling, *g2* growth of seedling to infant, *g3* growth of seedling to juvenile, *s2* infant survival, *r1* negative growth of infant, *g4* positive growth of infant, *s3* juvenile survival, *r2* negative growth of juvenile, *g5* positive growth of juvenile, *g6* growth of juvenile to immature, *g7* growth of juvenile to reproductive, *s4* immature survival, *g8* positive growth of immature, *s5* survival of reproductive, *f5* fecundity, the ratio of the number of new seedlings observed in $t + 1$ over the number of reproductives individuals in *t*. Zero entries represent transitions that are never observed

comparisons between populations should be made using elasticities of vital rates them-selves, rather than for matrix elements that are the product of those rates (Franco and Silvertown 2004). In addition, matrix element elasticities appear to be sensitive to the definition and number of size classes used in matrix construction (Franco and Silvertown 2004). Zuidema (2000) found that greatly increasing the number of size categories sig-nificantly changed the elasticities of matrix elements, but left vital rates elasticities almost unaltered. Thus, interspecific comparisons between species, which inevitably involve comparing matrix models that differ in their construction, will be less prone to error if they are based upon vital rates elasticities (Franco and Silvertown 2004). Note, however,
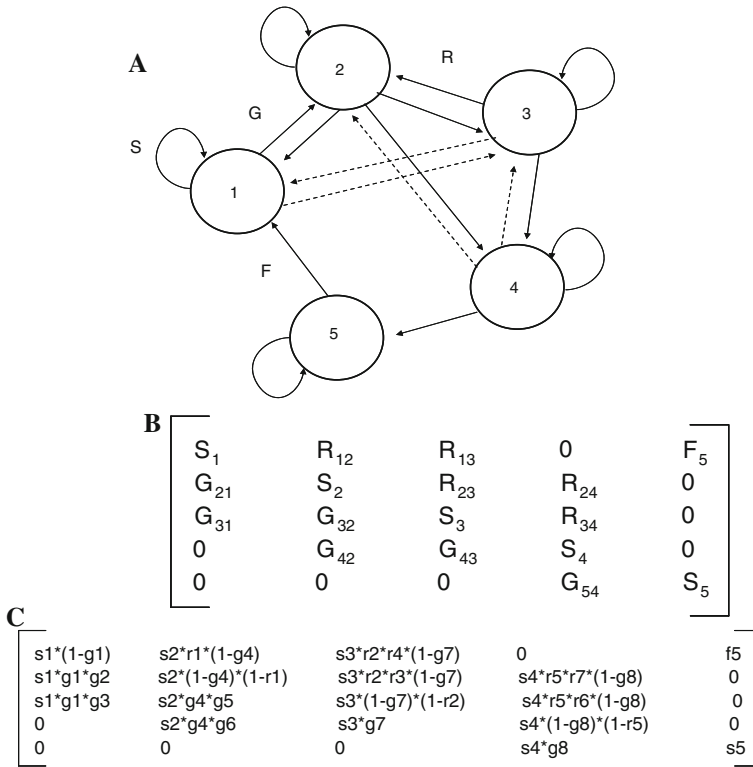
Fig. 2 **a** Life-cycle graph for *E. edulis*. Life-cycle graph legends in Fig. 1. **b** Population projection matrix legends in Fig. 1. **c** A population projection matrix corresponding to the life-cycle in **a** based on the lower levels vital rates. *s1* seedling survival, *g1* positive growth of seedling, *g2* growth of seedling to infant, *g3* growth of seedling to juvenile, *s2* infant survival, *r1* negative growth of infant, *g4* positive growth of infant, *g5* growth of infant to juvenile, *g6* growth of infant to immature, *s3* juvenile survival, *r2* negative growth of juvenile, *r3* negative growth of juvenile to infant, *r4* negative growth of juvenile to seedling, *g7* positive growth of juvenile, *s4* immature survival, *r5* negative growth of immature, *r6* negative growth of immature to juvenile, *r7* negative growth of immature to infant, *g8* positive growth of immature, *s5* survival of reproductive, *f5* fecundity, the ratio of the number of new seedlings observed in $t + 1$ over the number of reproductives individuals in t

that unlike matrix elements elasticities, vital rates elasticities do not sum to unity. All analyses were carried out in MATLAB version 7.5.0.342 (MathWorks, Natick, Massachusetts, USA).

