



UNIVERSIDADE ESTADUAL DE SANTA CRUZ
PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO
DA BIODIVERSIDADE

PPG Ecologia da Conservação

Universidade Estadual de Santa Cruz

**Efeitos da fragmentação florestal na predação de
sementes e estrutura populacional de *Euterpe edulis*
Mart. no sul da Bahia, Brasil**

Melina Oliveira Melito

Orientadora: Dra. Eliana Cazetta
Co-orientador: Dr. André M. Amorim

Ilhéus-Bahia
2011

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Dissertação apresentada para
obtenção do título de mestre
em Ecologia e Conservação da
Biodiversidade, à Universidade
Estadual de Santa Cruz.

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“Uma jornada de mil quilômetros começa com um único passo”

Lao Tsu

Agradecimentos

Este trabalho é fruto do esforço e colaboração de muitos, aos quais sou muito grata! Perdoem-me desde já possíveis esquecimentos de pessoas que deveriam constar aqui...

... à minha família amada que não importa o que eu faça ou onde eu esteja para me apoiarem incondicionalmente! Não seria quem eu sou hoje sem os conselhos, as broncas e o amor de vocês!

... à Eliana Cazetta que sempre me deu todo apoio e suporte para minhas aventuras e que muitas vezes botou meus pés no chão. Admiro muito o respeito que você sempre demonstrou por minhas opiniões! Muito obrigada por tudo e pela sua amizade!

... ao André Amorim por todos seus ensinamentos, conselhos e conversas seja nos botecos, no acarajé da Judith ou na longa estrada que liga o herbário CEPEC à Ilhéus. Além de ser o “chefia” é um amigo ótimo sempre disposto a me ajudar e a agüentar eu falando “aqueles fiozinhos da florzinha” entre outros...

... ao José Cláudio Faria e a Ana Schilling pelo imenso auxílio em estatística. Em especial ao Faria por ter ampliado minha estreita visão quanto à análise de dados e por todas as agradáveis conversas sobre o compromisso com a ciência e valores morais entre um e outro comando no R!

... ao Richard Vogt por ter acreditado em meu potencial e aceitado a co-orientação no projeto inicial do mestrado. Grata por todo o suporte para que eu pudesse realizar o projeto inicial e também pelo apoio quando foi preciso trocá-lo.

... aos docentes do PPG pela imensa dedicação em prol da qualidade do curso e da formação dos discentes! Sou muito grata também a Vanessa, secretária do PPG, que sempre foi muito solícita auxiliando sempre que pode.

... à FAPESB pela concessão da bolsa, ao PPGEGB pelo apoio financeiro para realização do campo, à UESC pelo custeio das gaiolinas de exclusão e suporte logístico nas coletas em campo e também ao ICMBio da REBIO e RVS Una pelo auxílio logístico.

... a galera da ecologia por terem compartilhado comigo tantas alegrias e dificuldades! Carinho especial a Sara, Lu, Lari, Flávia, Pedro, Gabriel, Thaline, Ricardo e Andes pela convivência prazerosa durante as disciplinas e, especialmente, nas mil e uma

confraternizações ao longo do mestrado! Também agradeço ao Heitor “beija-flor” por ter se mostrado sempre um grande amigo, daqueles que a gente pode contar sempre!

... ao pessoal do herbário CEPEC que me mostraram como é bom ser feliz trabalhando quando se está cercada de amigos! Em especial a Sara que me deu valiosas dicas sobre o R além das ricas conversas sobre a ecologia e a vida! Também agradeço ao Ricardo Perdiz pelas palavras de incentivo em momentos difíceis.

... à Carolina Pinheiro, Jamille Bonfim, Leiza Souza, Lukas Daneu, Michaelle Pessoa, Vinícius Vilaronga, Virgínia Fernandes, Thiago Araújo e, especialmente, ao Frederico Hobus pelo valioso auxílio em campo!

...à Flávia pela amizade e paciência durante os dois anos em que moramos juntas!

... ao Bruno Machena e Tatiana Alves por todo o auxílio para a realização desta pesquisa na REBIO e RVS de Una e, principalmente, pela amizade de vocês seja na Bahia como na Amazônia!

...à equipe do ICMBio REBIO Rio Trombetas, em especial ao Gilmar, Carlos, Carlitos e Eliézer por toda a ajuda e suporte logístico para a realização do projeto inicial.

...ao pessoal do grupo de pesquisa Quelônios da Amazônia, em especial a Camilla, Marcela, Rayath, Rosa, Virgínia e ao coordenador do grupo Richard Vogt por todo auxílio e suporte para a realização do projeto inicial além da amizade.

... à Virgínia e a Dri, por terem me acolhido tão bem em terras manauaras e por toda a amizade durante tempos difíceis e quentes!

... aos grandes amigos que fiz na Bahia: Tito, Lu Camillo, Maky, Alan (Tremendal), Vinícius (Petisco) e Chiquinho. Inúmeras são as histórias pra contar das viagens que fizemos e das aventuras que vivemos juntos! Obrigada pelos ensinamentos, conversas, carinho, lealdade e companheirismo! Quem tem amigos tem um tesouro!

...a Deus!

Resumo

A fragmentação florestal é uma das principais ameaças a Mata Atlântica, e um de seus efeitos mais severos são sobre as interações mutualistas e antagonistas entre fauna e flora pela síndrome das “florestas vazias”. Alterações nas comunidades de predadores de sementes podem acarretar na diminuição do recrutamento de plântulas afetando a estrutura demográfica das populações vegetais. No presente estudo foi avaliada a estrutura demográfica e o efeito da predação de sementes pós-dispersão no estabelecimento de plântulas em populações de uma espécie de palmeira endêmica e ameaçada, *Euterpe edulis*, em quatro classes de tamanho de fragmentos florestais na região sul da Bahia, Brasil. Não foi observado nenhum padrão relacionado ao gradiente e fragmentação florestal com relação a densidade total, estrutura em estádios de desenvolvimento ou tamanho das plantas de *E. edulis*. O maior fragmento florestal apresentou o maior número de indivíduos em todos os estádios de tamanho, exceto para plântulas, contrastando com o observado para o segundo maior fragmento que apresentou os menores parâmetros demográficos. Ambos apresentaram os maiores tamanhos de plantas com base na altura e diâmetro ao nível do solo, entretanto isto não refletiu em um padrão com relação à densidade de indivíduos. Possivelmente a população do fragmento grande esteja se regenerando de explorações de palmito ocorridas no passado. Em geral, as populações estudadas se apresentam em baixa densidade, especialmente no estágio de plântulas. Qualidade do hábitat e variações no microhabitat devem ser mais determinantes no padrão da estrutura populacional do que os efeitos da fragmentação florestal. No experimento de exclusão de predadores foram observados padrões relacionados a redução de habitat. A predação por vertebrados aumentou do maior fragmento para o menor, entretanto não linearmente. A taxa de predação de sementes por vertebrados foi mais elevada nos dois primeiros meses e variou entre 71% e 82%, para todos os fragmentos. Entretanto, os principais predadores no maior fragmento foram os besouros Scolytidae nos dois tratamentos. A predação por invertebrados ocorreu durante os seis meses de experimentos. A exclusão de vertebrados aumentou a probabilidade de uma semente germinada se estabelecer, exceto para o menor fragmento. Entretanto, um distinto aumento no número de plântulas estabelecidas foi observado apenas no fragmento de tamanho médio, especialmente no tratamento de exclusão de vertebrados. Provavelmente as altas taxas de predação estão gerando um gargalo populacional entre sementes e plântulas limitando o tamanho das populações de *E. edulis*.

Palavras-chave: demografia, estabelecimento, estrutura populacional, granivoria, predação pós-dispersão,

Abstract

Forest fragmentation is one of the main threats to the Atlantic forest. A severe effect of this process is at mutualistic and antagonistic interactions among animal-plant by the “empty forest” syndrome. Changes in granivorous guild may lead seedling recruitment decreases and thus impacting negatively demographic structure of plant populations. The palm *Euterpe edulis* is considered a key-resource for frugivorous at the Atlantic Forest and is threatened by palm heart exploitation. In this study we analyzed the demographic structure and the effect of post-dispersal seed predation on seedling establishment in populations of *E. edulis* at four sizes of forest fragment at southern Bahia, Brazil. We did not observe any pattern related to the gradient of forest fragmentation on plant density, structure of the developmental stages or plant size. Population density and number of plants into the stage classes, except for seedlings, were higher at the main-size habitat contrasting to the lower values observed at the large-size habitat. The main and large-size fragments showed the highest plant sizes but this was not correlated with plant abundance. The lowest population at the large-size remnant may reflect a regenerating population due to past harvesting activities. In general, populations at the studied sites show low densities, especially at the seedling stage. Habitat quality and microhabitat variation may be even more determinant in population structure of *E. edulis* than the isolated effect of forest fragmentation. Patterns associated with forest fragmentation were observed on seed fate experiments. Vertebrate predation increased across the gradient of habitat reduction although not linearly. Seed predation rates by vertebrates were higher in the first two months e ranged from 71% and 82% among fragments. However the foremost seed predator of the main habitat was the scolytine beetle for both treatments. Invertebrate predation occurred along all time of experiments. The exclusion of vertebrates increased probability of a germinated seed to established, except for the small habitat. Nevertheless a distinct great number of seedlings were observed just at the medium size fragment, especially on the exclusion treatment. High rates of seed predation may be driving a seed-to-seedling bottleneck that might be limiting population densities at the remnants.

Key-words: demography, establishment, granivory, population structure, post-dispersal seed predation

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INTRODUÇÃO

A redução da cobertura vegetal nos ambientes naturais formando ilhas de vegetação nativa imersas em uma matriz antropizada (Andreazzi *et al.* 2009), é uma das principais ameaças a biodiversidade presente na Mata Atlântica (Russo 2009). A fragmentação tem efeitos indiretos sobre a comunidade faunística podendo causar a síndrome das “florestas vazias”, em que populações animais são drasticamente reduzidas ou extintas localmente pela destruição de áreas críticas à sobrevivência, redução na disponibilidade de frutos, degradação do ambiente, entre outros fatores (Redford 1992).

Modelos sugerem que mudanças na composição da comunidade de frugívoros com a diminuição de espécies de grande porte, e.g. tucanos e antas, levam a um aumento momentâneo na diversidade de aves e mamíferos de médio porte, entretanto, em longo prazo estas populações declinam por se tornarem preferencialmente caçadas permitindo o crescimento acentuado da guilda de granívoros (Herrera 1989; Jordano *et al.* 2006). Alterações na composição faunística podem acarretar em mudanças nas interações mutualísticas e antagonísticas entre plantas e frugívoros (Redford 1992; Jordano *et al.* 2006), efeito que pode ser agravado em florestas tropicais onde de 50 a 90% dos frutos são consumidos por vertebrados (Howe e Smalwood 1982; Jordano *et al.* 2006) que correspondem a cerca de 80% da biomassa de herbívoros e frugívoros nos trópicos (Redford 1992).

A dispersão e predação de sementes por animais são processos com conseqüências diretas na estrutura, distribuição e dinâmica vegetacional (Schulze *et al.* 2004). A dispersão de sementes é o deslocamento das sementes para longe da planta-mãe, diminuindo os efeitos da mortalidade dependente de densidade, da predação pré-dispersão, de endogamia na população e amenizando a pressão da competição intrapopulacional pelo microsítio (Janzen 1970, 1971; Willson e Traveset 2000; Levin *et al.* 2003). Como a dispersão de sementes liga a polinização com o estabelecimento de novos indivíduos na população (Wang e Smith 2002), o local de deposição das sementes é um processo determinante na probabilidade da semente ser recrutada na população (Schupp 1993). Entretanto, a deposição das sementes em um substrato deixa os propágulos suscetíveis aos predadores.

A predação pós-dispersão geralmente é realizada por predadores especialistas, como insetos e roedores, que forrageiam oportunisticamente por sementes (Janzen 1971; Vander Wall *et al.* 2002), sendo que este processo se distingue da predação pré-dispersão pela variação temporal em que ocorrem e por geralmente envolverem diferentes espécies de predadores (Vander Wall *et al.* 2002).

O processo de fragmentação e defaunação reduzem o número de dispersores e predadores de sementes, causando impactos significativos na comunidade vegetal pela diminuição no recrutamento e estabelecimento de plântulas alterando secundariamente a demografia e diversidade da comunidade florística (Andreazzi *et al.* 2009).

