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Are protected areas really protecting populations? A test with an Atlantic rain forest palm

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Abstract

We compared the demography of the palm *Euterpe edulis* in a large forest fragment that is protected from palm harvesting with that in three smaller fragments where harvesting has occurred. Palms were censused from 2005 to 2007 in nine 30 m x 30 m plots in each forest fragment. Each individual was assigned to one of five stage classes: seedling, infant, juvenile, immature, and reproductive. Using summary matrices constructed for the fragments and a matrix for the population in the protected area, we compared the asymptotic growth rate (λ) in the protected and non-protected areas. We then quantified the contribution of each lower-level vital rate to the observed differences in λ using a fixed-design LTRE. *Euterpe edulis* populations in the protected area are projected to shrink at rates of 4.54 to 12.6% per year, and the populations of the fragments are projected to grow at rates of 3.44 to 9.43% per year. Our LTRE analysis revealed that the generally higher λ for the summary matrix based on the populations in fragments was due primarily to greater survival of immatures and reproductives. However, seedling growth contributed negatively to λ in the fragments. We also found that great numbers of immatures and reproductives were killed by the capuchin monkey (*Cebus nigritus*), which apparently also contributes to the differences between the protected area and the fragments. This study lends support to the idea that small fragments in a landscape actively managed and modified by humans can be very important in maintaining viable plant populations.

Key words: Atlantic rainforest fragments, capuchin monkey, *Euterpe edulis*, LTRE.

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Introduction

In light of the dramatic rate at which landscapes are being altered, perhaps the most effective tool for conserving biodiversity is the establishment of reserves [1]. However, protecting biodiversity in reserves is not enough because threatened populations frequently lie outside protected areas [2]. Any conservation strategy therefore needs to consider protected areas as one of several complementary approaches required to maintain viable populations and ultimately biodiversity [2]. Several studies have evaluated the extent to which “unprotected” fragments conserve species diversity [3-4]. However, little is known regarding the demography and population dynamics of species outside protected areas and whether they are at higher risk of extinction.

The Atlantic rainforest is an excellent system with which to address these issues because it is a mosaic of protected areas and privately owned fragments. This biome contains several reserves of different sizes in the coastal and interior region [5]. It is also a species-rich hotspot, with 40% of the plants from this biome endemic and high rates of landscape conversion [6]. Indeed, less than 8% of the original 1 million km² of Atlantic forest remains [7], and most of the remaining fragments are less than 100 ha in size [8]. Extinction rates are likely to be higher in biodiversity hotspots such as these that are geographically restricted, have high levels of endemism, extensive habitat loss, and rapidly increasing human populations [9]. Here we address the following question: Are populations of an abundant palm species demographically sustainable in a protected area and in privately owned fragments?

Methods

This study was carried out in four fragments of Atlantic forest – the Poço das Antas National Biological Reserve (referred to throughout as the “protected area”) and three fragments on private property (Santa Helena, Estreito, and Afetiva-Jorge, referred to throughout as “small fragments”; Fig. 1). The protected area is approximately 3,500 ha, while the small fragments range in size from 57 ha to 19 ha (Table 1). All are located in southeastern Brazil in Rio de Janeiro State in the municipalities of Silva Jardim and Casimiro de Abreu. These municipalities still have 33% and 30% forest cover, respectively [7]; the fragments were part of a large continuous expanse of forest until a century ago [10] when fragmentation began following the implementation of coffee production and other forms of agriculture.

Table 1. Density of *Euterpe edulis* in our study sites in the three census years (2005, 2006 and 2007) and the number of *E. edulis* harvested in each site in 2007.

Fragment	Density (individuals/ha)			<i>Euterpe edulis</i> harvested (individuals /0,81ha)
	2005	2006	2007	2007†
3,500-ha	1060.5	955.6	906.2	0
57-ha	192.6	171.6	166.7	8
21-ha	33.3	119.8	335.8	0††
19-ha	111.1	103.7	122.2	21

† We counted the number of *E. edulis* harvested in 2007, but these individuals were harvested before the beginning of the study. †† In 21-ha fragment we did not find individuals harvested in the plots, but we did observe harvested individuals outside the plots.

The habitat in all sites is lowland Atlantic rainforest (“floresta pluvial baixo Montana” *sensu* [11]). All sites are surrounded by pasture, agricultural fields, and secondary forest. The climate is classified as Walter and Lieth’s Equatorial type [12], with mean annual rainfall of ca. 2,100 mm [13]. Though there is no distinct dry season, there is often a drier period from May-August.

