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DINÂMICA POPULACIONAL E DIVERSIDADE GENÉTICA DE *Spondias tuberosa* ARR. EM RESPOSTA ÀS MUDANÇAS NO USO DO SOLO NA CAATINGA

Recife
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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco como um dos requisitos para obtenção do título de Doutor em Biologia Vegetal, na área de concentração Ecologia e Conservação e linha de pesquisa Ecologia de Populações e Comunidades.

Área de concentração: Ecologia e Conservação

Orientadora: Prof^{a}. Dra. Jarcilene Silva de Almeida Cortez

Coorientador: Dr. Arne Cierjacks

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RESUMO

A acelerada perda de hábitats e das funções ecológicas são exemplos de como as mudanças globais no uso da terra têm afetado os ecossistemas. Grandes projetos de construção, como os de reservatórios, podem ter grandes impactos, resultando em mudanças nos padrões de habitat e paisagens e afetando as populações. *Spondias tuberosa* Arr. é uma espécie frutífera, endêmica da Caatinga, com grande importância socioeconômico e ambiental, mas que tem sofrido com a baixa regeneração nos seus locais de ocorrência. O objetivo deste trabalho foi avaliar a dinâmica populacional, a regeneração natural e a diversidade genética de *S. tuberosa* em quatro tipos de usos da terra ("Caatinga protegida", "Caatinga degradada", "áreas de agricultura" e "áreas abandonadas"), em municípios ao redor do reservatório de Itaparica. A região se caracteriza por ser um mosaico de usos da terra que se estabeleceram após a construção do reservatório. Foram coletados dados de biometria, número de sementes na superfície do solo e número de plântulas para analisar a regeneração e a dinâmica populacional da espécies nos diferentes usos da terra. Como variáveis preditoras foram incluídos nas análises a distância para a casa mais próxima, a pressão por caprinos, o índice de cobertura vegetal (NDVI) e a densidade de casas ao redor de cada indivíduo. Para a análise da diversidade genética desses indivíduos foram utilizados dois marcadores: sete microssatélites e banda polimórficas de AFLP. Os resultados mostraram que o uso da terra tem impacto na biometria de indivíduos adultos, sendo as maiores árvores presentes nas áreas de Caatinga protegida e nas abandonadas. Plântulas de *S. tuberosa* foram encontradas em áreas agrícolas, provavelmente devido à abundância de água e à exclusão de caprinos. Quanto às análises genéticas, *S. tuberosa* apresentou, de um modo geral, baixa diversidade, mas que, entre os usos da terra, a área de Caatinga protegida foi maior. A diferenciação genética entre esses usos da terra também foi baixa. Os resultados evidenciam quão *S. tuberosa* está dependente da população local para sua regeneração, em especial quanto ao suprimento de água e exclusão dos caprinos. Isso também elucida que áreas agrícolas, apesar de ser resultado de uma perturbação antrópica, podem atuar como áreas de conservação para essas espécies endêmicas. Além disso, a maior diversidade genética encontrada na Caatinga protegida evidencia a importância de se destinar mais áreas para a conservação da Caatinga e aumentar a fiscalização das áreas já existentes para, assim, proteger a base genética atual existente de *S. tuberosa*.

Palavras-chave: Diversidade genética. Floresta tropical sazonalmente seca. Regeneração. Umbuzeiro.

ABSTRACT

The accelerated loss of habitats and ecological functions are examples of how global changes in land use have affected ecosystems. Large construction projects such as reservoirs can have major impacts, resulting in changes in habitat and landscape patterns, affecting tree populations. *Spondias tuberosa* Arr. is a fruit-bearing species, endemic to the Caatinga, with great socioeconomic and environmental value, but it has suffered from low regeneration in its places of occurrence. The aim of this work was to assess the population dynamics, natural regeneration and genetic diversity of *S. tuberosa* in four land-use types ("protected Caatinga", "degraded Caatinga”, "agricultural areas" and "abandoned areas"), in municipalities surrounding the Itaparica reservoir. The region is characterized by being a mosaic of land uses that were established after the construction of the reservoir. Tree biometry, number of seeds on the soil surface and number of seedlings were used to analyze the regeneration and the population dynamics of the species in different land-use types. As predictor variables, the distance to the nearest home, the pressure per goats, the vegetation cover index (NDVI) and the density of houses around each individual were included in analyzes. For the analysis of the genetic diversity of the trees, two markers were used: seven microsatellites and polymorphic AFLP. The results showed that land use has an impact on the biometry of adult individuals, with the biggest trees being present in the protected Caatinga and abandoned areas. Seedlings of *S. tuberosa* were found in agricultural areas, probably due to the abundance of water and the exclusion of livestock. Regarding the genetic analysis, *S. tuberosa* showed, in general, low diversity, but that among the land-use types, the protected Caatinga was higher. The genetic differentiation between these land-use types was also low. In conclusion, the results show that *S. tuberosa* is dependent on the local population for its regeneration, especially regarding water supply and exclusion of livestock. This also highlights that agricultural areas, despite being the result of anthropogenic disturbance, can act as conservation areas for these endemic species. In addition, the greater genetic diversity found in the protected Caatinga evidences the importance of afford more areas for the conservation of the Caatinga and increasing the inspection of the existing areas, in order to protect the present genetic base existing in *S. tuberosa*.