A estrutura e dinâmica de populações vegetais são desproporcionalmente influenciadas quando altas taxas de mortalidade afetam estádios críticos da história de vida da planta, como de plântulas (Clark *et al.* 2007) e adultos (Bruna *et al.* 2009). Extinções locais de plantas em habitats fragmentados são freqüentemente relacionadas a redução no recrutamento de plântulas (Silva & Tabarelli 2000). Portanto declínios populacionais levando a extinção é um processo essencialmente demográfico (Bruna *et al.* 2009).

Palmeiras em paisagens fragmentadas

Os frutos de palmeiras (Arecacea) são considerados um recurso-chave para vertebrados frugívoros (Galetti; Aleixo, 1998; Galetti *et al.*, 2006). Nos neotrópicos, 93 espécies de mamíferos consomem a polpa ou as sementes de palmeiras (Andreazzi *et al.*, 2009).

De modo geral, os efeitos da fragmentação e defaunação sobre as palmeiras estão relacionados com a diminuição na taxa e distância de remoção das sementes e inversão na proporção de sementes predadas entre besouros bruquídeos e roedores (Andreazzi *et al.*, 2009).

A fragmentação também pode alterar a interação entre mutualismos condicionais de roedores estocadores e palmeiras, como verificado entre *Astrocaryum aculeatum* e cutias na Amazônia (Jorge e Howe 2009). Desta forma, palmeiras neotropicais que dependem de roedores estocadores podem

enfrentar extinções locais pelos efeitos negativos da fragmentação florestal e defaunação (Galetti *et al.* 2006).

A caça afeta negativamente a abundância de mamíferos em florestais tropicais influenciando nas interações mutualistas e antagonistas entre mamíferos, insetos e palmeiras com um efeito em rede no estabelecimento de plântulas e, secundariamente, modificando a composição e diversidade da comunidade vegetal (Wright *et al.* 2000).

Além dos efeitos da fragmentação e da redução da fauna, algumas espécies de palmeiras também são pressionadas pela exploração comercial do palmito, com profundas implicações no recrutamento e regeneração destas populações (Galetti *et al.* 2006). As principais espécies de palmeiras exploradas para produção de palmito no Brasil são *Euterpe edulis* Martius e *Euterpe oleraceae* Martius (Galetti e Fernandez 1998).

Euterpe edulis, ou juçara, apresenta apenas uma estipe e a extração de seu meristema apical comestível, o palmito, leva à morte da planta (Matos e Watkinson 1998). A exploração predatória da juçara reduziu drasticamente suas populações naturais na floresta Atlântica e atualmente a espécie figura na lista brasileira da flora ameaçada de extinção (Galetti e Fernandez 1998; MMA 2008). A sobre-exploração de *E. edulis* também tem efeito ecológico por constituir um importante recurso para aves e mamíferos frugívoros (Galetti e Aleixo 1998; Galetti e Fernandez 1998), sendo considerada uma espécie-chave em ambientes fragmentados e em comunidades com escassez de recursos (Fadini *et al.*, 2009).

Estudos sobre a interação entre *Euterpe edulis* e a fauna associada de dispersores são mais freqüentes (e.g. Andreazzi *et al.* 2009; Galetti e Aleixo 1998; Galetti *et al.* 1999; Laps 1996; Matos e Watkinson 1998; Reis 1995), enquanto que as relações entre predadores e populações antropizadas de juçara são menos conhecidas.

Os principais predadores pós-dispersão de sementes de *Euterpe edulis* são besouros bruquídeos (*Coccotrypes palmarum* Eggers 1933) e roedores generalistas, como os do gêneros *Nectomys* e *Oryzomys* (Pizo e Simão 2001; Viera *et al.* 2003). Grandes mamíferos como *Tayassu pecari* (queixada) *Dasyprocta leporina* (cutia) também atuam como predadores de sementes de juçara (Galetti *et al.* 2010; Keuroghlian e Eaton 2009).

Fatores temporais parecem influenciar na proporção de sementes de *Euterpe edulis* predadas entre insetos e roedores, por exemplo, o período de frutificação (Von Allmen *et al.* 2004) e a estação do ano (Fadini *et al.* 2009). Fatores espaciais, como a diferenciação em microhábitats em fragmentos florestais, também levam a padrões distintos de exploração das sementes por predadores (Fleury e Galetti 2004).

Desta forma, a fragmentação florestal pode exercer um efeito negativo na estrutura demográfica de plantas e alterar as relações antagonísticas com a fauna associada de predadores que, por sua vez, afetam diretamente o recrutamento de plântulas. Sendo a região de Una formada por um mosaico de fragmentos florestais e área de distribuição de *Euterpe edulis*, é emergencial a avaliação da estrutura demográfica destas populações e o efeito dos predadores sobre a probabilidade de estabelecimento das plântulas. A caracterização destas populações e de suas relações ecológicas com a comunidade faunística possibilitarão que estratégias de conservação possam ser determinadas para *E. edulis*, que se encontra sobre ameaça de extinção.

Objetivo Geral

O principal objetivo deste trabalho foi avaliar a estrutura demográfica de *Euterpe edulis* em um gradiente de fragmentação florestal e os efeitos negativos da fauna associada de predadores no recrutamento de plântulas com a redução do hábitat.

Objetivos específicos:

Capítulo 1: Estrutura populacional de Euterpe edulis

Observamos se ocorrem efeitos negativos na densidade total de plantas, mudanças na estrutura demográfica das populações e alterações no tamanho dos indivíduos ao longo do gradiente de fragmentação florestal.

Capítulo 2: Predação de sementes e estabelecimento de Euterpe edulis

Analisamos o padrão do destino das sementes ao longo do gradiente de fragmentação florestal avaliando especificamente mudanças no padrão de exploração das sementes ao longo do tempo, inversões no processo de predação de sementes de acordo com a redução do hábitat, com aumento na taxa de predação por vertebrados e diminuição por invertebrados e, em última análise, o efeito negativo dos predadores no estabelecimento das plântulas.

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CAPÍTULO 1

Demographic structure of a threatened palm across a fragmented landscape at the northwestern Atlantic forest, Brazil¹

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¹ Article in preparation to *Revista Brasileira de Botânica*

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Abstract

Studies of the effects of habitat reduction in populations of the threatened *Euterpe edulis* rarely focused in changes at the demographic structure. We investigated the predictions that habitat loss could decrease plant density, reduce population structure and shifts plant size using four fragments with distinctive size classes at the Atlantic Forest in southern Bahia, Brazil. We did not find an effect of habitat reduction on any parameters evaluated. Mainly, population density and number of plants into the stage classes, except for seedlings, were higher at the main-size habitat contrasting to the lower values observed at the large-size habitat. The main and large-size fragments showed the highest plant sizes but this was not correlated with plant abundance. The lowest population at the large-size remnant may reflect a regenerating population due to past harvesting activities. Therefore, we discuss that habitat quality and microhabitat variation may be even more determinant in population structure of *E. edulis* than the isolated effect of forest fragmentation, especially in a landscape with great heterogeneity associated with a complex matrix connecting large forest patches.

Key-words: *Euterpe edulis*; habitat size; disturbance; life stages; recruitment; population structure.

1. Introduction

It is largely known that the Atlantic Forest suffers high deforestation rates in all range of its distribution leading to a severe threatening for the high biodiversity and endemism in this ecosystem (Myers *et al.* 2000; Russo 2009). The disruption of continuous habitat into forest remnants embedded in an anthropogenic matrix mainly promoting habitat reduction (Fahrig 2003) which is a major force underlying declines in species richness for several animal and plant taxa (see Laurance *et al.* 2011). Fragmentation associated with process and threats like forming edges, habitat reduction, logging and altered seed dispersal guild frequently unable viable populations of plants which can decline and being locally extinct (Tabarelli *et al.* 2004; Laurance *et al.* 2011).

Population decline to extinction is essentially a demographic process (Bruna *et al.* 2009). Changes in recruitment, survivorship, growth and fertility are often linked with habitat fragmentation with the smallest and more isolated habitats often showing the lowest population sizes and species richness (e.g. Scariot 1999; Benitez-Malvido & Martinez-Ramos 2003a,b; but see Bruna & Kress 2002; Neal *et al.* 2010). However, substantial species losses rate are expected even for fragments with 10.000 ha in area (Laurance *et al.* 2011).

High mortality rates at critical life-history stages, such as seedlings (Clark *et al.* 2007) and adults (Bruna *et al.* 2009), may disproportionately influence the structure and dynamics of plant populations and communities. Reduces in seedling recruitment is often related with plant extinctions in fragmented habitats (Silva & Tabarelli 2000). Moreover, the major processes underlying seedling recruitment are related with seed limitation and establishment limitation (Clark *et al.* 2007).

Plants in the largest size class modulate the flux of individuals from the seedling stage through the intermediate classes (Silva Matos *et al.* 1999). The number of reproductive individuals is directly related with fertility, expressed as seed output for example. Shifts in plant size can alter fertility (Horvitz & Schemske 1995) as also the capacity of resistance for abiotics events (Alves *et al.* 2004). In this way, ensure the survival and growth of the largest stage class is often identified as essential for maintenance of the population size and structure (Silva Matos *et al.* 1999; Freckleton *et al.* 2003).

Although inferences about population dynamics require long-term studies this is not always viable, as already pointed out by Bruna & Kress (2002) and Bruna *et al.* (2009). Besides much attention have been paid in investigate fragmentation effects in process linked to plant fertility (e.g. flowering and seed production) and seedling recruitment, the major impacts in population demography are in the survival and growth of the largest stages class (Bruna *et al.* 2009). As the actual demographic structure reflects past events occurred the assessment of the current population's stage structure can be an useful instrument for immediate conservationist proceedings (Bruna & Kress 2002) and for future sustainable management of tropical forests products.

Palms are important components of vegetation in the tropics and subtropics (Uhl & Dransfield 1987; Scariot 1999) with a key function to afford resources for vertebrate frugivores (Galetti & Aleixo 1998; Galetti *et al.* 2006; Andreazzi *et al.* 2009). Because of the easily recognition of palms and their ecological importance, the group has great suitability as subject on demographic studies (Uhl & Dransfield 1987).

Harvesting of economically important palms species, such as *Euterpe edulis*, have important effects in population structure especially in a fragmented landscape context (Portela *et al.* 2010). Palm heart exploitation lead to the declining of natural stands of *Euterpe edulis* (Galetti & Fernandez 1998) acting negatively on the natural regeneration and maintenance of the demographic structure (Reis *et al.* 2000). Even in protected fragments *E. edulis* populations were projected to be decreasing (Portela *et al.* 2010). In this context, we investigate the demographic structure of *E. edulis* and tested the following hypothesis: 1) densities of *E. edulis* are reduced across the forest fragmentation gradient; 2) habitat reduction has a negative effect on the demographic structure of the fragmented populations of *E. edulis*; and 3) plant size is affected by habitat fragmentation.

2. Material and methods

2.1 Study site

Southern of Bahia contains some of the last forest patches of the northeastern Atlantic Forest (Faria *et al.* 2009) being considered an area of towering biological importance because the high levels of richness and plant endemism (Thomas *et al.* 1998; Martini *et al.* 2007; Thomas *et al.* 2008). The Una region also presents great plant diversity and endemism structured in a tropical lowland rain forest with canopy, understory and emergents layers, and a rich epiphytic flora of bromeliads, orchids, ferns and lianas (Thomas *et al.* 1998; Amorim *et al.* 2008). Canopy layer is about 25-30 m with emergents reaching up 40 m (Faria *et al.* 2009).

We conducted this study at two federal protected areas, the Una Biological Reserve (REBIO Una) and the surrounding Una Wild Life Refuge (RVS Una), both located at the municipality of Una, Bahia, Brazil (15°10'S, 39°03'W) (Fig. 1). The REBIO Una is a high protected site established in 1980 with very restrictive purposes, as scientific research and protection of species and associated habitat. This conservation unit was amplified in 2007 mainly for fragments reconnection totally nowadays 18.900 ha (Table 1). Figure 1 shows the Maruim fragment that initially compounded the REBIO Una and the added Metal Forte remnant (see also table 1).

Table 1. Description of the study sites, size classification and date since each forest fragment was protected by two federal conservation units with different degrees of protection at Una, southern Bahia, Brazil.