Results

Asymptotic growth rate (λ)

Based on summary matrices, *A. aculeatissimum* asymptotic population growth rate was slightly but significantly greater than one in the first transition year (Table 2). In the second transition year the asymptotic population growth rate was slightly below but not significantly different from one, as evidenced by the 95% CI of λ overlapping 1. *E. edulis*
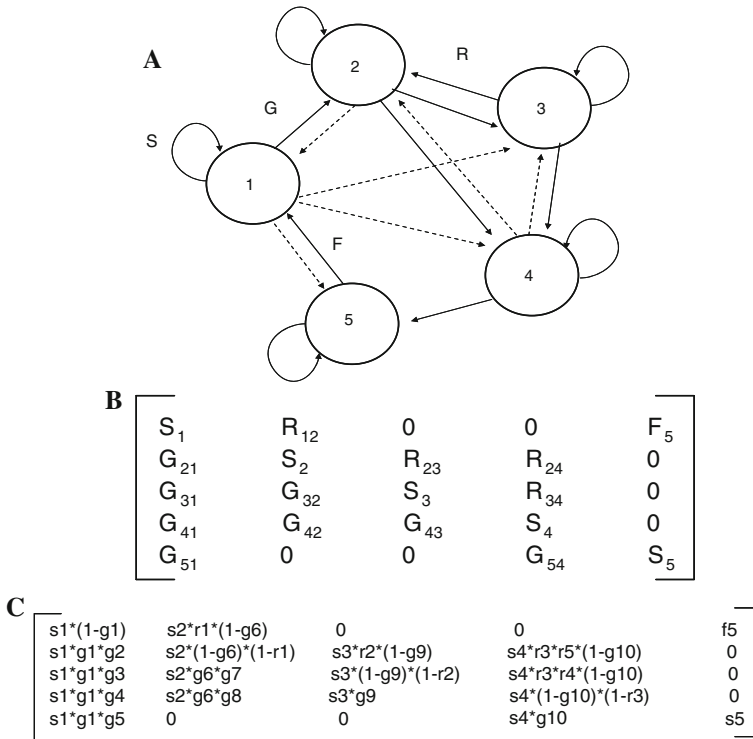
Fig. 3 **a** Life-cycle graph for *G. schottiana*. Life-cycle graph legends in Fig. 1. **b** Population projection matrix legends in Fig. 1 **c** A population projection matrix corresponding to the life-cycle in **a** based on the lower levels vital rates. *s1* seedling survival, *g1* positive growth of seedling, *g2* growth of seedling to infant, *g3* growth of seedling to juvenile, *g4* growth of seedling to immature, *g5* growth of seedling to reproductive, *s2* infant survival, *r1* negative growth of infant, *g6* positive growth of infant, *g7* growth of infant to juvenile, *g8* growth of infant to immature, *s3* juvenile survival, *r2* negative growth of juvenile, *g9* positive growth of juvenile, *s4* immature survival, *r3* negative growth of immature, *r4* negative growth of immature to juvenile, *r5* negative growth of immature to infant, *g10* positive growth of immature, *s5* survival of reproductive, *f5* fecundity, the ratio of the number of new seedlings observed in $t + 1$ over the number of reproductives individuals in t

Table 2 Asymptotic growth rate (λ) and the 95% CI for the three species studied (*A. aculeatissimum*, *E. edulis* and *G. schottiana*) in the five forest fragments of Atlantic rain forest

λ (95% CI)	*A. aculeatissimum*	*E. edulis*	*G. schottiana*
2005–2006	1.0093 (1.0017–1.0162)	0.9930 (0.9566–1.0234)	1.0043 (0.9843–1.0242)
2006-2007	0.9964 (0.9867–1.0025)	0.9569 (0.9163–0.9987)	0.9823 (0.9612–1.0040)

Sampled area: 4.05 ha

populations are projected to shrink at rates of 0.7 and 4.31% per year, though the 95% CI for these estimates failed to exceed one in the second transition year. *G. schottiana* asymptotic population growth rate was slightly above one in the first transition year; in the second transition year the 95% CI of the asymptotic population growth rate overlapped 1.