Keywords: Genetic diversity. Seasonally dry tropical forest. Regeneration. Umbuzeiro.

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1 INTRODUÇÃO

A busca pelo bem-estar, progresso ou simples vantagem econômica tem feito com que o ser humano realoque os recursos naturais, mudando a configuração do ambiente em que vive. No entanto, as perturbações ambientais causadas pelas ações humanas têm aumentado não só em frequência como em intensidade, ocasionando consequências catastróficas nos ecossistemas, como o declínio do número de espécies e a perda local e não aleatória de diversidade biológica, funcional e filogenética (LAWRENCE; CHASE, 2010). Dentre as principais perturbações antrópicas, o uso da terra tem impactado intensamente a superfície terrestre, onde mais de 25% das florestas foram completamente devastadas e mais de 30% são áreas de agricultura (HURTT et al., 2006).

A pressão antrópica pode ter efeitos críticos na diversidade e na estrutura genética a nível de indivíduo e de população (PITHER; SHORE; KELLMAN, 2003), alterando a proporção de loci polimórficos (LOWE et al., 2005), o coeficiente de endogamia (ANDRÉ et al., 2008), a riqueza de alelos e a heterozigosidade (BALDAUF et al., 2013; PITHER; SHORE; KELLMAN, 2003). Em alguns casos, a diversidade genética se correlaciona positivamente com a aptidão populacional (BIJLSMA; LOESCHCKE, 2012) e a diversidade da comunidade (BOOTH; GRIME, 2003).

Mudanças na paisagem em decorrência da construção de um grande reservatório também geram um impacto ambiental e social nos locais onde se inserem. Apesar de proverem diversos benefícios para as populações que vivem em áreas áridas e semiáridas, que vão desde a geração de energia até fins turísticos (LEME, 2007), a construção de reservatórios implica no envolvimento de diversos atores para a tomada de decisões (RODORFF et al., 2015), mas que nem sempre acontece de maneira pacífica ou vantajosa para todos os envolvidos.

No intuito de entender as respostas das populações vegetais aos impactos diretos e indiretos resultantes das mudanças no uso da terra decorrentes da construção do reservatório de Itaparica, nós estudamos a dinâmica populacional, regeneração natural e diversidade genética de *Spondias tuberosa* Arr. (umbuzeiro). O umbuzeiro é uma espécie endêmica da Caatinga de grande valor ecológico, social e econômico, mas que tem sofrido com a exploração predatória, além do baixo recrutamento de indivíduos jovens. De acordo com Cavalcanti et al. (2009), a ausência de plantas jovens em seu ambiente natural tem sido atribuída, principalmente, à irregularidade das chuvas na região, à dificuldade na germinação das sementes, ao desmatamento desordenado e aos danos causados às plântulas que emergem. A pressão por caprinos é outro fator que está associado à redução do recrutamento, do crescimento e da distribuição do umbuzeiro (CAVALCANTI; RESENDE; BRITO, 2009).

2 FUNDAMENTAÇÃO TEÓRICA

2.1 PERTURBAÇÕES NOS ECOSSISTEMAS

De acordo com Pickett e White (1985), as perturbações se caracterizam por ser qualquer evento, relativamente discreto no tempo, que modifica a estrutura de populações, comunidades e ecossistemas, além de alterar a disponibilidade de substrato e modificar as condições físicas do ambiente. A partir dessa definição, as perturbações foram classificadas como naturais ou antrópicas. A abertura de clareiras através da tombamento das árvores, a ocorrência natural do fogo no Cerrado ocasionada conjuntamente pelos raios e vegetação seca, o ataque de insetos às espécies vegetais sob condições de estresse, bem como enchentes, tempestades e movimentos de massa, são alguns exemplos de perturbações naturais. Tais perturbações proporcionam heterogeneidade espacial e temporal na estrutura e dinâmica de populações e comunidades naturais, como também desempenham o papel de agentes da seleção natural no processo evolutivo (SOUSA, 1984).

As perturbações antrópicas, causadas direta ou indiretamente por atividades humanas, têm sido apontadas como uma das principais causas da perda da biodiversidade, com modificações intensas no ambiente físico e que podem ser persistentes ao longo do tempo (LAWRENCE; CHASE, 2010). O desmatamento, a queima e a abertura para áreas agrícolas e de pastagens são exemplos de perturbações antrópicas que levam à perda acelerada do hábitat, uma das principais causas da extinção de espécies (SALA et al., 2000), sendo as áreas tropicais particularmente mais afetadas (BROOK; SODHI; BRADSHAW, 2008). Dessa maneira, os impactos nos habitats naturais não só ameaçam a diversidade biológica, mas também a provisão de serviços ecossistêmicos para o bem-estar humano, alterando o paradigma de uma "crise de extinção" (que geralmente se limita às espécies) para uma "crise dos biomas" mais ampla (que inclui a variedade de paisagens, interações ecológicas e pressões evolutivas que sustentam a biodiversidade; HOEKSTRA et al., 2005).

A intensidade e a frequência determinam o impacto causado pelas perturbações antrópicas em uma determinada área. Perturbações antrópicas agudas, mais intensas e menos frequentes, são altamente destrutivas e fáceis de identificar devido às mudanças extremas que induzem na estrutura dos sistemas ecológicos (DELLASALA et al., 2004). Assim, esse tipo de perturbação mostra uma clara dicotomia entre o que é perturbado e não perturbado.