Fragment	Area (ha)	Fragment size class	Protection status*	Time since protection	Plants density (~0.2 ha/habitat)
Maruim	12334.6	main	high	1980	877
Ecoparque	2655.8	large	low	2007	207
Metal Forte	946.4	medium	high	2007	559
Mazao	210.8	small	low	2007	499

* High = REBIO Una; low = RVS Una

The RVS Una was established in 2007 and has a lesser degree of protection due allowing private owners in the area in a system that attempt integrate land use, recovery of disturbed areas with reconnection and protection of forests remnants (Fig. 1, Table 1).

There is a mosaic of forests remnants broad by the two conservation units (Fig. 1) surrounded by a matrix composed mainly by pastures, second-growth forests and shaded cocoa plantations, respectively 27%, 15% and 6% (Pardini 2004). From these forest fragments we choose to sample four habitats with distinct sizes that showed no-visible signs of palm heart exploitation and with pre-existing trails.

The study area is characterized by two principal soil types: podzolized variety Cururupe (Tropodult) at east and laterite variety Tabuleiro (Haplorthox) more west (Carvalho Filho *et al.* 1987). Average annual temperature is 24 °C and mean rainfall about 2000 mm year⁻¹ without a clearly seasonality, although reduces might occur from December to March (Bovi *et al.* 1983).

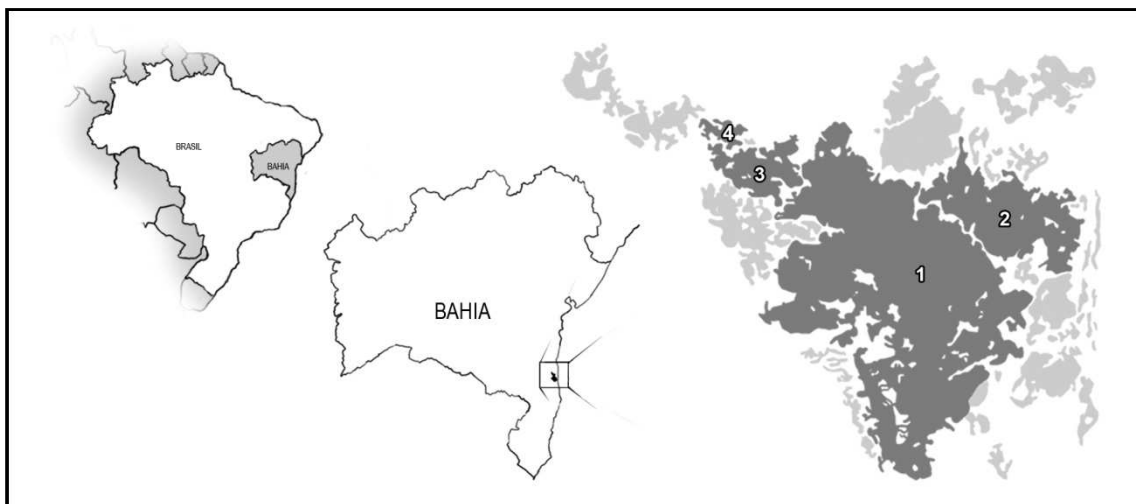


Figure 1. Map locating the forest fragments comprised by two conservation units at Una, southern Bahia, Brazil. Numbers corresponds to the (1) main, (2) large, (3) medium and (4) small-size habitats.

2.2. Focal species

Euterpe edulis (Arecaceae) occurs mainly at the Atlantic Forest (Henderson & Galeano 1996) and it is often related to the dominant component of the understory layer at southern Bahia (Thomas *et al.* 1998; Martini *et al.* 2007a,b). *Euterpe edulis* is mainly single-stemmed, 5-12 m tall, 10-12 cm diameter and it presents 8-15 pinnate leaves, leaflets horizontally spreading or

occasionally pendulous, with its apical meristem comestible (Henderson & Galeano 1996). Reproductive plants produce 1-5 inflorescences, fruits are globose drupes with one seed (mean \pm SD = 13.5 \pm 1.3 mm length, 14.2 \pm 1.2 mm width) (Von Allmen *et al.* 2004). The edible apical meristem is an exotic gourmet food of high monetary value (Wendt *et al.* 2011). Removal of the palm heart results in the death of the plant and this unplanned practice has led to the decline of the natural stands as also local extinctions across the Atlantic Forest (Galetti & Fernandez 1998).

Euterpe edulis is considered a key-species in fragmented forests or in habitats with restricted resource availability (Fadini *et al.* 2009) because it provides food resource for a variety of frugivores vertebrates, such as birds (Galetti & Aleixo 1998; Matos & Watkinson 1998), large mammals (Keuroghlian & Eaton 2008) and rodents (Vieira *et al.* 2003). By attracting several seed dispersers that influx seeds from the neighboring forest remnants, *E. edulis* can potentially facilitate forest recovering in degraded patches (Reis *et al.* 2000).

2.3. Demographic census samples

At each sampling site we established three plots of 25 x 25 m (~0.2 ha sampled/habitat) separated by at least 50 m from each other. The plots were displaced along pre-existing trails and more than 50 m far from the fragment boundary. For the main sized sampling site (Maruim, Table 1) we used a trail at the core of the forest fragment but under influence of a river that cross nearby. We assumed that density of *Euterpe edulis* is not related to river proximity, because a previous study did not find this pattern at Una probably due the high levels of humidity in the region (A. M. Z. Martini, unpubl. data).

The sampling plots were divided into a 5 m grid where all plants of *Euterpe edulis* were counted and measured. The morphometric characteristics related to plant size evaluated were number of leaves, height up to the leaves insertion and diameter at soil level (DAS) above the cone of the roots, which is a measurement shared by all individuals (Silva Matos *et al.* 1999). Thereafter, individuals were classified into development stages using biological criteria as reproduction and plant size (Table 2).

Table 2. Characteristics of the developmental stages for *Euterpe edulis* populations at Una, southern Bahia, Brazil based on morphometric measures.

Stage class	General characters
Seedling	One palmate leaf and presence of endosperm reserve
Infant	Pinnate leaves but palmate ones can be present, height $\leq 0.15\text{m}$
Juvenile	Only pinnate leaves and height up to 1 m
Immature	Stem $> 1\text{ m}$ with no signal of reproductive events
Adult	Stem with signal of reproductive events

2.4. Statistical analyses

2.4.1. *Euterpe edulis* density in a forest fragmentation gradient

We conducted an ANOVA to test the effect of the factor habitat size in reducing the density of *Euterpe edulis* populations along the fragmentation gradient. We considered the total number of plants from each sample plot as independent replicates of habitat category. In case of significant results we conducted a posteriori Tukey HSD test to identify which habitat(s) differs. We assumed the confidence level of 0.05 and used the R software (R Development Core Team, 2009).

2.4.2. Demographic structure based on development stages

We used log-linear models to test associations between habitat size, plot and their interaction on the demographic structure of *Euterpe edulis* from different habitat sizes. The null hypothesis verified was that the number of individuals at each development stage was independent of habitat size (four classes) and plot (three plots). First, we fitted a saturated model containing all single-factor effects, all two-way effects and the three-way effect resulting in a model containing all parameters and zero residual deviance. Then we followed hierarchical models by removing the highest-order term and comparing the deviance of the simplified model with the model that does contain that effect (Agresti 2007). We tested the effect of the interaction between habitat and plot

on the development stages (HPS) by removing this term from the saturated model. For testing the importance of habitat fragment (H) we fitted two models, one that excluded plot (marginal test) and other including plot (conditional test). The same procedure was conducted to test the importance of plot (P). All these hierarchical models are showed in more details in Appendix A. A posteriori Tukey HSD was used for differences among habitat assuming the confidence level of 95%. We used the R software (R Development Core Team 2009) to perform these Generalized Linear Models (GLMs) specifying poisson errors and a log link function (Crawley 2007).

2.4.3. Plant size

To evaluate if forest fragmentation has a negative effect on plant size we used a permutational multivariate analyses of variance based upon distance matrices. In this analysis we restricted the random permutations within each level of the development stages and performed 1000 permutations to obtain a trusty confidence level of 0.05, as recommended by (Anderson 2001). Additionally, we constructed a biplot of principal components for an exploratory analysis of the multivariate data (Gabriel 1971). The biplot is a graphical representation of both sampling units and the variables of an $n \times p$ matrix. The information represented permits the inspection of similarities or dissimilarities among objects (habitats) and correlations by the angulations formed between variables. For biplot construction the mean values were centered and standardized because of the different scales of measurement used. As the total number of individuals is a linear function of the development stages we used this parameter for associations with plant size. All the statistical analyses were performed using R software (R Development Core Team 2009)

3. Results

3.1. *Euterpe edulis* density in a forest fragmentation gradient

Overall, the mean (\pm SD) density of *Euterpe edulis* (per plot) is superior at the main-size fragment (292.3 ± 62.7) in relation to the others, namely large (69 ± 27.4), medium (186.3 ± 123) and small-size (166.3 ± 42.5) remnants (Fig. 2). Habitat had a significant effect on plant density ($F=4.6552$; $df=3,8$; $p=0.036$). Nevertheless, the *a posteriori* test showed that the significant differences was only between the two major habitats (Tukey-HSD, $p=0.024$) (Fig. 2).

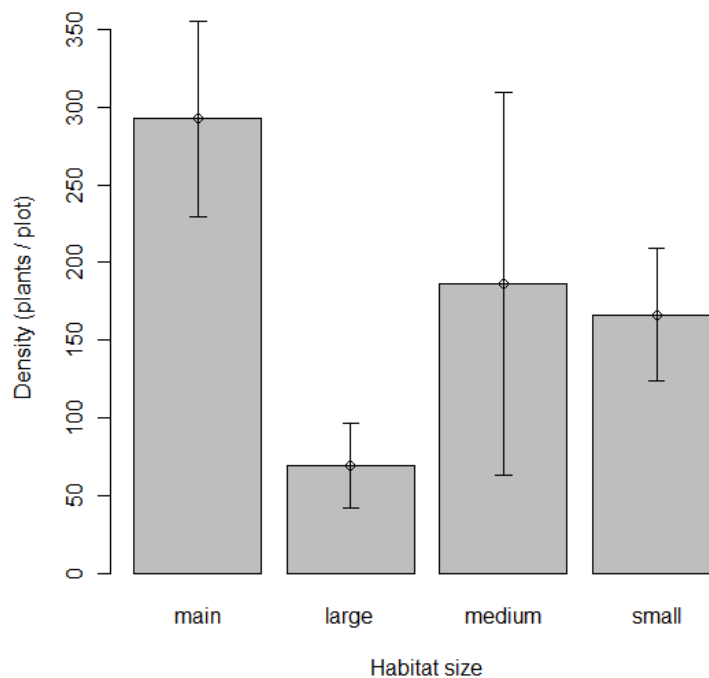


Figure 2. Mean *Euterpe edulis* density (\pm SD) per plot (~ 0.06 ha) across a habitat size gradient at Una, southern Bahia, Brazil.

3.2. Demographic structure based on development stages

We rejected the null hypothesis of independency between the number of individuals into the development stages for both habitat size and plot (Appendix A). The densities of plants in each stage showed significant effects of habitat size and plot level when each predictor variable was tested independently as when conditioned to the levels of the other variable (Table 3). However, the effect of the interaction between habitat size and plot was also significant in the demographic structure (Table 3).

Table 3. Log-linear analyses of the effects of habitat, plot and their interaction for predicting the density of *Euterpe edulis* in each five development stages (S) at Una, southern Bahia, Brazil. The term *given* relates to conditional test.

<i>Effect</i>	<i>DF</i>	<i>Deviance (G²)</i>	<i>P</i>
Habitat	12	107.95	<0.001
Plot	8	53.69	<0.001
Habitat, <i>given</i> plot	12	103.04	<0.001
Plot, <i>given</i> habitat	8	48.78	<0.001
Habitat X plot X stage	24	97.05	<0.001

The mean (\pm SD) densities of the seedling stage among the habitats varied from 6.3 (\pm 3.5), 0.3 (\pm 0.6), 4 (\pm 2) to 19.7 (\pm 11.7), respectively the main, large, medium and small-size remnants (Fig. 3). Significant differences were detected between the large and small-size remnants (Tukey-HSD, $p=0.02$, Fig. 3). For the infant stage the habitats did not differ in the mean densities due to a large between-plot variation at each site (Fig. 3). Significant higher density of juveniles were observed at main-size habitat compared to the others (Tukey-HSD, $p<0.01$ for all habitats). Immatures also showed increased densities in the main-size habitat in relation to the large and medium-size fragments (Tukey-HSD, $p<0.05$). The small-size habitat did not differ from the others for the immature stage. Densities of adults did not differ among habitats.