Lower levels vital rates

The survivorship of *A. aculeatissimum*, *E. edulis* and *G. schottiana* was high for all stage classes and exceeded 85% for postseedling stages (Tables 3, 4, 5). Immatures and reproductive *E. edulis* had lower survivorship in the 2006–2007 transition year. For seedling stages, *A. aculeatissimum* had the highest seedling survivorship: 83.3 and 87.2% in 2005–2006 and 2006–2007, respectively. *E. edulis* had intermediate seedling survivorship (73.9 and 74.7% in 2005–2006 and 2006–2007, respectively). *G. schottiana* had the lowest seedling survivorship: 28.7% in 2005–2006 and 38.3% in 2006–2007.

Very few individuals were capable of extremely rapid transitions among stage classes, most of then grow only into the next stage class. For *A. aculeatissimum*, the transition for seedling to a bigger stage (16.73%), occurs especially for infant stage (97.56%). For *E. edulis* growth, the higher values was found for infant (27.62 and 42.13%), with the majority growing to the next stage (78.48 and 90.91%). Seedlings of *G. schottiana* difficultly grow to a larger stage, 6.76 and 4.87%, and the majority grows to the next stage, 87.5 and 94.29%. A small proportion of the palms individuals (less than 10%) changed to a smaller stage after a 1-year period. For *A. aculeatissimum,* 42.02% of juveniles regress to infants in the second transition year. For *E. edulis*, 18.23% of juveniles regress, with the majority (97.3%) regressing only one stage.

Elasticities

For both transition years, elasticity patterns for the three palm species were very similar to each other. The highest elasticity values were for survival, especially for the later ontogenetic stages (Tables 3, 4, 5). Values for regressions were generally low. The highest vital rates elasticities for *A. aculeatissimum* and *G. schottiana* were similar between both

Table 3 LLVR and elasticities for summary matrices describing the demography of *A. aculeatissimum*. Abbreviations legends in Fig. 1

	2005–2006		2006–2007	
	LLVR	Elasticities	LLVR	Elasticities
s1	0.8333	0.0291	0.8722	0.0087
g1	0.1673	0.0051	0.1824	0.0011
g2	0.9756	0.0084	0.9821	0.0024
g3	0.0244	0.0007	0.0179	0.0001
s2	0.9897	0.2471*	0.9670	0.0638
r1	0.0087	−0.0011	0.0079	−0.0002
g4	0.0113	0.0059	0.0182	0.0021
s3	0.9820	0.1224*	0.9938	0.0078
r2	0.0316	−0.0025	0.4202	−0.0021
g5	0.0194	0.0059	0.0115	0.0021
g6	0.9474	0.0076	1.0000	0.0022
g7	0.0526	0.0005	0	0
s4	0.9941	0.0742	0.9883	0.0154
g8	0.0893	0.0011	0.1361	0.0001
s5	0.9937	0.5191*	0.9940	0.9021*
f5	0.4340	0.0081	0.3123	0.0022

* Highest elasticities

	2005–2006		2006–2007	
	LLVR	Elasticities	LLVR	Elasticities
s1	0.7394	0.0792	0.7479	0.1180*
g1	0.1583	0.0202	0.1547	0.0258
g2	1.0000	0.0295	0.9286	0.0369
g3	0	0	0.0714	0.0031
s2	0.9408	0.1192*	0.9109	0.0916
r1	0.0420	−0.0023	0.0085	−0.0003
g4	0.2762	0.0095	0.4213	0.0049
g5	0.7848	0.0280	0.9091	0.0368
g6	0.2152	0.0118	0.0909	0.0047
s3	0.9398	0.0881	0.9227	0.2072*
r2	0.1823	−0.0018	0.0262	−0.0004
r3	0.9730	0.0110	1.0000	0.0041
r4	0.0270	0.0001	0	0
g7	0.1478	0.0069	0.1466	0.0079
s4	0.8960	0.2133*	0.8401	0.2743*
r5	0.0194	−0.0013	0.0104	−0.0006
r6	0.8333	0.0020	0.6667	0.0013
r7	0.1667	0.0003	0.3333	0.0006
g8	0.0323	0.0222	0.0242	0.0341
s5	0.9367	0.4719*	0.8333	0.2690*
f5	1.4304	0.0284	3.2857	0.0399