Perturbações antrópicas crônicas, apesar de mais frequentes, são mais sutis e ocorrem durante longos períodos de tempo. De um modo geral, florestas secas ou áreas com baixa produtividade são mais impactadas por esse tipo de perturbação, já que a sua completa recuperação não é alcançada antes da ocorrência de um novo impacto (MARTORELL, 2007; MARTORELL; PETERS, 2005). Além disso, essas áreas estão sujeitas à alta densidade populacional, cujas principais atividades envolvem a criação de caprinos, extração de madeira e uso de recursos florestais não-madereiros (MARTORELL; PETERS, 2005; SINGH, 1998). Com isso, mensurar perturbações crônicas implica em medi-las em uma escala contínua, já que há um gradiente entre os locais intocados e muito degradados (WATT, 1998).

Populações vegetais são, muitas vezes, sujeitas a múltiplas fontes de distúrbios antrópicos, especialmente em áreas tropicais, onde cerca de 90% das florestas ficam fora das áreas protegidas (WWF, 2002). Dentre os efeitos negativos que as perturbações têm nas populações vegetais pode-se citar a mortalidade dos indivíduos, seja através do desmatamento ou pela retirada contínua ou frequente de material vegetal. O baixo recrutamento de indivíduos em função do pastejo de animais domesticados também tem sido uma questão preocupante que tem levado ao declínio populacional. Por sua vez, os padrões de regeneração após essas perturbações antrópicas são determinados por interações entre o regime de perturbação (como intensidade, frequência, escala) e a biologia das espécies (história de vida, fisiologia, comportamento; PICKETT; WHITE, 1985).

2.2 GENÉTICA DA PAISAGEM

Apesar do reconhecimento de que as perturbações, tanto naturais como antrópicas, têm um papel fundamental na formação da biodiversidade (MILLER; ROXBURGH; SHEA, 2011; TURNER, 2010), seu papel como *driver* dos padrões e da distribuição da diversidade genética é relativamente mal compreendido. Esta é uma grande lacuna de conhecimento já que a diversidade genética tem consequências importantes para todos os níveis de biodiversidade, influenciando a aptidão dos indivíduos, a viabilidade das populações, a adaptabilidade das espécies às mudanças ambientais, a evolução das novas espécies, a estrutura das comunidades e a função dos ecossistemas (AMOS et al., 2001; HUGHES et al., 2008; KELLER; WALLER, 2002). Portanto, as interações entre perturbações e diversidade genética provavelmente terão ramificações ecológicas e evolutivas disseminadas (BROCKHURST; BUCKLING; GARDNER, 2007; HUGHES et al., 2008).

A perda e a fragmentação do habitat em função das perturbações antrópicas criam descontinuidades na distribuição de recursos críticos (como alimento, cobertura, água) ou nas condições ambientais (por exemplo, microclima). Do ponto de vista de um organismo, tais descontinuidades na distribuição de habitats adequados levam a uma redução da conectividade entre os fragmentos populacionais (KINDLMANN; BUREL, 2008). À medida que o habitat é perdido e as populações se fragmentam, a conectividade funcional através da troca individual e do fluxo gênico torna-se criticamente importante (KOOL; MOILANEN; TREML, 2013). Especificamente, a subdivisão e isolamento de populações leva à redução no sucesso de dispersão e nas taxas de colonização, que resultam em um declínio na persistência das populações e uma maior probabilidade de extinção regional através de uma paisagem (LANDE, 1987; KING et al., 1999). Além disso, a teoria da metapopulação mostra que a extinção e a recolonização da população têm efeitos substanciais na diferenciação genética das populações. (WADE; MCCAULEY, 1988).

As análises genéticas permitiram novos conhecimentos acerca das consequências ecológicas de grandes mudanças ambientais, como a fragmentação do habitat, mas essas análises têm sido menos aplicadas a outros tipos de perturbações (ver AGUILAR et al., 2008). Consequentemente, o potencial dessas análises genéticas para melhorar a inferência biológica de acordo com a dinâmica ambiental e/ou condições demográficas tem sido limitado. Em virtude das mudanças nos regimes de perturbações naturais e do aumento na frequência e na intensidade das perturbações antrópicas (TURNER, 2010), é urgente o conhecimento sobre como essas mudanças afetarão a biodiversidade em seu nível mais fundamental, a diversidade genética.

Um dos pontos que mais tem se estudado com relação à fragmentação de habitats devido às perturbações antrópicas é o fluxo gênico entre as (sub) populações remanescentes. O fluxo gênico entre populações, seja por troca de indivíduos em animais, pólen e sementes em plantas ou esporos em criptogâmicas, é necessário para manter a viabilidade a longo prazo de populações. É ele que mantém a variação genética local neutralizando a deriva genética e espalhando potencialmente genes adaptáveis. Do ponto de vista da biologia da conservação, é, portanto, essencial para inferir a conectividade funcional das populações através das paisagens (VAN DYCK; BAGUETTE, 2005).