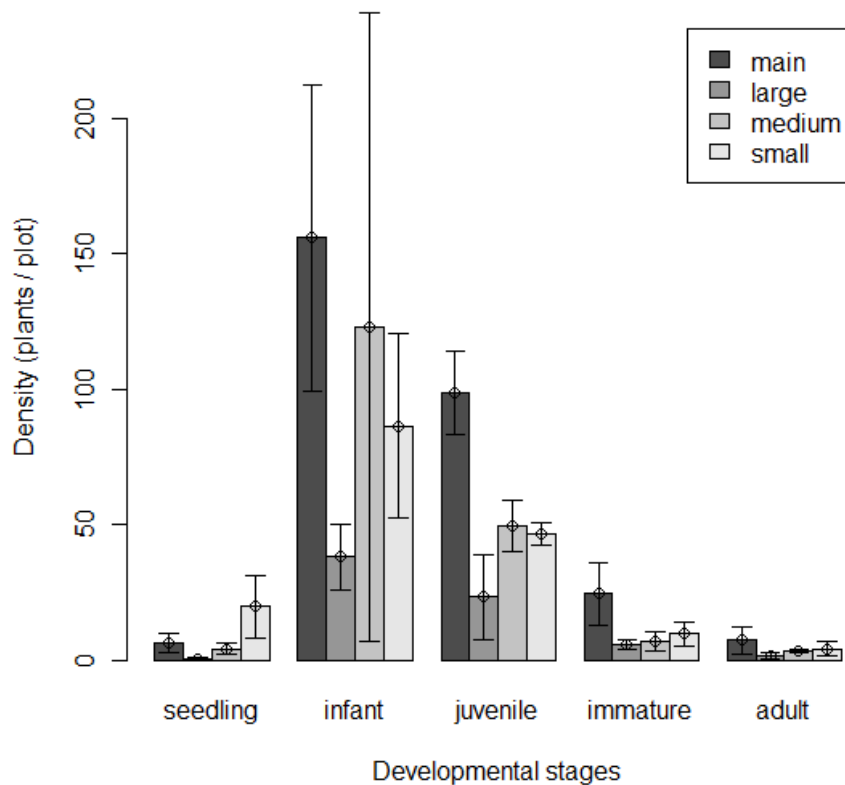


Figure 3. Density (mean \pm SD) of plants observed at each development stage of *Euterpe edulis* populations across different habitat sizes classes in Una, southern Bahia, Brazil.

3.3. Plant size

There was a significant difference in plant size between habitats (pseudo- $F=8.6076$, $p<0.001$). The biplot showed a weak association between density of *Euterpe edulis* and plant size (Fig. 4). The first principal component (PC1) explained 61.58% of the variation and corresponds to the morphometric variables (Table 4). Similarities in plant size, mainly as function of higher height and DAS, approximated the main and large-size remnants followed by the small-size fragment (Fig. 4). In the opposite side of the first principal component is the medium-size fragment, with lower means for plant size variables (Fig 4).

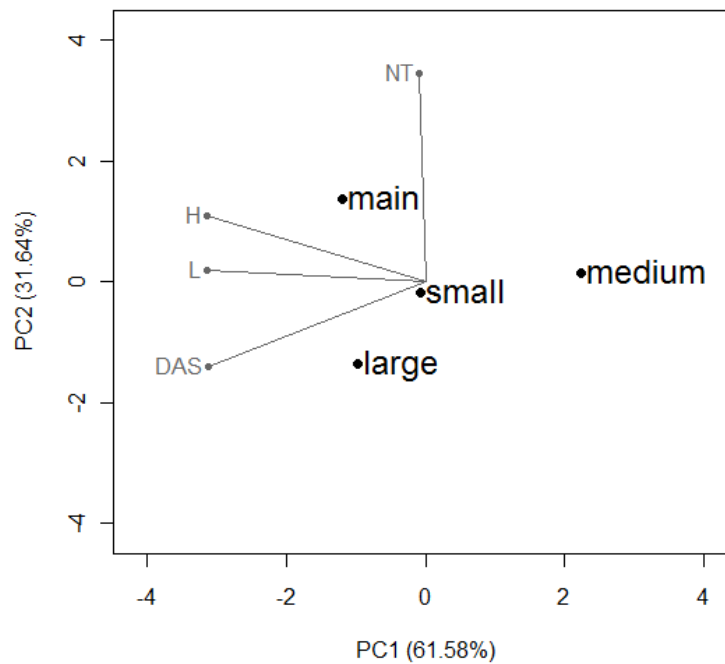


Figure 4. Biplot of the relation between variables (red vectors) and the habitat sizes with *Euterpe edulis* populations at Una, southern Bahia, Brazil. DAS=diameter at soil level, L=number of leaves, H=height, NT=number of plants.

The second component (PC2) explained 31.6% of the remaining variation discriminating the habitats based in the number of plants and height contrasting diameter at soil level (DAS) (Table 3). The main-size remnant presented higher density of *Euterpe edulis* and taller plants, populations of the small and medium-size fragment form an intermediate group. Contrasting the main-size populations is the large-size habitat with low density of *E. edulis* and plants smaller but with high DAS (Fig 4, Table 3).

Table 4. Results from principal components (PC) of the biplot analysis based on the morphometric variables and density of *Euterpe edulis* populations at Una, southern Bahia. NT=number of plants, DAS=diameter at soil level, H=height, L=number of leaves.

		PC1	PC2
Eigenvectors	NT	-0.02	-0.89
	DAS	-0.58	0.36
	H	-0.58	-0.28
	L	-0.58	-0.05
Eigenvalues (λ)		2.72	1.95
Variation retained (%)	Partial	61,58	31.64
	Accumulated	61.58	93.21

The morphometric variables were strongly correlated, especially number of leaves, plant abundance and height (Fig. 4, Table 5). Height and DAS showed also high positive correlation values (Fig. 4, Table 5). Main-size habitat showed the highest value in the height vector, followed by the intermediate group (large and small-size fragments), and the lowest by the medium-size habitat (Fig. 4). the large-size remnant presented the higher value for the DAS parameter. The main and small-size habitats are intermediate for DAS and the medium-size has the lowest value (Fig. 4). Mean number of leaves were very similar among the small, main and large-size sites and because of this the position of the small-size habitat in the biplot was more weighted by the DAS and height vectors (Fig. 4). The medium-size site has the lowest mean value of number of leaves (Fig. 4). We did not verify any pattern related to habitat reduction.

Table 5. Correlation matrix among plant size parameters diameter at soil level (DAS), height and number of leaves and mean number (NT) of plants of *Euterpe edulis* populations at Una, southern Bahia, Brazil.

	NT	DAS	Height	Leaves
NT	1	-0.3793	0.3395	0.0852
DAS		1	0.7319	0.7367
Height			1	0.7252
Leaves				1

4. Discussion

We evaluated the effects of forest fragmentation on the demography of an important palm species. We have shown that differences in plant density occur only between the two major habitats. In general, our main-size remnant showed the highest densities and number of individuals in all stages classes. Nevertheless, we did not find any pattern related to habitat loss for the parameters observed. Although the effects of forest fragmentation on plant demography is largely documented in the literature (Bruna *et al.* 2009) we suggested that the high structural heterogeneity among fragments, the peculiar matrix connecting the remnants, the cabruças, and the sizes of our small fragments (>200ha) might influence the population ecology of *E. edulis*. So our attempt here was primarily point out possible patterns related to our sampled populations as an useful information for posteriori testing.

4.1. *Euterpe edulis* density in a forest fragmentation gradient

Population densities observed at Una remnants are very below the estimated threshold of 1.7 plants/m² for *Euterpe edulis* populations at southern Brazilian's Atlantic Forest (Reis *et al.* 2000). Lower density in a fragment at Una region was already pointed out in other study (Silva *et al.* 2009) and two factors may be influencing this pattern. First, the two principal soil types in Una region (more specifications in study site) are poor in nutrients which can directly limit establishment and growth of plants as can increase intra and interspecific competition for resources. Second, at southern Bahia is being investigated a phenotypic and genetic differentiated population of *E. edulis* (Coelho 2010), the "Bahia" ecotype, mainly characterized by the reddish crownshaft coloration and the reduced number of rachillae which imply in a lower number of fruits produced by plant (Bovi *et al.* 1987). Reduced fertility, as seed output, decreases the probability of seeds being deposited in favorable sites and to be recruited into the population.

Euterpe edulis is an abundant species at Una landscape being regularly found at fragments understory or even in disturbed areas (Martini *et al.* 2007). Although abundant, the lowest expected densities of *E. edulis* observed may be

justified by the high equability of the plant community observed at forest fragments with different sizes at Una (Mariano-Neto 2004) implying in a restrictive force in growth and survival due to high competition process.

In spite of this, the similarities of densities between Maruim, Metal Forte and Mazao remnants, respectively the main, medium and small-size fragments, possibly reflects a natural variation of *Euterpe edulis*. However, the greatly decrease in density of *E. edulis* at the Ecoparque site (large-size fragment) probably does not represent this natural variation.

Decreased density of plants in Ecoparque (large-size fragment) is not related with habitat reduction properly but possibly to secondary effects of a disturbance gradient already revealed within this landscape (Faria *et al.* 2009). Harvesting, logging, hunting and forest burning are some examples of threats facilitated by fragmentation process (Tabarelli *et al.* 2004). Even though we tried to avoid visible harvested areas, we can not exclude the possibility of palm heart exploitation, as this practice was already observed at Una (A.M.Z. Martini, pers. com.).

Harvesting could also explain the great differences in *E. edulis* density in our study (0.110 plants/m²) comparing to Silva *et al.* (2009) (0.423 plants/m²) at the Ecoparque remnant. Although both studies were conducted at the same fragment, samples plots in Silva *et al.* (2009) corresponds to a longer protected area since this fragment is divided into two parts, one of a particular owner, our sampled area, and the other a conservation unit established in 1997 where Silva *et al.* (2009) sampled. We also need to highlight that the samples of Silva *et al.* (2009) were conducted in 2001 and considering the colonizing ability of *Euterpe edulis* in variable habitat quality (Martini *et al.* 2007) we expected a homogenize dominance across this fragment past 10 years.

Protection status of the site and time since protection are probably also imperatives factors influencing the demography, as the higher mean density belongs to the more long-protected remnant. Pires (2006) founded even lower densities of *Euterpe edulis* in seven forest fragments compared to our study, allying this pattern probably to fragmentation effects, harvesting and lack of protection of the remnants.

4.2. Demographic structure based on development stages

The subpopulations sampled differed in the developmental stages frequencies however there was a significant difference in densities among plots. These results indicate that even in short distances there is a natural variation in the demographic structure within the forest fragments possibly as an outcome of microhabitat effects (Reis 1995). Increase in sampling efforts may reduce this great variability.

The demographic structure of *Euterpe edulis* at the sampled forest fragments presents the reverse “J” shape when we consider jointly seedling and infant stages, which represent the regeneration bank. This kind of distribution shows that the regeneration is maintained by the continuum recruitment of the earlier stages into larger size classes (Reis 1995). In *E. edulis* populations there is also a strongly density-dependence by which high densities of the regeneration bank limit densities of the intermediate stages (Silva-Matos *et al.* 1999). Density-dependence mortality might reflect both the strength of intraspecific as interspecific competition. Although *E. edulis* is allied to the understory dominant component in Una landscape, there is a quite equability in the forest communities in Una (Mariano-Neto 2004) showing that establishment could result from successful competition abilities or by chance.

The relative proportion of seedlings ranged roughly from 0.5 to 12% in our study, a number well below the 73% estimated by Reis *et al.* (2000) as is characteristic of the species the strategy of forming an abundant seedling bank (Reis *et al.* 1996). Similar seedling abundance was related to forest fragmentation by Pires (2006) but our results did not support the effect of habitat reduction.

Annual variation in seed production is common in *Euterpe edulis* populations because the number of seed-bearing trees and inflorescences per plant oscillate year-by-year (Matos & Watkinson 1998; Fantini & Guries 2007). Following the year of low-production usually there is compensation in reproduction maintaining the influx of individuals to the previous formed regeneration bank (Matos & Watkinson 1998; Fantini & Guries 2007). This pattern is corroborated by the larger density at the infant stage class observed

in all sampled habitats representing the successive incoming of individuals securing the natural regeneration of the subpopulations.