The focal species of our study was *Euterpe edulis* Mart. (i.e., “palmito Juçara”). It is a monoecious, solitary, slow-growing, and shade-tolerant palm. Though it can reach 20 m in height and 10-15 cm in diameter at breast height, it is considered a subcanopy palm. While it occurs primarily along the Atlantic coast of Brazil, it can be found inland as far as Argentina and Paraguay [14]. It occupies the crests or slopes of hills and flooded sites up to 1,000 m elevation [14-15]. The palm must be 8 years old before it is large enough to be harvested [16].

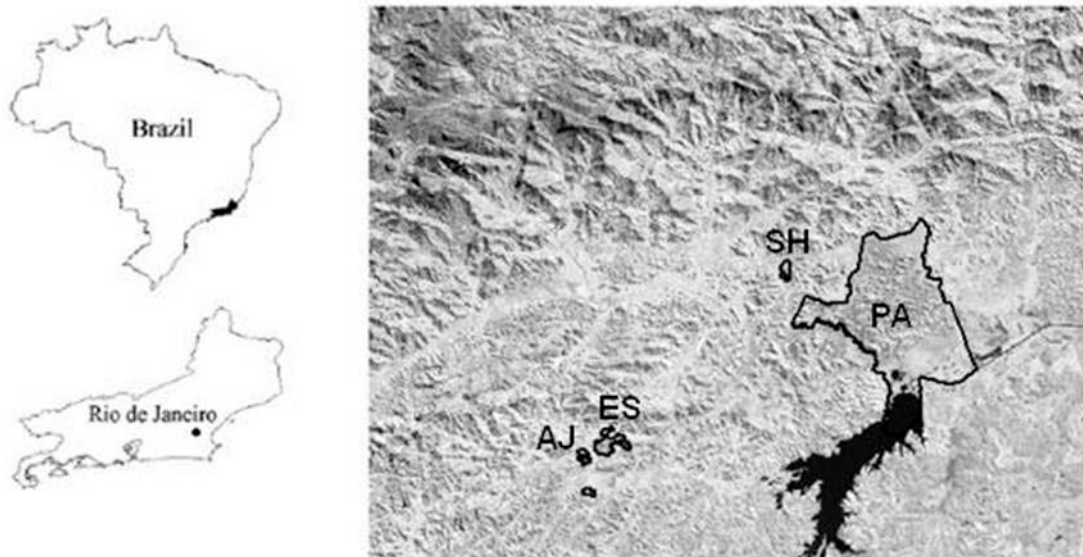


Fig. 1. Location of Poço das Antas National Biological Reserve (PA) and the three fragments on private property called Santa Helena (SH), Estreito (ES), and Afetiva-Jorge (AF) in the state of Rio de Janeiro, Brazil.

In each fragment we censused palms in nine 30 m x 30 m plots that were distributed systematically in three blocks. Each block had three plots that were 50 m apart, with each block 100 m apart. 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 protected area we used a previously established trail close to the center of the fragment. From June to September of 2005 we tagged all *Euterpe edulis* individuals with a numbered aluminum tag. The survival of plants was then monitored between June-September of 2006 and 2007, when all new plants were also tagged. During each census each plant was assigned to one of five stage classes based on morphological and morphometric analysis: (1) seedling, individuals with palmate leaves; (2) infant, individuals

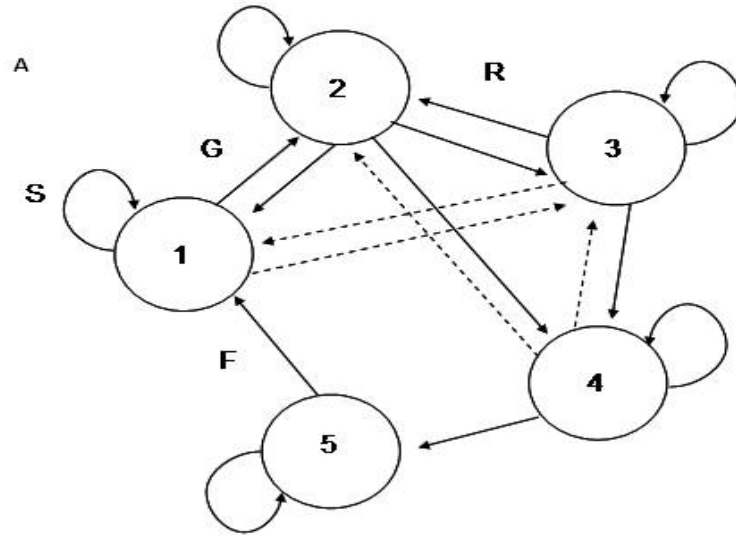
with at least some completely segmented leaves; (3) juvenile, individuals with only completely segmented leaf blades and a maximum diameter at ground level of 52 mm but still stemless; (4) immature, individuals with completely segmented leaf blades, an apparent stem with diameter at ground level >52 mm but no evidence of prior reproduction, and (5) reproductive, individuals with evidence of flower and fruit production. For additional details on the surveys and stage classifications see [17].