A genética da paisagem (área transdisciplinar que que integra a genética de populações, a ecologia da paisagem e as estatísticas espaciais) tem estimulado a pesquisa sobre o efeito das paisagens nos processos evolutivos, a fim de contribuir na avaliação das mudanças globais e na conservação e gestão das áreas tropicais e urbanas. Levando vantagem dos recentes desenvolvimentos estatísticos (por exemplo, no campo da estatística espacial ou análise Bayesiana), ele tem como objetivo detectar o impacto da fragmentação no fluxo gênico e determinar como a seleção e a variação ambiental modelam a variação genética adaptativa em populações naturais. Assim, os métodos utilizados na genética da paisagem podem contribuir, por exemplo, na inferência do fluxo gênico, na compreensão de como as características da paisagem impulsionam o fluxo gênico, bem como na inferência de estratégias adequadas no manejo de conservação.

2.3 O RESERVATÓRIO DE ITAPARICA

Além das citadas práticas de manejo agrícola, grandes construções, como a de um reservatório, também têm grande impacto na paisagem. A construção de reservatórios tem sido uma solução viável ao desenvolvimento e bem estar de populações que vivem em regiões áridas e semiáridas, onde a precipitação é irregular e concentrada em poucos meses do ano (LIEBE; VAN DE GIESEN; ANDREINI, 2005). No entanto, a edificação dessas barragens também é bastante conflituosa, já que envolve e interfere no cotidiano de muitos atores, como o poder público, a iniciativa privada, a população e os ambientalistas (RODORFF et al., 2015).

O Rio São Francisco, localizado no Nordeste brasileiro, possui nove reservatórios, planejados, principalmente, para a geração de energia e projetos de irrigação. Um desses reservatórios é o Reservatório de Itaparica (atual Luís Gonzaga), cuja construção foi finalizada em 1985. Desde antes da sua construção, a relação entre a população e os órgãos governamentais responsáveis pela construção da barragem tem sido delicada. Cerca de três-quartos da população realocada dependia somente da agricultura e, porque a Companhia Hidrelétrica do Vale do São Francisco (CHESF) não tinha planos de reassentamento para a maioria dos deslocamentos, muitos da população local só receberam a compensação financeira (HORGAN, 1999). Essa relação conflituosa perdura até os dias atuais e, mesmo os que foram compensados com terras para a agricultura, de alguma forma foram prejudicados, em especial porque grande parte das terras férteis que margeavam o São Francisco havia sido inundada. Assim, existe um mosaico na paisagem da área ao redor do reservatório, principalmente formado por áreas de agricultura e áreas em diferentes estádios de regeneração.

2.4 CAATINGA – UMA FLORESTA TROPICAL SAZONALMENTE SECA

As florestas tropicais sazonalmente secas (FTSS) ocuparam uma grande quantidade de terras tropicais – mais de 40% de todas as florestas tropicais - antes do desmatamento em larga escala (MURPHY; LUGO, 1986). Elas possuem extrema importância devido à sua biodiversidade (riqueza de espécies, endemismo e diversidade funcional), aos serviços ecossistêmicos e outros valores (em termos recreativos, estético e cultural) que elas fornecem (SUNDERLAND et al., 2015). Acerca de estrutura da vegetação, as FTSS podem ser tão ou mais diversas do que as florestas tropicais, podendo variar de floresta alta semidecidual e decídua até mata arbórea com suculentas (APGAUA et al., 2014; MORO et al., 2016; VALE et al., 2010). Muitas das propriedades únicas das FTSS dependem de seus regimes pluviométricos. Os regimes de precipitação das FTSS são caracterizados pela alternância de temporadas secas e úmidas, sendo que, em algumas florestas, a estação seca (≤ 100mm) pode ser de seis meses ou mais. Apesar de abrigar 7 dos 25 *hotspots* de biodiversidade, as FTSS ainda possui alguns dos mais ameaçados ecossistemas, já que, em função das mudanças climáticas, a previsão para áreas áridas e semiáridas é de chuvas cada vez mais escassas e inconsistentes (ALLEN et al., 2010; IPCC, 2013; ALLEN et al., 2017).

A Caatinga é uma das maiores FTSS (LINARES-PALOMINO et al., 2011; SÄRKINEN et al., 2011) e possui uma grande diversidade e alto grau de endemismo quando comparado com outras FTSS. A diversidade de cultural reflete a diversidade vegetal existente na Caatinga, devido à presença de diversos grupos étnicos, como os indígenas, os quilombolas e as comunidade rurais (Diegues e Arruda 2001). De um modo geral, esses grupos utilizam as plantas da Caatinga para fins alimentícios, medicinais e ornamentais, no entanto, a utilização desses recursos pode variar de acordo com o grupo em função dos aspctos sociais, culturais, econômicos e ecológicos (ALBUQUERQUE; ANDRADE; SILVA, 2005; PAULINO; ALBUQUERQUE, 2007).

Apesar de negligenciada por muitos anos, o interesse acerca da Caatinga tem sido crescente nas últimas décadas e informações sobre sua flora nativa, cobertura vegetal, análise biogeográfica, etnobotânica e políticas de proteção já têm sido documentadas (MORO et al., 2016). No entanto, assim como outras FTSS, a Caatinga tem sofrido com a intensa perturbação humana, primeiro por ser uma das regiões mais populosas do mundo (26 habitantes per km^2; MEDEIROS et al. 2012), e segundo porque grande parte da população possui baixa renda (em média US$ 300 por ano, IPEA 2010), fazendo com que muitas famílias dependam dos recursos naturais para sua sobrevivência ou complementação da renda familiar. Somada à essa superexploração, a extensa criação de caprinos e a agricultura de subsistência também têm sido fatores preocupantes e que tem gerado sucessivos níveis de degradação que variam desde a redução do estoque de carbono à completa desertificação (LEAL et al., 2005; SCHULZ et al., 2016). Assim, conhecer a dinâmica ecológica que se estabelece após as perturbações nas FTSS, bem como as que influenciam em sua regeneração, é de extrema importância para a promoção de medidas mitigadoras para amenizar os impactos da perturbação antrópica na Caatinga.