Seed establishment may also have been regulated by increased post-dispersal seed predation rates (Fadini *et al.* 2009). Seed predation can be caused by vertebrates, such as small rodents (Vieira *et al.* 2003) and white-lipped peccaries (Keuroghlian & Eaton 2008), as also through the specialist scolytoid beetle (Von Allmen *et al.* 2004). We observed in other study at the same trails high rates of seed predation that ranged from 71% to 82% among the habitats. Possibly seed predation is a process leading to a seed-to-seedling bottleneck as we also observed a low probability of seedling establishment at these fragments. Interaction between insects and vertebrate seed predators may vary along seasons (Von Allmen *et al.* 2004), microhabitats (Fleury & Galetti 2004) and by the defaunation level of the habitat (Galetti *et al.* 2006) and can result in distinct effects on long-term demographic structure. Monitoring these effects in a landscape is a further issue to be elucidated.

There are some possible explanations to the higher number of seedlings at the small-size fragment. First, it was observed in this forest remnant the practice of logging trees (M. O. Melito, pers. obs.) which promote gap formation that increase light incidence and could stimulate an increase in the number of adults flowering and fruiting or seed output per plant. Increases in resource availability might further attract the associated fauna that disperse the diaspores, corroborating the seedling-clumped pattern by defecated dispersed seeds of some samples in the small-size fragment. Some seed dispersers that swallow fruits can favor establishment by increasing germination rates and/or the percentage of seeds recruited as also can promote a suitable microhabitat by a fertilized effect on growth of the defecated seeds (Traveset 1998). However, seedlings from clumped seeds may suffer intraspecific competition especially through shoot competition (Pizo & Simão 2001). Other possibility is a year of an episodic recruitment (Bruna *et al.* 2009) in this habitat or even this proportion of seedlings represents the natural production expected for the area, contrasting to a year of low recruitment in the other remnants. For instance, the number of seedlings of the small-size fragment is not reflecting, at least yet, in a higher density of infants.

In general, lower survival rate is expected for seedlings (Portela *et al.* 2010) and regeneration bank (Silva Matos *et al.* 1999). The bottleneck observed between the infant and juvenile stages, except for the large-size habitat, may be related to density-dependent effects on survival and growth (Matos & Watkinson 1998), as herbivory (Fadini *et al.* 2009) and intra and interspecific competition (Silva Matos *et al.* 1999; Fantini & Guries 2007;).

More opened canopy conditions appears to favor recruitment of the lower-stages into the immature size class (Fantini & Guries 2007) possibly explaining the higher densities observed at main and small-size patches. As already discussed, there is logging activities at the small-size fragment affecting canopy integrity. Higher light incidence in main-size remnant may be due to the proximity of a river and/or through the effects of a past disturbance at the sampled plots. Before the establishment of Una Biological Reserve it was presented in the region an agroforestry system of shaded cacao plantation in the surroundings of the Maruim river. After 30-40 years of disturbance plant densities markedly increased at southern Bahia (Piotto *et al.* 2009). Corroborating with this disturbance hypothesis is the presence of *Macrocarpaea* spp. (Gentianaceae) at the medium-size fragment, a plant observed just in high preserved forests.

Impacts in the number of immature may be a concern since they represent the future reproductive individuals (Bruna *et al.* 2009). Models estimate more profound impacts in the demographic structure when mortality, expressed as harvesting, achieves the immature rather than the reproductive plants of *Euterpe edulis* (Freckleton *et al.* 2003). Both recruitment into the immature stage as survival and growth must be followed, especially at the large and medium-size habitat, to better elucidate the regeneration potential of this populations.

The density of reproductive plants sampled corresponds to the estimated in natural stands (Reis *et al.* 2000), although the large-size fragment was two-times lower contrasting to the main-size that was two-times higher. The main-size fragment is a protected area about at least 30 years, possibly sufficient time for population recovery of past harvesting and avoidance of actual exploitation. Although the other areas are also protected they differ in the degree of protection (except medium-size habitat) and, more importantly, were

incorporated to conservation units just recently (see Table 1). Although important, the protection status does not secure palm population survival and maintenance across fragmented landscapes at the Atlantic Forest (Portela *et al.* 2010).

Although we did not detect a statistical differentiation in the average stages density of *Euterpe edulis* at the large-size remnant in comparison to the others areas (Fig. 3), it is visible that this subpopulation shows the lowest densities for all developmental stages. The fact of we observed just a single seedling in the samples plus the lowest density of the infant stage may reflect a past-occurred palm heart exploitation in this area (Raupp *et al.* 2009) and probably the population is in a process of natural regeneration. The sympatry with the higher protected subpopulation in the same fragment (Silva *et al.* 2009) may be regulating this recovering by a source-sink process (Dunning *et al.* 1992) facilitated by the seed dispersers. The crucial role of seed disperses in seed arrival was already pointed out for other *E. edulis* subpopulation at Una Biological Reserve (Martini & Santos 2007). Seed limitation process is common in disturbed areas which suffered removal of adults and soil disturbance regimes leading to a restriction in seed recruitment (Clark *et al.* 2007).

When an individual is established in the adult stage there is a high probability of survival (Silva Matos *et al.* 1999; Portela *et al.* 2010) and the structural parameters (density and abundance) of the plant community seems not to influence survival, flowering and reproduction (Fantini & Guries 2007). If the actual density of adults is continually maintained over the time the natural regeneration probably will be secured in Una landscape due to the presence of protected areas and persistence of populations at small fragments (Portela *et al.* 2010). Broadly, *Euterpe edulis* populations from the study plots probably are shown in lower densities at seedling-to-immature stages due to competition effects in this richness and soil poor landscape but they have potential for successful reproductive establishment.

4.3. Plant size

In general, more accentuated differences in plant sizes were observed into the larger sizes classes, especially for the DAS and height parameters.

Number of leaves seems to be a less variant character than diameter and height for *Euterpe edulis* (Reis 1995). The shape of *E. edulis* changes with growth because stem diameter does not evenly vary with tallness (Alves *et al.* 2004). Plants up to 1.25 m allocate resources to achieve a wide stem base allowing support for a posterior growth in height (Silva 1991; Alves *et al.* 2004).

Possible the soil composition and humidity level among the main and large-size remnants may influence for higher plant sizes (DAS and height) in these populations than medium and small-size fragments that are probably distributed at a most sandy soil. This could possible explain the lack of even taller plants at the small-size habitat that possibly have an opened canopy due logging activities at the site. The combination of a nutrient-poor soil and community structure may be restricting the development at the medium-size fragment as *Euterpe edulis* growth has a slightly negative relation with density of woody plants (Piotto *et al.* 2009)

Similarity in plant sizes between the main and large-size remnants did not reflect in abundance of *Euterpe edulis* (Fig. 1). Although both remnants showed the higher mean plant sizes (in DAS and height) they differed in what kind of morphometric parameter was responsible for the plant size. Site quality influences plant size reflecting also on resources allocation for reproduction (Nathan & Muller-Landau 2000). Plants from main-size plots are taller than the others habitats probably by a directly response to solar irradiation as observed for the species (Silva 1991), most likely due to a more opened canopy in face of past disturbance. Fertility are related with higher sunlight radiation (Silva 1991), but no with stem diameter (Matos & Watkinson 1998), and can influence positively population's abundance. Investment in radial growth at large-size habitat might reflect a strategy for competition in a more closed canopy observed in older forests or, most likely, indicate a regenerating population due to past harvesting.

Acknowledgements

We thanks to Carolina M. Pinheiro, Lukas H. Daneu and Thiago R. F. Araújo for field assistance and Yonaldo Guedes for permit to conduct the research in his property. Special thanks go to José Cláudio Faria for the biplot analyses and Bruno Machena (ICMBio REBIO Una) and Tatiana Alves (ICMBio RVS Una) for all support to conduct this research. This study was possible due to the grant from FAPESB (BOL0524/2009) and UESC (00220.1100.773), financial support of the master program in Ecology and

Conservation (UESC) and the logistic facilities provided by UESC, CEPEC herbarium and the ICMBio from Una Biological Reserve.

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Appendix A. Log-linear analyses of the effects of habitat (H) and plot (P) and their interaction for predicting the density of *Euterpe edulis* individuals into five development stages (S) in Una, southern Bahia, Brazil.

Effect	Contrast	df	G ²	P
Habitat	HP, S*	44	253.78	<0.001
	HP, HS	32	145.83	-
	Δ	12	107.95	<0.001
Plot	HP, S*	44	253.78	<0.001
	HP, OS	36	200.09	-
	Δ	8	53.69	<0.001
Habitat, given plot	HP, OS	36	200.09	-
	HP, HS, OS	24	97.05	-
	Δ	12	103.04	<0.001
Plot, given habitat	HP, HS	32	145.83	-
	HP, HS, OS	24	97.05	-
	Δ	8	48.78	<0.001
Habitat X plot X stage	HP, HS, OS	24	97.05	-
	HPS	0	0	-
	Δ	24	97.05	<0.001

* corresponds to the null model

CAPÍTULO 2

Seed fate of a threatened palm in forest fragments at the Atlantic Forest, southern Bahia, Brazil³

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Abstract

Forest fragmentation can affect the composition of mammal community and granivorous abundance. Therefore, patterns of seed exploitation by vertebrates and invertebrates might change in forest remnants affecting negatively seedling establishment. We evaluated using selective exclosure experiments patterns of seed predation and seed recruitment of the threatened palm *Euterpe edulis* across four size classes of forest fragments at the Atlantic Forest of southern Bahia, Brazil. Patterns associated with forest fragmentation were observed on seed fate experiments. Vertebrate predation increased across the gradient of habitat reduction although not linearly. Seed predation rates by vertebrates were higher in the first two months and ranged from 71% and 82% among fragments. However the foremost seed predator of the main habitat was the scolytine beetle for both treatments. Invertebrate predation occurred along all time of experiments. The exclusion of vertebrates increased probability of a germinated seed to established, except for the small habitat. Nevertheless a distinct great number of seedlings were observed just at the medium size fragment, especially on the exclosure treatment. High rates of seed predation may be driving a seed-to-seedling bottleneck that might be limiting population densities at the remnants thus conservation strategies for population recovery are discussed.

Key-words: *Euterpe edulis*, seed predation, seed establishment, seedling, scolytine beetles, vertebrate

1. Introduction

Southern of Bahia contains some of the last forest patches of the northeastern Atlantic Forest (Faria *et al.* 2009) being considered an area of towering biological importance because of the high levels of richness and plant endemism (Martini *et al.* 2007a; Thomas *et al.* 2008; Thomas *et al.* 1998). The Una region at southern Bahia have been suffered heavy deforestation rates and intense logging activities since 70's (Alger & Caldas 1994) and the remaining forest patches are estimated to comprise 3-5% of the original cover (Thomas *et al.* 1998).

The processes of forest fragmentation lead to the disruption of continuous habitat into forest remnants mainly promoting habitat loss thus impacting negatively biodiversity (Fahrig 2003). One of the most severe processes linked with forest fragmentation is the disruption of mutualistic and antagonistic relationships among plant and animals (Jordano *et al.* 2006; Tabarelli *et al.* 2004). Seed dispersal is a spatial process of diaspores' movement away from vicinities of their parent plant which may increase seed survival by mainly escaping from mortality-dependent process and/or arrival at suitable sites for germination (Janzen 1970; Nathan & Muller-Landau 2000). Despite the importance of seed dispersal seed arrival is not a guarantee of successful recruitment (Nathan & Muller-Landau 2000). Nevertheless post-dispersal seed predation is a process that directly impact plant demography (Hulme 1998).

Forest fragmentation and synergic effects can impact vertebrate community (Tabarelli *et al.* 2004). Depletion of the mammal community can lead to a compensatory increase in rodent and bird abundance that are voracious seed predators (Wright 2003). High granivorous abundance in forest fragments can greatly increase seed predation rates (Donoso *et al.* 2003). Therefore defaunation intensity and fragment size may underlie distinct patterns of seed predation and seedling recruitment (e.g. Galetti *et al.* 2006).