The life-cycle graph of *Euterpe edulis* (Fig. 2A) is summarized in a stage-based matrix model [18] with five stages. We constructed summary matrices describing the dynamics of the populations in each fragment in each transition year (i.e., 2005-2006 and 2006-2007) by pooling the data from the nine plots in a site to create a “summary matrix” [19]; summary matrices are the best means of synthesizing the demography of multiple populations because they account for the disproportionate weight that low plant numbers in some size classes in some locations can give to transition probabilities [19-20]. In our study, using pooled matrices is advantageous because it allows the estimation of several vital rates not observed in some of the small forest fragments due to low plant density.

From one year to the next plants can grow into next stage class (G), remain in the same stage (S), shrink into a smaller one (R), or die. The matrix elements representing these stage-specific transition probabilities, as well as elements representing stage-specific fertility, are the product of lower-level vital rates [21-22]. We build our matrix models using these lower-level vital rates, which allows us to investigate the underlying demographic mechanisms responsible for differences among species or populations in population growth rates [23] (Fig. 2 B).

For each matrix, we calculated the asymptotic population growth rate (λ) and the sensitivities of λ to each lower-level vital rate [21-22]. The standard matrix population model will project exponential growth if the dominant eigenvalue (λ) of a matrix is > 1.0 (implying no resource limitations or competition) or exponential decline if $\lambda < 1.0$ (24). We concluded that estimates of λ were significantly different from 1.0 if the bias-corrected 95% confidence intervals (CI) failed to include 1.0. Confidence intervals were estimated by bootstrapping; the raw data (individuals) were resampled 2,000 times to obtain 2,000 transition matrices for which we estimated λ . We then used the distribution of these estimates of λ to calculate the upper and lower 95% confidence intervals using the procedure detailed in [24].

To quantify the contribution of each lower level vital rate to the differences in λ observed between the protected area and the smaller fragments, we used a Life Table Response Experiment (LTRE [24-25]). The construction of LTRE and their analysis is described in detail elsewhere [24-25]; we used a fixed-design LTRE in which the matrix for the protected area was the “control” matrix, and the summary matrix built with data from the three fragments was the “treatment” matrix. We conducted two LTRE comparisons: the protected area vs. the small fragments in each of the two transition years. All analyses were carried out in MATLAB (MathWorks, Natick, Massachusetts, USA).



B

$s_1(1-g_1)$	$s_2r_1(1-g_4)$	$s_3r_2r_4(1-g_7)$	0	f_5
$s_1g_1g_2$	$s_2(1-g_4)(1-r_1)$	$s_3r_2r_3(1-g_7)$	$s_4r_5r_7(1-g_8)$	0
$s_1g_1g_3$	$s_2g_4g_5$	$s_3(1-g_7)(1-r_2)$	$s_4r_5r_6(1-g_8)$	0
0	$s_2g_4g_6$	s_3g_7	$s_4(1-g_8)(1-r_5)$	0
0	0	0	s_4g_8	s_5

Fig. 2. (A) Life-cycle graph for *Euterpe edulis*. 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%). Ontogenetic stages: 1- seedling, 2- infant, 3- juvenile, 4- immature and 5- reproductive. (B) A population projection matrix corresponding to the life-cycle in Fig. 2A based on the lower levels vital rates. s_1 , seedling survival; g_1 , positive growth of seedling; g_2 , growth of seedling to infant; g_3 , growth of seedling to juvenile; s_2 , infant survival; r_1 , negative growth of infant; g_4 , positive growth of infant; g_5 , growth of infant to juvenile; g_6 , growth of infant to immature; s_3 , juvenile survival; r_2 , negative growth of juvenile; r_3 , negative growth of juvenile to infant; r_4 , negative growth of juvenile to seedling; g_7 , positive growth of juvenile; s_4 , immature survival; r_5 , negative growth of immature; r_6 , negative growth of immature to juvenile; r_7 , negative growth of immature to infant; g_8 , positive growth of immature; s_5 , survival of reproductive; f_5 , fecundity, the ratio of the number of new seedlings observed in $t + 1$ over the number of reproductive individuals in t . Zero entries represent transitions that are never observed.