Table 4 LLVR and elasticities for summary matrices describing the demography of *E. edulis*. Abbreviations legends in Fig. 2

* Highest elasticities

transitions years, with the highest elasticities representing survival of reproductive. For *E. edulis* in the first transition year, the highest vital rate elasticities were for the survival of reproductive plants, but in the second transition year, elasticities for immature and reproductive were very similar and nearly followed by juvenile.

For all three palms, the survival of reproductives was the most important LLVR for λ and should be the primary targets of management efforts. Although there were others stages survival that were also contribute to lambda, especially for *E. edulis*.

Discussion

Our results suggest that populations of *A. aculeatissimum* and *G. schottiana* in our focal landscape are stable, but that *E. edulis* populations will decline. Elasticity patterns for the three palm species were very similar to each other for both transition years analyzed, with the survival rates in larger stages having the highest elasticity values. This result is consistent with that from other systems indicating that survival is critical for population maintenance in long-lived plant species (Franco and Silvertown 2004; Bruna et al. 2009). Our results suggest that ensuring the survivorship of large, reproductive individuals should be a major focus of conservation strategies for these species, especially *E. edulis*.

Table 5 LLVR and elasticities for summary matrices describing the demography of *G. schottiana*. Abbreviations legends in Fig. 3

	2005–2006		2006–2007	
	LLVR	Elasticities	LLVR	Elasticities
s1	0.2879	0.0373	0.3881	0.0446
g1	0.0676	0.0266	0.0487	0.0270
g2	0.8750	0.0193	0.9429	0.0256
g3	0	0	0.0286	0.0011
g4	0.0833	0.0042	0.0286	0.0012
g5	0.0417	0.0038	0	0
s2	0.8579	0.0576	0.8693	0.0785
r1	0.0187	−0.0007	0.0065	−0.0003
g6	0.2500	0.0093	0.2941	0.0095
g7	0.6375	0.0111	0.6444	0.0183
g8	0.3625	0.0102	0.3556	0.0115
s3	0.9275	0.0388	0.9733	0.0893
r2	0.0938	−0.0008	0.0685	−0.0014
g9	0.1719	0.0040	0.1781	0.0025
s4	0.9093	0.1041*	0.8952	0.1856*
r3	0.0181	−0.0006	0.0222	−0.0007
r4	0.8333	0.0008	0.7143	0.0022
r5	0.1667	0.0001	0.2857	0.0006
g10	0.1390	0.0105	0.0633	0.0172
s5	0.9683	0.7348*	0.9368	0.5742*
f5	4.5344	0.0273	5.8921	0.0278

* Highest elasticities

That populations of *A. aculeatissimum* were neither growing nor decreasing in our study landscape suggests that it is tolerant of the altered environment found in fragments. Interestingly, this is the only species we studied that is not harvested, and more than 50% of the population grows clonally (Portela 2008). These two characteristics may favor the persistence of similar palm species (e.g., *Bactris setosa* and *Desmoncus polyacanthos*, Pires 2006) in fragmented Atlantic forests. In contrast, *E. edulis* is heavily harvested for its palm heart in the Atlantic forest (Fantini and Guries 2007), leading to its local extirpation from many sites (Galetti and Fernandez 1998; Silva-Matos and Bovi 2002). Our elasticity analyses indicate this is probably due to the harvesting methods—stem cutting strongly influences survival (Svenning and Macia 2002; Franco and Silvertown 2004). It is also important to note that two of our study sites were National Biological Reserves, and even when including these protected areas in our analyses we project that *E. edulis* populations are decreasing across our landscape. In addition to the anthropogenic pressure for palm heart, populations we studied also suffered attack by Capuchin monkeys (*Cebus nigritus*), which kill individuals by breaking the stems to consume the palm heart (Taira 2007; Portela 2008). This was particularly true in the second transition year for "immatures" and "reproductives" in the National Biological Reserve of Poço das Antas. Although the long-term impacts for *E. edulis* of herbivory by monkeys remain to be seen, similar feeding by Capuchin monkeys was blamed for the decline of the palm *Geonoma brevispatha* in an Atlantic rain forest fragment in the state of São Paulo (Souza and Martins 2006).