Different guilds of granivorous may have distinct spatial and temporal scale effects on seed predation (Christianini & Galetti 2007; Hulme 1998). Invertebrates also subject seeds to high levels of predation and they are usually host-specific (Dracxler *et al.* 2011). Scolytine and bruchine beetles are typically

associated with palm seed exploitation impacting negatively seedling recruitment (e.g. Dracxler *et al.* 2011; Janzen 1972). Although vertebrates and invertebrates granivorous are usually related with negative effects on plant populations seed damaged not always limit germination and establishment (Pizo *et al.* 2006; Rodríguez-Pérez *et al.* 2011).

In this context, our main objective was to evaluate the effects of habitat reduction on patterns of seed fate of the threatened palm *Euterpe edulis*. Analyzing multiple interactions we studied the impact of predator agents on the regeneration of *E. edulis*. Therefore using selective exclosure experiments we tested the following predictions: (1) patterns of seed exploitation shifts across time (2) vertebrate predation increases according to the gradient of forest fragmentation as insect predation decreases; (3) seedling establishment decrease across the forest fragmentation gradient as a negative effect of vertebrate predation.

2. Material and methods

2.1. Study site

The Una region presents great plant diversity and endemism structured in a tropical lowland rain forest with canopy, understory and emergents layers, and a rich epiphytic flora of bromeliads, orchids, ferns and lianas (Amorim *et al.* 2008; Thomas *et al.* 1998). We conducted this study at protected areas, two remnants at the Una Biological Reserve (REBIO Una) and other two at the Una Wild Life Refuge (RVS Una), both conservation units located at the municipality of Una, southern Bahia, Brazil (Table 1, Fig. 1).

The REBIO Una is a high protected site established in 1980 with very restrictive purposes, as scientific research and protection of species and associated habitat. This conservation unit was amplified in 2007 mainly for fragments reconnection totally nowadays 18.900 ha (Table 1). Figure 1 shows the Maruim (main-size) fragment that initially compounded the REBIO Una and the added Metal Forte (medium-size) remnant (see also table 1). The RVS Una was established in 2007 and has a lesser degree of protection due to the presence of private owners in the area in a system that attempt integrate land

use, recovery of disturbed areas with reconnection and protection of forests remnants (Fig. 1, Table 1).

Table 1. Characteristics of the study sites and populations of *Euterpe edulis* in Una, southern Bahia, Brazil.

Fragment	Area (ha)	Fragment size class	Plants density (m ²)
Maruim	12334.6	main	0.468
Ecoparque	2655.8	large	0.110
Metal Forte	946.4	medium	0.298
Mazao	210.8	small	0.266

There is a mosaic of forests remnants broad by the two conservation units (Fig. 1) surrounded by a matrix composed mainly by pastures, second-growth forests and shaded cocoa plantations, respectively 27%, 15% and 6% (Pardini 2004). Average annual temperature is 24 °C and mean rainfall about 2000 mm year⁻¹ without a clearly seasonality, although reduces might occur from December to March (Bovi *et al.* 1983). Canopy layer is about 25-30 m with emergent trees reaching up 40 m (Faria *et al.* 2009).

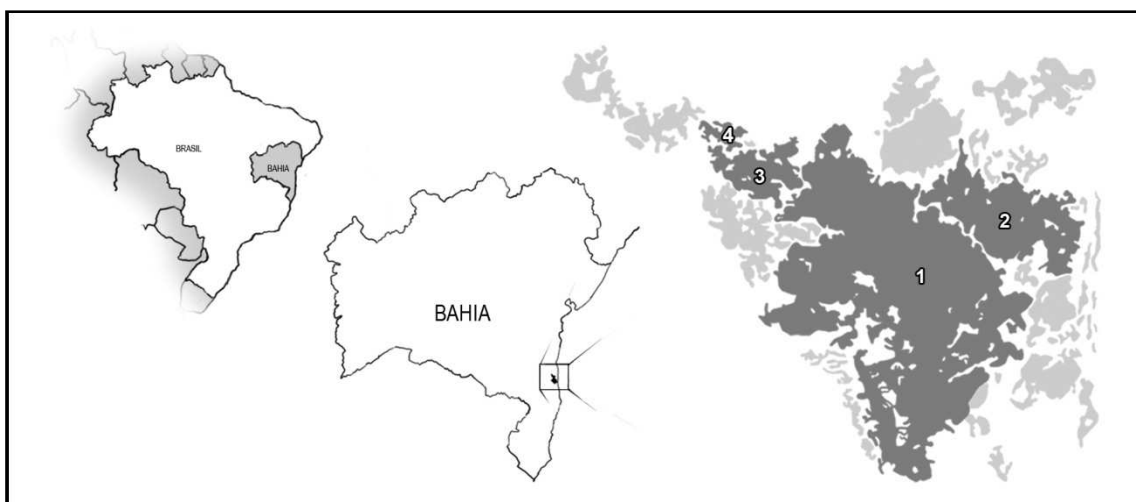


Figure 1. Map locating the forest fragments comprised by two conservation units at Una, southern Bahia, Brazil. Fragments from REBIO Una are 1 (main size) and 3 (medium size) and RVS Una are 2 (large size) and 4 (small size).

2.2. Focal species

Euterpe edulis (Arecaceae) occurs mainly at the Atlantic forest (Henderson & Galeano 1996) and it is abundant at southern Bahia (Martini *et al.* 2007a; Martini *et al.* 2007b; Thomas *et al.* 1998). *Euterpe edulis* is mainly single-stemmed, 5-12 m tall, 10-12 cm diameter and it presents 8-15 pinnate leaves (Henderson & Galeano 1996). Reproductive plants produce mean (\pm SD) of 1.6 (\pm 0.6) inflorescences within 128 (\pm 22) rachillae (Wendt *et al.* 2011). Fruits are globose drupes (mean \pm SD = 13.5 \pm 1.3 mm length, 14.2 \pm 1.2 mm width) (Von Allmen *et al.* 2004) containing a slightly fleshy-fibrous mesocarp involving a hard-fibrous endocarp containing one seed.

Euterpe edulis is considered a key-species in fragmented forests or in habitats with restricted resource availability (Fadini *et al.* 2009) because it provides food resource for a variety of frugivores vertebrates, such as birds (Galetti & Aleixo 1998; Matos & Watkinson 1998), large mammals (Keuroghlian & Eaton 2008) and rodents (Vieira *et al.* 2003). Removal of the edible apical meristem results in the death of the plant and this unplanned practice has led to the decline of the natural stands as also local extinctions across the Atlantic Forest (Galetti & Fernandez 1998). Even though illegal exploitation still continues depleting natural stands with ecological consequences at the vertebrate communities (Galetti & Fernandez 1998).

2.3. Seed fate experiment

We tested the effect of vertebrate and invertebrate predation on seed fate at different habitat sizes by enclosure experiments. The experimental unit consists of an open treatment (inclusion) 1-2 m apart of the vertebrate treatment (exclusion). The inclusion treatment was marked with a stick at the center with a numbered label. The exclusion treatment consisted of a wire cage (20 X 20 X 10 cm) covered with a mesh of 1.5 cm in which only invertebrates were capable to have access. We systematically set up the 20 experimental units per habitat 10 m off a trail and separated from each other by 50 m securing independence among samples.

We removed the endocarps from ripe fruits collected directly from rachillae and set up six endocarps in each treatment directly in soil surface simulating the natural clustering pattern found after primary dispersion (Fleury & Galetti 2004). Hereafter we use the term “seed” for the pyrene structure that consist of the hard endocarp protecting the seed and embryo. Experimental units were checked about every 30 days during six months as seed establishment ranges from three to six months (Bovi *et al.*, 1987). We used rubber gloves to avoid bias by olfactory predator cues when we manipulated seeds and the experimental units (Duncan *et al.* 2002).

We classified seed fate as (1) invertebrate predated (IP), (2) vertebrate predated (VP), (3) germinated seed (SG), (4) seed germinated and with signs of predation (GP), (5) recruited seed, i.e. established seedling (SE), and (6) intact seeds (SI). We classified vertebrate and invertebrate predation by the print left on the seeds as tooth marks from rodents and typical entrance hole of scolytine beetles (*Coccotrypes palmarum* Eggers). In addition to visible signs we also considered seed predation by vertebrates the seeds not observed in a radius of 30 cm from the inclusion treatment (Galetti *et al.* 2010). Protrusion of the radicle indicated germination. We evaluated rates of seeds germinated and predated because establishment is possible to occur in damaged seeds (Pizo & Simão 2001). To avoid manipulation of the seeds germinated we only inspected manually signs of predation in seeds not firmly fixed on substrate, in this way our estimative could be underestimated. Establishment was determined by the presence of one palmate leave. We assumed the absence of secondary dispersal by ants due to the lack of seed removal by ants in observational and experimental studies at the area (Santana 2011).

2.4. Data analysis

Biplot based on principal component analyses (Gabriel 1971) was used to observe the temporal variation and multiple interactions among seed fate categories and to discriminate related patterns between habitats and treatments. Correlation matrix of seed fate categories was constructed based on the mean values of the experimental units of each variable. Matrix data of seed fate were not cumulative for each revision (~30 days), i.e. is represented

just the variation of “new” events at each month from the beginning of experiments. Data were centered in means and not scaled to unitary variance preserving the variability of the length vectors by factoring method (Galindo 1986). Replicates from the exclusion treatment that failed to avoid vertebrate access were discarded from analyses. The biplot was constructed using R software (R Development Core Team 2009). Transition probability was used to estimate survival of a germinated seed to establishment (Rey & Alcántara 2000). Thus we divided the mean number of seeds established by the germination rate for the inclusion and exclusion treatment and habitats.

3.Results

After six months seeds preyed when accessed by vertebrates ranged from 71% to 82% at all fragments (Table 2). Rates of seed predation varied among treatments (Table 2). In general, insects are important agents underlying seed mortality at the largest fragments in inclusion treatments (Table 2). There was a decrease of roughly 2-fold in seed predation at the exclusion treatment in the smallest habitats (medium and small) (Table 2).

Table 2. Seeds preyed by vertebrates and invertebrates from exclusion and inclusion treatments among habitat size classes at Una, southern Bahia, Brazil. Mean \pm SD per experimental unit (n=6).

Habitat size	Exclusion		Inclusion	
	mean \pm SD	%	mean \pm SD	%
Main	4.95 \pm 1.54	81.8	4.25 \pm 1.29	70.80
Large	4.11 \pm 1.70	68.4	4.94 \pm 1.18	82.46
Medium	2.18 \pm 1.81	36.3	4.31 \pm 1.49	71.93
Small	2.78 \pm 1.52	46.3	4.95 \pm 1.23	82.50

Germination was higher at the sites (medium and small habitats) where seed predation on exclusion treatment was lower (Table 2, 3) indicating a negative impact of invertebrates on seed germination. The exclusion of vertebrates resulted in a higher probability of seedling establishment but not for the small fragment (Fig. 2). The medium-size fragment showed higher transition

probability rate in the exclusion (0.57) and inclusion (0.26) treatments (Fig. 2). The main habitat presented the lowest transition rate (0.04) when accessed by vertebrates (Fig. 2). Seedling establishment increased in a range of 2 to 4-fold in the absence of vertebrates for all habitats (Table 3). Thus vertebrates can directly influence the bottleneck among seed-to-seedling stages, except for the small habitat. Although germination at the small habitat seems to be improved on exclusion treatment this did not reflect at the transition probability to seedling stage (Fig. 2)

Table 3. Seeds germinated and established on treatments of exclusion and inclusion of vertebrates among habitat size classes at Una, southern Bahia, Brazil. Values are mean \pm SD per experimental unit (n=6).