Results

Euterpe edulis populations in the protected area were projected to decline at rates of 4.54% per year ($\lambda = 0.9546$, CI= 0.9101-0.9959, 2005-2006) and 12.6% per year ($\lambda = 0.8740$, CI= 0.8162-0.9256, 2006-2007), with 95% confidence intervals for these estimates failing to exceed one in either year. In contrast, populations in the unprotected fragments are projected to grow at rates of 3.44% per year ($\lambda = 1.0344$, CI= 0.9900-1.1134, 2005-2006) and 9.43% per year ($\lambda = 1.0943$, CI= 1.0275-1.1774, 2006-2007), with significantly greater population growth projected with the data from transition year one than transition year two.

Survivorship was high for all stage classes, and often exceeded 85% for post-seedling stages (Table 2). However, the survival rates of immatures and reproductives in the protected area were 76.96% and 80%, respectively, in the second transition year. Seedling survivorship ranged from 68.42% in the first transition year to 83.49% in the second transition year in the unprotected fragments.

Table 2. Lower-level vital rates for *Euterpe edulis* populations in the Poço das Antas National Biological Reserve (protected area) and for the summary matrices from the private fragments of Santa Helena, Estreito, and Afetiva-Jorge (small fragments). Abbreviations are as in Fig. 2.

	2005-2006		2006-2007	
	Protected área	Small fragments	Protected area	Small fragments
s1	0.7517	0.6842	0.6911	0.8349
g1	0.1927	0.0385	0.2941	0.0330
g2	1.0000	1.0000	0.9200	1.0000
g3	0	0	0.0800	0
s2	0.9446	0.8966	0.9048	0.9600
r1	0.0391	0.0385	0.0096	0
g4	0.2852	0.1923	0.4115	0.4583
g5	0.7808	0.8000	0.9070	0.9091
g6	0.2192	0.2000	0.0930	0.0909
s3	0.9467	0.9180	0.9122	0.9434
r2	0.2324	0.0714	0.0370	0
r3	0.9697	1.0000	1.0000	0
r4	0.0303	0	0	0
g7	0.1690	0.1071	0.1630	0.1200
s4	0.8462	0.9837	0.7696	0.9600
r5	0.0267	0.0083	0.0180	0
r6	0.8000	1.0000	0.6667	0
r7	0.2000	0	0.3333	0
g8	0.0374	0.0248	0.0180	0.0333
s5	0.9265	0.9900 [†]	0.8000	0.9900 [†]
f5	0.3676	7.5455	0.8000	15.3571

[†] s5 for the smaller fragments was estimated because during the study no reproductives died (n=11 in 2005-2006 and n= 14 in 2006-2007 transition year). We estimated that this species could survive to 100 years old (long), and when s5=1, it should be substituted by s5=1-(1/long).

The proportion of individuals that grew to a larger stage after one year varied widely. For *E. edulis* stages growth, the higher values were found for infant (45.83% and 41.15%) in the second transition year for the unprotected fragments and the protected fragment, respectively. Most growth was to the subsequent stage (90.91% and 90.70 %). Smaller values were found for the growth of immatures to reproductives (smaller fragments: 2.48% and 3.33%; bigger fragments: 3.74% and 1.8%) in both transition years, and of seedlings to infants in the unprotected fragments in both transition years (3.85% and 3.30%). For *E. edulis*, most individuals that grow advance to the next stage class.

A small proportion of the palm individuals – less than 10% – regressed to a smaller stage in a sampling interval. A total of 23.24% of *E. edulis* juveniles regressed in the protected area, and the majority of them (96.97%) regressed one stage.

Our LTRE analysis revealed that the generally higher λ in the unprotected fragments was due primarily to greater survival of immatures and reproductives in both transition years (Fig. 3A). Survival of seedlings, growth of immatures, and fertility also contributed to the greater λ in the unprotected fragments, but only in the second transition year (Figs. 3A, 3B, 3D). The contribution of regression was negligible, but the majority was also to the greater λ in the unprotected fragments (Fig. 3C). This is particularly true of terms describing seedling growth, which contributed to the lower λ in unprotected fragments (Fig. 3B).