2.5 *Spondias tuberosa* ARR. – A ÁRVORE SAGRADA DO SERTÃO

> [p. 46]
>
> […]
> *É a arvore sagrada do sertão. Sócia fiel das rápidas horas felizes e longos dias amargos dos vaqueiros. Representa o mais frizante exemplo de adaptação da flora sertaneja. Foi, talvez, de talhe mais alentado e alto — e veiu descahindo, pouco a pouco, numa intercadencia de estios flammivomos e invernos torrenciaes, modificando-se á feição do meio, desinvoluindo, até se preparar para a resistência e reagindo, por fim, desafiando as seccas duradouras, sustentando-se nas quadras miseráveis mercê da energia vital que economisa nas estações benéficas, das reservas guardadas em grande copia nas raizes*.
>
> Trecho de 'Os Sertões' (Euclides da Cunha, 1905)

Spondias tuberosa Arr., pertence à família Anacardiaceae e é uma espécie endêmica da região semiárida brasileira. Conhecida como umbuzeiro ou imbuzeiro e poeticamente descrita por Euclides da Cunha como a "árvore sagrada do sertão", *S. tuberosa* apresenta grande importância sócioeconômica, ecológica e cultural. Seus frutos são amplamente utilizados pela população local para consumo *in natura* ou para a fabricação de sucos, doces, sorvetes, licores e da tradicional umbuzada, além de serem aproveitados na alimentação de animais domésticos (LINS NETO; PERONI; ALBUQUERQUE, 2010; RESENDE; CAVALCANTI, 2004). A coleta dos frutos é uma atividade realizada em conjunto, seja entre membros da família ou entre vizinhos, e, portanto, é uma atividade recreativa (observação pessoal). A venda dos frutos e manufaturados gera uma movimentação econômica local, contribuindo com a renda mensal de muitas famílias. Folhas e madeira também são utilizadas para fins medicinais e lenha, respectivamente (FERRAZ et al., 2012). Além de ser fonte de alimento para diversos animais presentes na Caatinga [como o cateto (*Tayassu tajacu*), o veado catingueiro (*Mazama gouazoubira*), a ema (*Rhea americana*), a raposa (*Dusicyon thous*), o tatu-peba (*Euphractus sexcinctus*) e a cotia (*Dasyprocta cf. prymnolopha*; Oliveira et al. 2003], *S. tuberosa* também é uma importante fonte de néctar e pólen para diversos polinizadores, já que é uma das primeiras espécies a florescer ainda no final da estação seca (MACHADO; BARROS; SAMPAIO, 1997)(NADIA; CRISTINA; VALENTINA, 2007). Além da estreita relação com a população das comunidades rurais, *S. tuberosa* é a planta símbolo do festejo Pankararu "Corrida do Umbu".

Dados do IBGE mostraram que no início dos anos 90 a produção extrativista do umbuzeiro alcançou 20.000 toneladas de frutos por ano com áreas de coleta espalhadas por todo o Nordeste brasileiro. No entanto, as consequências desse modelo exploratório têm sido refletidas no declínio constante da produção de frutos na última década (SANTOS et al. 2005). Além disso, tem-se reportado a ausência do recrutamento de plântulas em seu ambiente natural, cuja causa ainda tem sido atribuída, em sua maioria, à dificuldade que as sementes do umbuzeiro apresentam para germinar, aos danos causados às sementes e às plântulas que emergem (tanto por insetos como por mamíferos) a irregularidade das chuvas na região e ao desmatamento desordenado (CAVALCANTI; RESENDE; BRITO, 2009).

Um dos fatores que dificultam a propagação do umbuzeiro em larga escala é a dormência das suas sementes, o que propicia uma emergência lenta e não uniforme, conforme os trabalhos de Araújo et al. (2001), Costa et al. (2001) e Souza et al. (2005). A semente de umbuzeiro está envolvida por endocarpo rígido, lenhoso e lignificado e, segundo Carvalho e Nakagawa (2000), o endocarpo resistente impede o crescimento e a expansão do embrião, além de restringir a entrada de água e oxigênio no interior da semente.

Cavalcanti e Resende (2004), através de observações realizadas nas áreas de ocorrência do umbuzeiro em diversos municípios da região semiárida nos Estados de Pernambuco, Paraíba, Rio Grande do Norte e Bahia, constataram que a maioria das sementes de umbu encontrada no solo sob a copa de indivíduos adultos, não germinou devido à predação por insetos, principalmente pelo besouro *Amblycerus dispar*. A herbivoria por caprinos é outro fator que está associado à redução do recrutamento, do crescimento e da distribuição do umbuzeiro, já que esses animais consomem, além das plântulas, folhas e flores do umbuzeiro (CAVALCANTI; RESENDE; BRITO, 2009). A dispersão das sementes de umbu pelos caprinos é considerada negativa. As sementes regurgitadas nos chiqueiros são levadas normalmente com o esterco caprino para áreas de agricultura e, ainda que algumas sementes consigam germinar, muitas serão eliminadas nas áreas irrigadas (CAVALCANTI; RESENDE; BRITO, 2009).