Habitat size	Germinated		Established	
	exclusion	inclusion	Exclusion	inclusion
Main	0.90 \pm 1.21	1.30 \pm 1.34	0.10 \pm 0.45	0.05 \pm 0.22
Large	1.74 \pm 1.66	1.05 \pm 1.08	0.32 \pm 1.00	0.11 \pm 0.46
Medium	3.00 \pm 2.09	1.58 \pm 1.30	1.71 \pm 1.45	0.42 \pm 0.77
Small	3.00 \pm 1.53	1.25 \pm 1.25	0.33 \pm 0.69	0.15 \pm 0.37

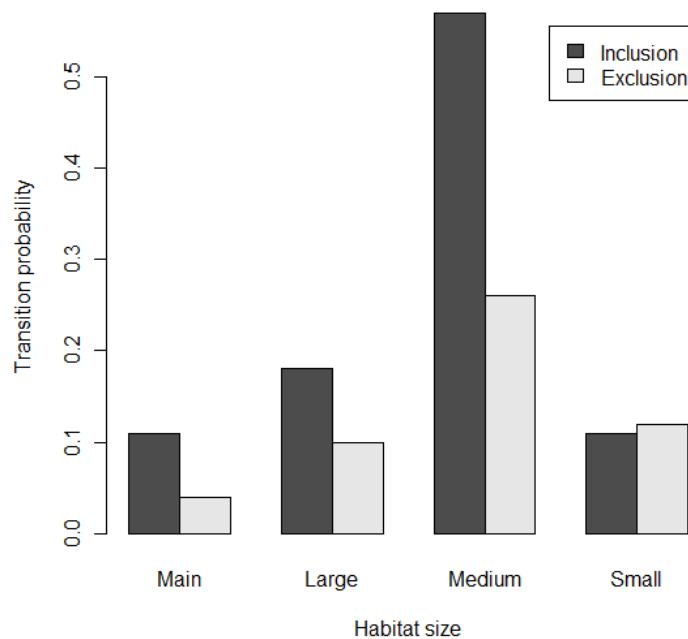


Figure 2. Transition probability of a germinated seed to establish on vertebrate exclusion and inclusion treatment among a gradient of habitat size at Una, southern Bahia, Brazil.

Seed fate patterns varied temporally among treatments and habitats. The first three months of experiments better elucidate dissimilarities among habitats due to the greater variation in seed fate between the treatments and fragments.

After 30 days the first component (PC1) retained 78.14% of the variation distinguishing at the right side of this axis the habitats with higher means of intact seeds (SI) and predation by invertebrate (IP) contrasting with habitats with higher vertebrate predation rates (VP) at the left side (Table 4, Fig. 3a). Observing just the inclusion treatment high rates of seeds preyed by vertebrates were found at the large and small remnants thus these areas are closer to the extremity of the VP vector (Fig. 3a). Vertebrate predation rate was intermediate in the medium-size habitat (Fig. 3a). The main-size habitat showed the lowest level of seeds preyed by vertebrates after 30 days and therefore presented the higher number of seeds intact and preyed by invertebrates (Fig. 3a).

As expected, the exclusion treatment was more clustered at right in the first axe on 30 days of experiments by the absence of vertebrate predation. Thus the second component (PC2) better discriminated the patterns of the exclusion treatment. PC2 after 30 days explained 13.67% of the variation and is negatively related with invertebrate predation (IP) and positively with the number of seeds intact (SI) and germinated (SG) (Table 4). The smaller habitats presented the higher proportion of seeds intact and germinating in the absence of vertebrates (Fig. 3a). Contrarily, the biggest remnants (main and large) showed the highest rates of seeds preyed upon by invertebrates and lowest number of germinated seeds and intact in the presence or absence of vertebrate access (Fig. 3a). However, the major process underlying seed mortality was predation by vertebrates at the large-to-small remnants in the inclusion treatment.

After 60 days there was a decrease on vertebrate predation and the variables that formed the PC2 at 30 days (SI and SG contrasting to IP) gain strength forming the PC1 (64.58%) at this time (Table 4, Fig. 3a,b). From the seeds that remained intact from previous month we observe a proportional decrease in insect predation and increase on germination and seeds intact in the large remnant (exclusion treatment) (Fig. 3a,b). The others habitats conserved the same pattern observed at 30 days (Fig. 3b). High rates of insect predation were still observed in the main habitat regardless the access of

vertebrates, but more intensified in the exclusion treatment (Fig. 3b). PC2 (32.21%) basically discriminate habitats by the number of seeds preyed by vertebrates contrasting with the variables of the PC1 (SI, SG and IP). The small-to-large fragments were even more clustered when accessed by vertebrates showing the homogeneity for this variable.

High decrease in the mean number of seeds germinating (SG) at all sample units was observed after 90 days of experiments, this pattern is showed by the small length of the SG vector in the biplot (Fig. 2c). Number of seeds preyed by vertebrates (VP) reduced even more at 90 days of experiments. Besides VP has no more explicative power for the next months. We also can observe by the angle of almost 180° among the SG and VP vectors that they are strongly negative correlated (Fig. 3c).

Table 4. Principal component analysis of seed fate experiments from 30 to 90 days at forest fragments at Una, southern Bahia, Brazil. IP= invertebrate predation, VP= vertebrate predation, SG= seeds germinated, SI= intact seeds.

		30 days		60 days		90 days	
		PC1	PC2	PC1	PC2	PC1	PC2
Eigenvectors	IP	0.23	-0.80	0.63	0.73	0.01	-0.99
	VP	-0.81	0.11	0.04	-0.39	0.05	0.10
	SG	0.03	0.31	-0.50	0.36	-0.05	-0.14
	SI	0.53	0.50	-0.59	0.44	-1.00	0.01
Eigenvalues (λ)		4.02	1.68	2.52	1.78	1.38	0.79
Variation retained (%)	Partial	78.14	13.67	64.68	32.21	73.61	24.6
	Accumulated	78.14	91.81	64.68	96.89	73.61	98.21

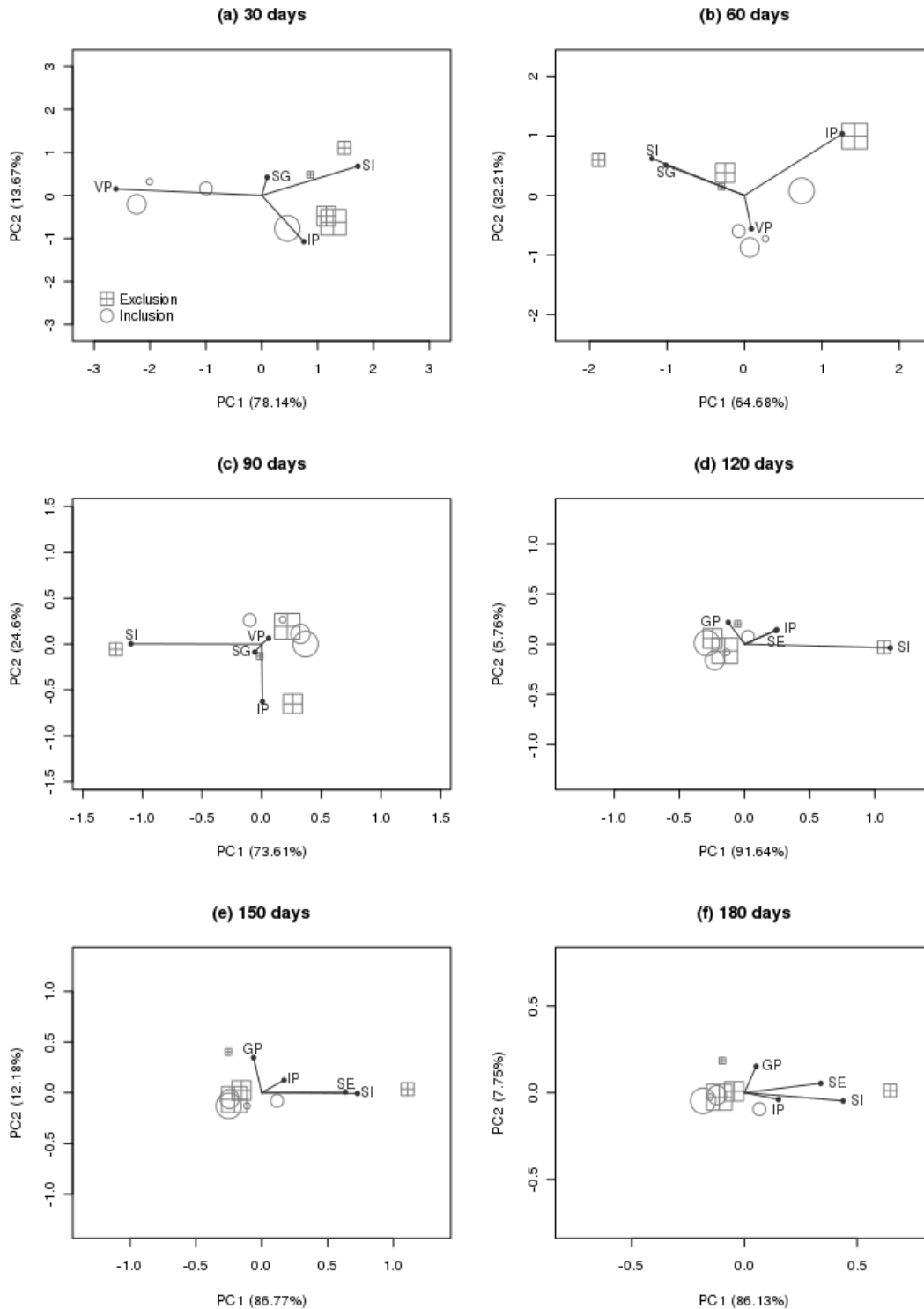


Figure 3. Biplot based on principal components showing the sequence of variation of *Euterpe edulis* seed fate from treatments of vertebrate exclusion and inclusion in a forest fragmentation gradient at Una, southern Bahia, Brazil. Size of the symbols is congruent with the gradient of habitat size going to the main (bigger symbol) to small (smaller symbol) fragment. Vectors correspond to response variables of seed fate: IP= invertebrate predation; VP= vertebrate predation, SG= seed germinated; GP= seed germinated and predated; SE= seed eaten; SI= intact seeds.

After 90 days the PC1 (73.61%) discriminated the habitats by the number of intact seeds (SI) (Table 4). In the absence of vertebrates the medium-size fragment continued to present a higher number of seeds intact greatly contrasting with the other habitats (Fig. 3b,c). When vertebrates accessed seeds the medium-size habitat also showed higher number of seeds intact. Possibly the intermediate rate of seed predated by vertebrates at the medium-size habitat in the beginning of experiments (Fig. 3a) resulted after 90 days in a higher number of intact seeds (Fig. 3c). We highlight that in the inclusion treatment at the main remnant had no more intact seeds after 90 days and the major process underlying seed mortality was insect predation (Fig.3a-c). The PC2 (24.6%) discriminated habitats by invertebrate predation (Table 4). In the exclusion treatment seeds preyed by insects were highest at the large-size habitat contrasting lowest on the main fragment (Fig. 3c). Insect predation when accessed by vertebrates was slightly higher on the large remnant (Fig. 3c). There was no correlation among number of seeds preyed by insects and seeds intact as observed by the angle of 90° among variables (Fig. 3c).

Germinated seeds showing signs of predation (GP) were observed every month but they appeared to be important to discriminate the habitats only after 120 days (Table 5). Seeds with signs of germination and predation (GP) were not correlated with insect predation (IP) after 120 days (Fig. 3d). Both variables were also positively correlated with the remaining intact seeds (SI) (Fig. 3d).

Seedling establishment was observed after 120 days of experiments (Fig. 3d) except for the large-size remnant that started next month. At this time PC1 (91.64%) is represented by number of seeds intact (SI), similarly to the observed after 90 days of experiment (Table 5, Fig. 3c,d). Broadly, we can distinguish the medium-size habitat when not accessed by vertebrates by higher mean number of intact seeds contrasting to the remaining habitats (inclusion and exclusion) that are clustered at the left side of the first axe (Fig. 3d). Observing just the open treatment the medium remnant also presented a higher number of seeds intact (SI). PC2 retained just 5.76% of the variation and little discriminated the habitats and treatments.

The same pattern observed at 120 days is conserved after 150 and 180 days but with a better distinction among sample units (Table 5, Fig. 3d-e). PC1 at 150 (86.77%) and 180 (86.13%) days were composed by the sum of number

of seeds intact (SI) and seeds established (SE). In general, the medium-size habitat was positioned at the right side of the first axis contrasting the remaining areas clustered in the left side with low means of the parameter SE and SI (Fig. 3e-f). PC2 after 150 (12.18%) and 180 days (7.75%) discriminated the small-size habitat (exclusion treatment) mainly by the seeds germinated and predated (GP). This high rate of GP elucidates the lack of transition probability improvement on exclusion treatment at the small habitat.

Seeds established (SE) are greatly correlated with the number of intact seeds (SI) since 120 days (Fig. 3e-f). Insect predation is also correlated with SE and SI since 120 days (Fig. 3d-f), indicating the importance of invertebrates as predators along the time of experiments especially when vertebrate predation decreased (Fig. 3).