Unlike *E. edulis*, which always dies when harvested, *G. schottiana* can survive if only the leaves are removed; this is the harvesting strategy most observed in our study landscape (Portela 2008). Defoliation studies have shown that understory palms are remarkably tolerant to complete defoliation (Oyama and Mendoza 1990; Chazdon 1991). For instance Zuidema et al. (2007) found that ramet survival of *Geonoma deversa* was not changed following defoliation if the stem is undamaged. However, others have found that defoliation has a strong negative effect on reproduction (flowering and fruiting in *Chamaedorea elegans*, Martínez-Ramos et al. 2009). The results of these defoliation studies, coupled with our projections of λ, suggest the harvesting of *G. schottiana* leaves is probably sustainable if it continues at current levels. However, if individuals are killed during the harvesting of the leaves, it is likely to cause dramatic decreases in λ (*sensu* Svenning and Macia 2002).

Previous work with *Astrocaryum mexicanum* has shown low survivorship in early stages but almost no mortality during the reproductive ones (Piñero et al. 1984). However, while we also found reproductive stages of *A. aculeatissimum* had high survival rates (99.3 and 99.4%), the survival of seedlings and infants were also extremely high in both transition years (seedlings: 83.3 and 87.2%; infants: 98.9 and 96.7%). We suggest that the reason our *A. aculeatissimum* seedling and infants survival rates are so much higher than *A. mexicanum* smaller individuals may be because our *Astrocaryum* species grows predominantly clonally or because de fruits of this species is bigger (*A. aculeatissimum* 5–6 cm and *A. mexicanum* 4–6 cm, Lorenzi et al. 2004).

Implications for plant populations in fragmented Atlantic rain forest

For long lived plant species, the most "important" vital rates are typically those describing the survival of larger ontogenetic stages (Franco and Silvertown 2004). Consequently, the best way to enhance the likelihood of persistence of harvested species is to protect larger, often reproductive individuals. Our results are consistent with this conclusion, and suggest that palm harvesting that kills adults for palm heart or thatch is likely to be unsustainable in our sites. However, in species in which adults are not harvested (e.g., *A. aculeatissimum*), protecting adults is unlikely to have a large impact on λ because survivorship of these stages is already quite high (de Kroon et al. 2000). We therefore propose that, in addition to protecting large plants, protecting smaller size classes whose elasticity values are lower but for which survivorship can still increase is the best means by which to enhance λ (*sensu* de Kroon et al. 2000).

Our results also demonstrate that even in a highly fragmented and impacted forest such the Atlantic rain forest, populations of non-pioneer plant species are capable of persisting or even growing. The mechanisms underlying this propensity for persistence are complex, and could include such life-history traits as clonal growth or the capacity to reproduce asexually. Regardless, our results underscore the idea that in addition to protected areas, small fragments can play an important role in plant conservation in tropical forests (Turner and Corlett 1996).

Several caveats to these conclusions bear discussion. First, although sensitivity and elasticity analyses are frequently and effectively used in conservation biology (Caswell 2000), they have some important limitations (de Kroon et al. 2000). For example, elasticity analysis does not analyze the effects of actual variation in the transition elements of populations, but analyses the impact of hypothetical changes in these elements. Then, if large changes in transition values and growth rates are involved, the predicting effects of

sensitivity and elasticity analyses could be imprecise (de Kroon et al. 2000). Also, these analyses are local estimates around a particular value of λ. If λ changes, the relative importance of different transition values and ecological interactions may change as well (Bruna 2003). Second, the study was done during a relatively short period (3 years); longer studies are clearly needed to elucidate the role of environmental stochasticity in long-term population dynamics. Finally, the environmental causes of the observed interannual variation in λ are unclear. We suggest future researcher experimentally explore the role of biotic and abiotic factors influencing plant growth and reproduction as well as the processes occurring in the matrix surrounding fragments, all of which have been shown to have important effects on plant demography in fragmented tropical landscapes. When integrated with demographic data, these studies could elucidate long-term trends in abundance as well as provide insights as to their restoration.