A escassez hídrica também é um fator que impede o estabelecimento das plântulas de umbuzeiro em regiões semiáridas. O umbuzeiro tem como principal característica a formação de raízes tuberosas (xilopódios), cuja principal função é armazenamento de água e sais minerais. Durante a estação seca, as reservas nos xilopódios são utilizadas para manter o balaço hídrico da planta (LIMA FILHO, 2004). Apesar da rápida formação dessa estrutura após a germinação (30 dias após a emergência, o xilopódio tem comprimento em torno de 12 cm e um diâmetro na porção tuberculada de 20 mm), poucas plântulas conseguem sobreviver ao período de seca e chegar à próxima estação chuvosa como uma muda com condições de desenvolvimento (LIMA, 1996).

Dado o exposto, o objetivo geral dessa tese foi entender como *S. tuberosa* responde aos impactos diretos e indiretos resultantes das mudanças no uso da terra decorrentes da construção do reservatório de Itaparica, através da dinâmica populacional, da regeneração natural e da diversidade genética.

3 MÉTODO

3.1 ÁREA DE ESTUDO

A área de estudo inclui os municípios de Petrolândia [com três localidades: Comunidade Soares (08º53´S, 38º13´W), Apolônio Sales (08º57´S, 38º14´W) e Icó Mandantes (08º49´S, 38º23´W)], Itacuruba (08º47´S, 38º40´W), Inajá (08º56´S, 37º58´W), Tacaratu (09º05´S, 38º05´W) e Floresta (08º30´S, 38º26´W), Pernambuco , Brasil. Todos os municípios estão localizados na microrregião de Itaparica, com exceção de Inajá (que faz fronteira com Tacaratu e Floresta), no nordeste do Brasil, cujo principal tipo de vegetação compõe uma floresta tropical sazonalmente seca, a caatinga. O tipo de clima é BSh do semiárido brasileiro, caracterizado como quente e seco (Alvares, Stape, Sentelhas, Gonçalves, & Sparovek, 2013), sendo a estação seca pronunciada e interrompida por uma estação chuvosa entre novembro e abril. Em nossa área de estudo, a temperatura média anual é de 28 ° C, a precipitação média varia de 300 a 1.200 mm por ano e a estação seca pode se prolongar por até 10 meses (Assis, Souza, & Sobral, 2015).

A construção de barragens e as consequentes inundações resultaram na perda de terras aráveis e a agricultura de irrigação foi promovida para compensar os reassentados e reduzir a pobreza tradicionalmente alta nesta região semiárida (Camelo Filho, 2005). No entanto, nem todas as pessoas se beneficiaram; mais de 30 anos após a construção do reservatório, há grande competição entre os agricultores locais por terras irrigáveis. Em áreas sem instalações de irrigação, os pequenos agricultores dependem da pecuária, principalmente de caprinos devido à sua tolerância às condições semiáridas, bem como dos recursos naturais, como madeira ou derivados (Ferraz, Albuquerque, & Meunier, 2006; LL Santos Ramos, Silva, Sales & Albuquerque, 2009). Devido à falta de manejo adequado do uso do solo, a pressão por caprinos e a extração de recursos naturais, a área de estudo sofre com distúrbios antropogênicos em diferentes níveis e intensidades. É dentro deste mosaico de perturbação antrópica e regeneração que indivíduos de *S. tuberosa* utilizados nesse estudo foram encontrados.

3.2 TIPOS DE USO DO SOLO

Classificamos o uso do solo ao redor de cada árvore em quatro categorias: (1) Caatinga protegida por lei (PC): a única área de vegetação da Caatinga protegida por lei era a Serra da Canoa, que se tornou oficialmente uma estação ecológica em 2012 (Decreto Estadual nº 38.133/2012). Comparado com os outros tipos de uso da terra, PC mostrou maior biodiversidade (índice de diversidade de Shannon-Wiener: 0,57, p> 0,05; dados não mostrados), com vegetação nativa lenhosa em torno de 70%, maior distância até a casa mais próxima e menor densidade de casas ao redor das árvores, o que geralmente indica menor pressão de coleta dos frutos e outras partes úteis da planta. Apesar de um bom estado geral de conservação legal, ainda há acesso aberto descontrolado aos recursos naturais dentro da área, especialmente durante a estação seca, devido ao apoio mínimo de instituições ou do governo. Os agricultores locais permitem que as cabras pastem nestas terras e a pressão desses animais domesticados pode ser alta. Apesar dessa alta pressão de pastejo, escolhemos essa área como nosso “controle”, já que a intensidade geral do distúrbio antrópico foi menor (ver descrição abaixo).