Discussion

Protected areas are an important strategy for buffering threatened populations from further declines. We were therefore surprised to find that projections of λ for *Euterpe edulis* population in the Poço das Antas Reserve were significantly lower than those in the smaller unprotected fragments in both transition years. Furthermore, the population of *E. edulis* in this site – in which palm populations are protected from harvesting by humans – is projected to decline (i.e., $\lambda < 1$) based on analyses of transition matrices. This is in contrast to the populations in the three unprotected forest fragments, where harvesting has occurred but populations are nevertheless projected to grow. Thus, it is likely that the *E. edulis* population is declining in the protected area and is increasing in the chronically disturbed fragments.

Our LTRE analysis revealed that the generally higher λ in the small unprotected fragments was due primarily to greater survival of immatures and reproductives in those sites. This result is strikingly different from that of other studies that have used LTRE to study the demography of palms. For instance, Zuidema et al. [26] found that the higher λ of undisturbed populations of *Geonoma deversa* when compared to those subject to defoliation resulted predominantly from lower sexual and vegetative reproduction following defoliation. Rodríguez-Buriticá et al. [27] studied *Geonoma orbignyana*, an understory palm used as foliage, and found that this species is very sensitive to harvest if defoliation implies alteration of high-elasticity survival transitions. Although the kind of harvesting used is very different, we observed a similar result for *E. edulis*. The low survival of immatures and reproductives in our protected area (15.38% and 7.35% mortality in year one and 23.04% and 20% mortality in year two, respectively) was the result of herbivory by capuchin monkeys (*Cebus nigritus*), which break the palm stems and feed on palm heart [28, see also 29 for a description of similar herbivory in the palm *Geonoma brevispatha*). Although capuchin monkeys do not appear to occur in the small unprotected fragments in which we established demographic

plots (C. Ruiz, pers. comm.), they are found in other Atlantic forest fragments. Nevertheless, mortality of larger individuals is rare in these sites – in a three-year study conducted in a 252 ha fragment, only one individual with diameter greater than 120 mm died [30], and there was no evidence of herbivory by monkeys despite their presence in the site [29]. Our results suggest herbivory by monkeys could profoundly alter the dynamics of palm populations in some locations.