References

Anten NPR, Martínez-Ramos M, Ackerly DD (2003) Defoliation and growth in an understory palm: quantifying the contributions of compensatory responses. Ecology 84:2905–2918

Bruna EM (2003) Are populations in fragmented habitats recruitment limited? Tests with an Amazonian herb. Ecology 84:932–947

Bruna EM, Oli MK (2005) Demographic effects of habitat fragmentation on a tropical herb: life-table response experiments. Ecology 86:1816–1824

Bruna EM, Fiske IJ, Trager MD (2009) Habitat fragmentation and plant populations: is what we know demographically irrelevant? J Veg Sci 20:569–576

Carvalho FA (2005) Efeitos da fragmentação florestal na florística e estrutura da Mata Atlântica submontana de região de Imbaú, município de Silva Jardim, RJ. Dissertation, Universidade Estadual do Norte Fluminense

Caswell H (2000) Prospective and retrospective perturbation analysis: their roles in conservation biology. Ecology 81:619–627

Caswell H (2001) Matrix population models. Sinauer Associates, Massachusetts

Chazdon RL (1991) Effects leaf and ramet removal on growth and reproduction of *Geonoma congesta*, a clonal understory palm. J Ecol 79:1137–1146

de Kroon H, Groenendael JV, Ehrlén J (2000) Elasticities: a review of methods and model limitations. Ecology 81:607–618

Escalante S, Montaña C, Orellana R (2004) Demography and potential extractive use of the liana palm, *Desmoncus orthacanthos* Martius (Arecaceae), in southern Quintana Roo, Mexico. For Ecol Manag 187:3–18

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Bio Rev 81:117–142

Fantini AC, Guries R (2007) Forest structure and productivity of palmiteiro (*Euterpe edulis* Martius) in the Brazilian Mata Atlântica. For Ecol Manag 242:185–194

Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. Glob Ecol Biogeogr 16:265–280

Franco M, Silvertown J (2004) A comparative demography of plants based upon elasticities of vital rates. Ecology 85:531–538

Gaiotto FA, Grattapaglia D, Vencovsky R (2003) Genetic structure, mating system and long distance gene flow in *Euterpe edulis* Mart. J Hered 94:399–406

Galetti M, Aleixo A (1998) Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil. J Appl Ecol 35:286–293

Galetti M, Fernandez JC (1998) Palm heart harvesting in the Brazilian Atlantic forest: changes in industry structure and the illegal trade. J Appl Ecol 35:294–301

Henderson A, Galeano G, Bernal R (1995) Field guide to the palms of the Americas. Princeton University Press, New Jersey

Horvitz CC, Schemske DW (1995) Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecol Monogr 65:155–192

Kalisz S, McPeek MA (1992) Demography of an age-structured annual: resampled projection matrices, elasticity analyses, and seed bank effects. Ecology 73:1082–1093

Lefkovitch LP (1965) The study of population growth in organisms grouped by stages. Biometrics 21:1–18

Lorenzi H, Souza HM, Medeiros-Costa JT, Cerqueira LSC, Ferreira E (2004) Palmeiras brasileiras e exóticas cultivadas. Editora Plantarum, São Paulo

Martínez-Ramos M, Anten NPR, Ackerly DD (2009) Defoliation and ENSO effects on vital rates of an understorey tropical rain forest palm. J Ecol 97:1050–1061

Morris WF, Doak DF (2002) Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates Inc., USA

Morris WF, Doak DF (2005) How general are the determinants of the stochastic population growth rate across nearby sites? Ecol Monogr 75:119–137

Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nodari RO, Fantini AC, Reis A, Reis MS (2000) Restauração de populações de *Euterpe edulis* Martius (Arecaceae) na Mata Atlântica. In: Reis MS, Reis A (eds) *Euterpe edulis* Martius (Palmiteiro): biologia, conservação e manejo. Herbário Barbosa Rodrigues, Itajaí

Oyama K, Mendoza A (1990) Effects of defoliation on growth, reproduction, and survival of a neotropical dioecious palm, *Chamaedora tepejilote*. Biotropica 22:119–123

Peres CA, Baider C, Zuidema PA et al (2003) Demographic threats to the sustainability of Brazil nut exploitation. Science 302:2112–2114

Piñero D, Martinez-Ramos M, Sarukhán J (1984) A population model of *Atrocaryum mexicanum* and a sensitivity analysis of its finite rate of increase. J Ecol 72:977–991

Pires AS (2006) Perda da diversidade de palmeiras em fragmentos de Mata Atlântica: padrões e processos. Thesis of PhD, Universidade Estadual Paulista

Portela RCQ (2008) Dinâmica populacional de três espécies de palmeiras em uma paisagem fragmentada no domínio da Mata Atlântica, RJ. Thesis of PhD, Universidade Estadual de Campinas

Ranta P, Blom T, Niemelä J, Elina J, Sitonem M (1998) The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. Biodivers Conserv 7:385–403

Rizzini CT (1979) Tratado de fitogeografia do Brasil, aspectos sociológicos e florísticos. HUCITEC/Ed. Da Universidade de São Paulo, São Paulo

Silva-Matos DM, Bovi MLA (2002) Understanding the threats to biological diversity in southeastern Brazil. Biodivers Conserv 11:1747–1758

Silva-Matos DM, Watkinson AR (1998) The fecundity, seed and seedling ecology of the edible palm Euterpe edulis in south-eastern Brazil. Biotropica 30:595–603

Silva-Matos DM, Freckleton RP, Watkinson AR (1999) The role of density dependence in the population dynamics of a tropical palm. Ecology 80:2635–2650

Silvertown J, Franco M, Menges E (1996) Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. Conserv Biol 10:591–597

SOS Mata Atlântica (2008) Atlas dos Remanescentes Florestais da Mata Atlântica—Período de 2000–2005. São Paulo

Souza AF, Martins FR (2004) Population structure and dynamics of a neotropical palm in fire-impacted fragments of the Brazilian Atlantic forest. Biodivers Conserv 13:1611–1632

Souza AF, Martins FR (2006) Demography of the clonal palm *Geonoma brevispatha* in a Neotropical swamp forest. Aust Ecol 31:869–881

Svenning JC, Macia MJ (2002) Harvesting of *Geonoma macrostachys* Mart. leaves for thatch: an exploration of sustainability. For Ecol Manag 167:251–262

Tabarelli M, Silva JMC, Gascon C (2004) Forest fragmentation, synergisms and the impoverishment of Neotropical forests. Biodivers Conserv 13:1419–1425

Taira JT (2007) Consumo de palmito Juçara (*Euterpe edulis* Mart.) por macacos-prego (*Cebus nigritus*): estratégia de forrageamento ótimo ou requinte de um gourmet? MS. Dissertation, Universidade de São Paulo

Terborgh J (1986) Keystone plant resources in the tropical forest. In: Soule ME (ed) Conservation biology: the science of scarcity and diversity. Sinauer, New York, pp 330–344

Turner IM, Corlett RT (1996) The conservation value of small, isolated fragments of lowland tropical rain forest. Trends Ecol Evol 11:330–333

Walter H (1971) Ecology of tropical and subtropical vegetation. Oliver and Boyd, Edinburgh

Zuidema PA (2000) Demography of exploited tree species in the Bolivian Amazon. Thesis of PhD, Utrecht University
Zuidema PA, Kroon H, Werger MJA (2007) Testing sustainability by prospective and retrospective demographic analyses: evaluation for palm leaf harvest. Ecol Appl 17:118–128