(2) Caatinga Degradada (DC): este tipo de uso do solo estava localizado principalmente em áreas rurais onde a terra era usada para fins agrícolas e de pastagem. A cobertura vegetal foi de 45% e espécies pioneiras de Caatinga [como *Cenostigma pyramidale* (Tul.) Gagnon e G.P.Lewis e *Aspidosperma pyrifolium* Mart.] predominaram nessa área. Assim, o índice de diversidade foi menor que em PC (índice de diversidade de Shannon-Wiener: 0,29, p> 0,05; dados não mostrados). Este tipo de uso da terra também foi caracterizado pela proximidade de casas e aldeias e as árvores eram facilmente acessíveis pela população local. Moradores relataram que, devido à pressão humana, grandes mamíferos nativos desapareceram. Por outro lado, a presença de cabra permaneceu alta.

(3) Áreas agrícolas (AGR): as áreas agrícolas eram aquelas com sistemas agrícolas irrigados com o cultivo de monoculturas e, portanto, onde o gado e caprinos eram quase completamente ausentes (para mais informações, ver Cierjacks, Pommeranz, Schulz, & Almeida-Cortez 2016). A maioria dessas áreas foi desmatada há aproximadamente 30 anos, após a construção da barragem. Não houve diversidade de plantas lenhosas e a cobertura vegetal por árvores nativas foi inferior a 10%. Em geral, os agricultores mantinham os indivíduos de *S. tuberosa* dentro da lavoura por causa dos frutos e da sombra que as árvores fornecem (Araújo, Castro, Amorim, &

Albuquerque, 2012). Como os indivíduos de *S. tuberosa* estavam em áreas privadas, a coleta de frutos era normalmente restrita à família do proprietário, apesar da proximidade e densidade das casas.

(4) Áreas abandonadas (ABN): Estas áreas foram anteriormente utilizadas como terras de cultivo, mas foram abandonadas entre 5 e 25 anos atrás. A cobertura vegetal era inferior a 30%, caracterizada por arbustos dispersos e pequenas árvores e principalmente pelo solo exposto. O índice de diversidade de Shannon-Wiener foi de 0,07 ($p > 0,05$; dados não mostrados). Indivíduos de *S. tuberosa* presentes nestas áreas estavam mais sujeitos à superexploração devido à proximidade e à densidade de casas ao redor, bem como ao pastoreio de cabras.

3.3 AMOSTRAGEM E COLETA DE DADOS

A coleta de dados foi realizada entre março de 2014 e março de 2015, durante a estação chuvosa. Considerando cada árvore como unidade de amostragem, selecionamos 80 indivíduos adultos de *S. tuberosa* com diâmetro do caule ao nível do solo (dsl) > 5 cm. A densidade de árvores foi extremamente baixa na área de estudo. Por isso, usamos a informação da população local para encontrar um número suficiente de indivíduos. Para cada árvore, medimos o diâmetro, altura e dsl da copa; as coordenadas de GPS de todas as unidades de amostragem foram gravadas utilizando um receptor GPS portátil Garmin eTrex 20. Equações alométricas foram usadas para estimar a biomassa aérea de cada árvore (Luoga, Witkowski, & Balkwill, 2002; Ouédraogo, Bondé, Boussim & Linstädter, 2015). Abaixo do dossel de cada indivíduo, contamos as sementes na superfície do solo em quadrantes de 50 × 50 cm para estimar o número de sementes por metro quadrado (sementes.m^{-2}). O sucesso do recrutamento foi avaliado pela contagem de plântulas de *S. tuberosa* dentro de um círculo de 20 m de diâmetro ao redor de cada árvore.

4 RESULTADOS

4.1 ARTIGO 1 - LAND-USE CHANGES AFTER DAM CONSTRUCTION AFFECT POPULATION DYNAMICS OF A THREATENED FRUIT TREE IN NORTHEASTERN BRAZIL

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ABSTRACT

Global land-use changes have led to accelerated habitat loss, which is one of the major causes of species extinction. Large construction projects, such as reservoirs for hydropower generation, can have great impacts, resulting in changes in habitat and landscape patterns that profoundly affect species populations. *Spondias tuberosa* Arr. is an endemic fruit-bearing tree of the Brazilian semiarid region with great socio-economic and environmental importance. The species currently shows a striking lack of seedling recruitment in its natural environment. In this study, we aimed to assess whether the failure of *S. tuberosa* to regenerate is related to different land-use types or intensities that have arisen following the construction of the Itaparica reservoir. We used tree biometry, the number of seeds on the soil surface, and seedling number to analyze regeneration and population dynamics of the species and compared these indicators across agricultural areas, abandoned areas, degraded forest, and in a protected area of the Caatinga, officially an ecological station since 2012. Indicators of land-use intensity included distance to the nearest house or road, grazing pressure, NDVI, and kernel density. Our results showed that land use has an impact on the biometrics of adult individuals, with the biggest trees being present in the protected Caatinga and abandoned areas. However, tree size was not related to greater regeneration success. On the contrary, we found seedlings of *S. tuberosa* mostly in irrigated agricultural areas, probably due to the abundance of water and the exclusion of livestock. Differences in the population dynamics of *S. tuberosa* among land-use classes were not detectable. The dependence of *S. tuberosa* regeneration on an adequate water supply and low grazing pressure highlights the threat faced by this highly adapted species, as these conditions are rarely met in most of the Brazilian semiarid region. At the same time, our findings imply that anthropogenic agricultural habitats may act as conservation areas for this endemic species.

Keywords: Caatinga; grazing; regeneration; reservoir construction; seasonally dry tropical forest; *Spondias tuberosa*.