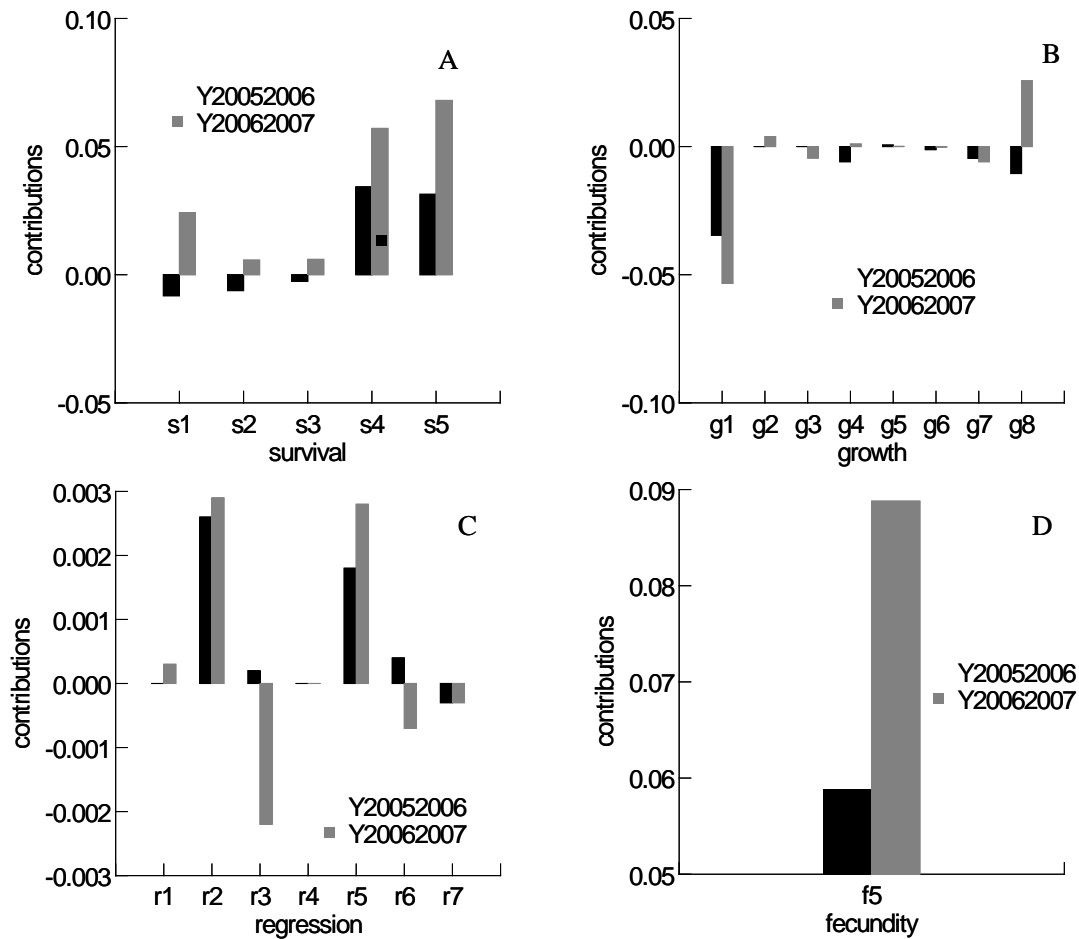


Fig. 3. (A) The contributions of each of the stage-specific vital rates -- (A) survival, (B) growth (C) regression and (D) fertility -- to the difference in λ between *Euterpe edulis* populations in the protected area and the three small fragments. Abbreviations are as in Fig. 1.

Several caveats to our conclusions bear discussion. First, although sensitivity and elasticity analyses are frequently and effectively used in conservation biology [24], they have some important limitations [31]. For example, elasticity analysis does not describe the effects of actual variation in the transition elements of populations, but rather how hypothetical changes in these elements would influence λ . Furthermore, elasticities 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 [20]. Second, the study was conducted over a relatively short period (three years). Longer studies are clearly needed to elucidate the role of environmental stochasticity in long-term population dynamics. Third, Silva Matos et al. [30] suggested that the inclusion of density-dependence could alter conclusions about *E. edulis* dynamics. It is important to note, however, that the density of plants in the single population studied by Silva-Matos et al. [30] was much higher than that found in any of our sites, including the protected area (25184-40900 number of individuals/ha vs. 906.2-1060.5 individuals/hectare, respectively). Considering density dependence may indeed be critical in some parts of *E. edulis*' range – other studies of *E. edulis* also reported a greater density than we observed (e.g., Fantini & Guries [32] – 17334 and 11537 individuals/hectare, Reis et al. [33] – 17198 individuals/hectare). With densities in our sites up to 40-fold lower than in other locations, however, we believe that our density independent models accurately describe the dynamics in our field sites.



Fig. 4. (A) An unprotected fragment studied. (B) The studied species *Euterpe edulis*. (C) The damage caused in *E. edulis* by Capuchins monkey. Photos by Portela, R.C.Q.

Implications for conservation

Euterpe edulis is heavily harvested for its palm heart in the Atlantic forest [32]. Our results suggest that harvesting methods involving stem cutting – similar in many ways to how Capuchins harvest palm hearts (Fig. 4) – likely reduce population viability because they exert strong effects on survivorship and other vital rates that have a large influence on λ [34-35]. Silva-Matos et al. [30], who studied *E. edulis* in a 252-ha Atlantic forest reserve protected since 1979, estimated an annual growth rate of 24%. However, Silva-Matos et al. [30] did not report any case of Capuchin monkey predation, which in our study was the principal cause of population decline. Taira (28)

reported that the frequency of palm heart consumption by capuchins was negatively related to insect foraging and invertebrate abundance, indicating that palm heart is an alternative source of proteins. It could be that the intense herbivory by monkeys we observed indicates that Poço das Antas does not have the quantities of high-quality food necessary for some vertebrates. Furthermore, Silva-Matos et al. [30] argued that the high rate of population increase they observed reflected either a response to changes in the environment resulting from forest fragmentation and isolation or recovery from past exploitation. In concert with a lack of monkeys, both of these explanations may be driving the increases in population growth we observed in the three small fragments we studied.

Fragmented animal communities often pass through unstable transition states that do not otherwise occur in nature [36]. These can cause serious ecological distortions (e.g., a collapse of predator and parasite populations, and a hyperabundance of herbivores and ecological generalists) that have cascading impacts on plant communities [37]. We suggest that this is what is driving the patterns we observed in our protected area. This study also lends support to the idea that small, unprotected fragments embedded in a landscape that is actively managed and modified by humans can be very important for maintaining viable plant populations [reviewed in 38]. To truly understand the current status and forecast the future state of tropical biodiversity, we need to understand levels and patterns of diversity in this kind of landscape [39].

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