Table 5. Principal component analysis of seed fate experiments from 120 to 180 days at forest fragments at Una, southern Bahia, Brazil. IP= invertebrate predation, SE= seed established, GP= seeds germinated and predated, SI= seeds intact.

		120 days		150 days		180 days	
		PC1	PC2	PC1	PC2	PC1	PC2
Eigenvectors	IP	0.21	0.49	0.17	0.34	0.26	-0.22
	SE	0.21	0.46	0.65	0.02	0.59	0.31
	GP	-0.11	0.73	-0.06	0.94	0.09	0.88
	SI	0.95	-0.13	0.74	-0.02	0.76	-0.27
Eigenvalues (λ)		1.18	0.30	1.23	0.46	0.72	0.22
Variation retained (%)	Partial	91.64	5.76	86.77	12.18	86.13	7.75
	Accumulated	91.64	97.4	86.77	98.95	86.13	93.88

4. Discussion

Studies of seed fate rarely focused on the temporal sequence of events combining the importance of each predator at the dynamics of seed germination and establishment. In our study we have shown that seed predation by vertebrates was high and severe at the beginning of seed exposition, insects detected and preyed seeds more equally along the time. Insect predation was a

function of the number of the remaining intact seeds after the peak of vertebrate seed predation. This temporal shift on predator importance corroborated to our predictions. We also verified that vertebrates greatly increased seed predation rates with habitat reduction although not linearly.

Vertebrates greatly impacted seed survival in the first two months, especially in the first 30 days of experiments. Small and medium mammals can accelerate about two times the median time of seed removal as also significantly decreased seed and seedling survival (Paine & Beck 2007). The peak of fruit removal of *Euterpe edulis* by animals is about 40 days after experimentally exposed to frugivores (Reis 1995) corroborating to our findings. As far as we know, the high percentage of *E. edulis* seeds preyed when accessed by vertebrates in Una were only lower to the findings at Anchieta island an area with a high agoutis density in the Atlantic Forest (Fadini *et al.* 2009).

In Una landscape richness and abundance of small mammals increased in forest fragments in comparison to continuous forest (Pardini 2004), which correspond to our main-size remnant. The genus *Oryzomys* is frequently associated to palm seed predation (e.g. Pinto *et al.* 2009; Vieira *et al.* 2003) and in Una is represented by *O. russatus*, *O. subflavus* and *O. laticeps* (Pardini 2004). *O. laticeps* is the most abundant small mammal at Una landscape and is associated to mature forest interiors of fragments (Pardini 2004).

We also verified in field signs of seed predation by peccaries indicating a possible effect of large mammals on seed predation. *Dasyprocta leporina* (agouti) is a large mammal observed in Una landscape with a negative response in abundance to habitat reduction (R. Pardini, unpubl. data). Agouti and white-lipped peccary (*Tayassu pecari*) are important seed predators of *E. edulis* (Galetti *et al.* 2010; Keuroghlian & Eaton 2008).

Granivory by birds may also be an important process in forest fragments (Christianini & Galetti 2007). Birds are the most diverse animal group in Una landscape and generalist species are more associated with interior of small fragments than on large ones (Pardini *et al.* 2009). Donoso *et al.* (2003) suggested that rodents and birds are the main predators in the interior of small fragments compared to continuous forest in an intensively scattered landscape at Neotropics. In summary, the high levels of seeds preyed upon by vertebrates

indicate the importance of *E. edulis* seeds as resource within fragments at Una landscape.

Seed predation at the main-size fragment was due to insects and may be correlated with the higher densities of *Euterpe edulis* adults observed in the area (0.012 adults/m²; M. O. Melito, unpubl. data). Insect predation predominated at unharvested sites where *E. edulis* density is supposed to be higher, possibly due to the host-specificity of scolytid beetles (Pizo & Vieira 2004). Besides high insect predation rates are related to habitats where rodent abundance is lowest (Wright *et al.* 2000). However rodents play a key role in dispersing seeds and maintaining *Astrocaryum aculeatissimum* population when high intensity of seeds preyed by scolytines greatly increase seed mortality (Dracxler *et al.* 2011).

Seed predation by insects at the large habitat was also high but probably it was not related with *Euterpe edulis* density as we observed the lowest population size in this area (see Table 1). Maybe other palm species at the remnant act as host attracting the scolytid beetle (Janzen 1972). There was a temporal oscillation on patterns of seed exploitation by insects at this remnant until the first 3 months of experiments. Probably this results from different generations of scolytine beetles ecdysis after the eggs being laid into the endocarps (Janzen 1972). Generation time of the congeneric *Coccotrypes carpophagus* is of 30 days (Janzen 1972). Abiotic characteristics as humidity and light variation may also influence invertebrate foraging behavior (Christianini & Galetti 2007).

In general, the probability of seedling establishment decreased with vertebrate predation, except in the small habitat, but it did not follow the forest fragmentation gradient as predicted. *Tinamus solitarius* (Tinamidae) and *Odontophorus capueira* (Odontophoridae) are birds species associated with predation of germinated seeds (Barroso *et al.* 2010). Nevertheless the biplot only captured a distinct great number of seedlings established at the medium size habitat, especially at the exclusion treatment. Seedling establishment at this site might be favorable by microhabitat conditions and low rates of insect predation.

Transition probability of seed establishment at the small habitat did not improve with vertebrate exclusion and this was due to the high rates of seeds

preyed after germination. Although germination seems not to be affected by predation the negative effects of damage can reflect on seedling survival (Pizo *et al.* 2006). However in other study at the same area the small remnant showed a significant higher density of seedlings compared to the other habitats (M. O. Melito, unp. data). Plant density is not always greatly reduced by high rates of granivory (Hulme & Kollmann 2002) because animals can act as seed predator or dispersal agents and this is a time-dependent characteristic (Janzen 1971). As we did not evaluate deposition patterns by vertebrates is possibly that some vertebrates also perform as seed dispersals. Models evaluating costs and benefits of seed ingestion by ungulates suggest that there is a trade-off among increasing post-dispersal seed predation mortality but improving germination by secondary dispersal (Rodríguez-Pérez *et al.* 2011). Besides seed ingestion by ungulates compensates the negative effects of seed predation by bruchids beetles having a positive response on population growth rates (Rodríguez-Pérez *et al.* 2011). This process could be true at the small habitat as we observed sometimes the seedling-clumped pattern by defecated dispersed seeds.

We highlight that although seedling bank density at the small remnant is higher in general the regeneration bank of *Euterpe edulis* in our studied transects has low density, as we observed in other study (M. O. Melito, unp. data). This pattern corroborated the high seed predation rates and the low probability of seedling establishment when vertebrates have access to the post-dispersed seeds. Possibly seed predation by insects and vertebrates is a process driving a seed-to-seedling bottleneck.

4.1. Conservation remarks

Una region is considered a complex landscape composed by few large old-growth forests and a gathering of small fragments where a disturbance gradient related with edge effects was already identified (Faria *et al.* 2009). The surrounding matrix connecting these few forest remnants is dominated by an agroforestry system of shaded cacao plantations cultivated mainly under a thinned native canopy, called “cabruças” (Faria *et al.* 2007). The shade cacao plantations can harbor an extremely high diversity of ferns and animal

assemblages (Pardini *et al.* 2009) but this capacity rely on the proximity and extent of native forest at the landscape (Faria *et al.* 2007).

Euterpe edulis can potentially facilitate forest recovering in degraded patches by attracting several seed dispersers that influx seeds from the neighboring forest remnants (Reis *et al.* 2000). Besides the ecological importance, *E. edulis* has an economic value and a high potential for sustainable management (Reis *et al.* 2000). The edible apical meristem, the “palm heart”, is a gourmet food with a market value well established. Sustainable management of natural populations was successfully developed and tested on stands at southeast and south of Atlantic forest (Reis *et al.* 2000). Models also support the ability of *E. edulis* populations to be robust for high levels of harvesting when considering timing and life stage affected (Freckleton *et al.* 2003). However, incentives for legal regulation of this profitable commodity are essential to avoid illegal harvesting (Galetti & Fernandez 1998). Illegal palm heart production may be twice more profitable than legal activity (Orlande *et al.* 1996) and with low penalties when discovered (Galetti & Fernandez 1998). Local extinction and depletion of natural stands are associated with the unplanned illegal harvesting practiced at the Atlantic forest (Galetti & Fernandez 1998; Reis *et al.* 2000).

Euterpe edulis is a shade tolerant understory species which requires a forest canopy for successful regeneration and initial growth (Reis *et al.* 2000). In this way, the maintenance of a canopy layer on shade cacao plantations may provide a favorable environment for establishment and growth of *E. edulis*. Management of *E. edulis* into thinned natural forests or in consort with other cultures was already recommended by Bovi *et al.* (1987). We also believe that *E. edulis* would diversify local economy aggregating value to the shade cacao plantations and concomitantly reconnect natural stands of this threatened species.

In our studied we observed high levels of seed predation and low density of *Euterpe edulis* populations (M. O. Melito, unpubl. data). In such areas planting of seedlings and juveniles should be considered in spite of sowing seeds (Pizo & Vieira 2004). Protection of plants in the earlier stages may also be needed to avoid herbivory (Fadini *et al.* 2009). Seedlings could be provided in partnership between farmers and a federal cacao research institution present at the region

which has plant nurseries. Fruit pulp extraction on natural populations can also be implemented to complement economy of farmers securing profits until adult establishment. After pulp removal the seeds can be used for reforestation and handicraft.

Therefore identify and map the natural stands in Una and monitoring population dynamics is an essential step for conservation strategies. We highlight that the conservation unit RVS Una was created allowing private owners in a system that attempt integrate land use, recovery of disturbed areas with reconnection and protection of forests remnants. Thus, conservation strategies joining sustainable management and population recovery and maintenance of this threatened species are able to be implemented at Una landscape.

Acknowledgements

We thanks to Frederico Hobus, Jamille Bonfim, Leiza Souza and Michaele Pessoa for field assistance and Yonaldo Guedes for permit to conduct the research in his property. Special thanks go to Bruno Machena (ICMBio REBIO Una) and Tatiana Alves (ICMBio RVS Una) for all support to conduct this research. This study was possible due the grant from FAPESB (BOL0524/2009) and UESC (00220.1100.773), financial support of the master program in Ecology and Conservation (UESC) and the logistic facilities provided by UESC, CEPEC herbarium and the ICMBio from Una Biological Reserve.

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CONCLUSÕES GERAIS

Em geral, as populações de *Euterpe edulis* estudadas nos fragmentos de Una apresentaram baixas densidades populacionais. Com relação aos parâmetros demográficos (densidade de indivíduos e estrutura dos estádios de desenvolvimento) contrastes expressivos foram observados entre os dois maiores fragmentos. Nos mesmos fragmentos os indivíduos apresentaram os maiores valores de tamanho de planta (altura e DAS), entretanto este padrão não refletiu em um aumento na abundância de indivíduos. A menor densidade de indivíduos foi observada para o estágio de plântulas, que pode ser o indicativo de processos limitantes no estabelecimento ou sobrevivência dessas plântulas.

Desta forma, os padrões observados não estão relacionados à redução de área sobre a demografia das populações de *Euterpe edulis* analisadas. Possivelmente variações do microhabitat, a grande heterogeneidade estrutural entre os fragmentos e a permeabilidade da matriz que conecta os remanescentes sejam fatores preponderantes aos padrões observados.

Constatamos elevadas taxas de predação de sementes nos fragmentos estudados gerando um efeito negativo na proporção de plântulas estabelecidas. Predação por invertebrados foi importante no maior fragmento enquanto que vertebrados, possivelmente pequenos roedores e aves granívoras, foram os principais predadores para os outros remanescentes florestais. É possível que a intensa predação de sementes possa estar limitando o banco de plântulas de *Euterpe edulis*, padrão corroborado pela baixa densidade de indivíduos neste estágio no estudo demográfico das populações.

Vários estudos analisaram aspectos demográficos e o efeito de predadores sobre populações naturais de *Euterpe edulis*. Entretanto são escassos trabalhos enfocando as populações desta espécie na Floresta Atlântica meridional. As condições edafo-climáticas somadas à paisagem peculiar da região de Una em que grandes fragmentos se encontram imersos em uma matriz permeável, as cabruças, distinguem as populações de *E. edulis* estudadas daquelas distribuídas no sudeste e sul do Brasil. Desta forma, os

padrões e processos observados neste estudo são de grande importância para a conservação da espécie em escala global.