INTRODUCTION

The construction of large hydrological reservoirs involves complex land-use changes with different impacts at the landscape, ecosystem, and species scales (Schulz, Koch, Cierjacks, & Kleinschmit, 2017; Schulz et al., 2016). Reservoirs provide water for irrigation and power generation and may facilitate flood control, transportation, and recreational opportunities, thereby offering an economically viable way to improve the well-being of populations living in arid and semiarid regions (Bauni, Schivo, Capmourteres, & Homberg, 2015; Ghobadi, Pradhan, Shafri, & Kabiri, 2015; Zafarnejad, 2009). However, dam building remains highly conflictive, since it results in a huge array of environmental effects, such as landscape structure change and habitat and ecosystem fragmentation. In addition, water flows are transformed, greenhouse gas are emitted, wetlands dry up, and valleys and lowland sites are flooded (Horgan, 1999; Kellogg & Zhou, 2014; Rodorff, Siegmund Schultze, Köppel, & Gomes, 2015; Selge, Matta, Hinkelmann, & Gunkel, 2016). The impacts of these changes on biodiversity and populations of animal and plant species are usually not sufficiently understood to allow for the proposal of adequate conservation measures. Thus, to counteract the ongoing decline in global biodiversity (Ceballos, Ehrlich, Soberón, Salazar, & Fay, 2005), a better understanding of how land use affects species populations and the subsequent implementation of efficient conservation measures are urgently needed.

In northeastern Brazil, the Itaparica reservoir, also called Luís Gonzaga, is one of nine reservoirs along the São Francisco River used for flood regulation and power generation (Romano & Garcia, 1999). The construction of the Itaparica reservoir, completed in 1988, caused the resettlement of about 40,000 inhabitants and the reconstruction of two urban nuclei at the new lake shore. Most of the resettled families had been highly dependent on natural resources such as land for agriculture and water for fishing, which were also severely affected by the construction of the artificial lake (Siegmund-Schultze, Köppel, & Sobral, 2015). The land-use changes after dam construction included the establishment of irrigation farming schemes and changes in livestock production and grazing regimes, but also brought about urbanization and rural depopulation, which resulted in the regrowth of degraded secondary forests (Corrêa, Silva, Freire, Gunkel, & Castro, 2015; Selge et al., 2016; Siegmund-Schultze et al., 2015).

Environmental compensation measures were created to offset the disturbance or loss of natural ecosystems and have been adopted by several countries (Jay, Jones, Slinn, & Wood, 2007). The Brazilian legislation does require compensation methods after reservoir flooding such as the establishment of new conservation areas. The Itaparica reservoir is located within one of the most extensive seasonally dry tropical forest (SDTF) ecosystems, known as Caatinga. These forests are characterized by a high biodiversity, which partly exceeds others seasonally tropical dry forests (SDTF), along with a high degree of endemism (Leal, Tabarelli, & Silva, 2003). However, the biodiversity of Caatinga has been neglected for many years and the protection state of its biota is low in comparison with others Brazilian biomes (Moro, Lughadha, de Araújo, & Martins, 2016) and even with the environmental compensation only a minor percentage of the original Caatinga is protected in the surrounding of the reservoir (Koch, Almeida-Cortez, & Kleinschmit, 2017).

Spondias tuberosa Arr. is an endemic tree of the Caatinga (Giulietti et al., 2003) that shows pronounced adaptations to semiarid conditions. Due to its tuberous roots (known as xylopodium), which are able to store water and minerals, the trees can survive during the dry season, which lasts approximately 7 to 9 months per year (Cavalcanti, Resende, & Brito, 2010; Lima Filho, 2011). In the region of the Itaparica reservoir, the species is of great environmental and socioeconomic importance. One of the adaptations of *S. tuberosa* to the semiarid conditions is its bloom during the dry season, thus providing floral resources for several pollinator species (Nadia, Machado, & Lopes, 2007). In the rainy season, its fruits are a food source for several wild species as well as for domestic animals and the human population itself (Cavalcanti, Resende, & Brito, 2009; Resende & Cavalcanti, 2004). The fruit, which varies in size, color, and taste (Melo & Andrade, 2010; C. A. F. Santos, 1997), is widely used by the local people for commercial purposes, either sold as fresh fruit or processed to pulp for the production of jellies, sweets, and ice creams. The leaves are also used for medicinal purposes and the wood as fuel (Ferraz, Ferreira, Santos, & Meunier, 2012). Income generated from these trees can represent a significant proportion of a household’s income (Borges, Maia, Gomes, & Cavalcanti, 2007; Lins Neto et al., 2010). For the Pankararu indigenous communities of the area, *S. tuberosa* also has an important cultural value as the symbol of one of the most important religious manifestations of the tribe, the “Umbu Race”, which takes place after the first rains of the rainy season (Athias & Pankararu, 2017).

Despite its value for local communities, *S. tuberosa* seems to be in decline as it shows a pronounced lack of natural recruitment in the region of the São Francisco River (personal observation). Due its socioeconomic importance and its possibly threatened status, we used *S. tuberosa* as a model species to analyze land-use effects after dam construction. In this study, we aimed at a better understanding of the responses of *S. tuberosa* to different land-use types and intensities that have arisen following the construction of the Itaparica reservoir. We used tree biometry, seeds on soil surface, and seedling number to analyze possible effects in agricultural areas, abandoned areas, degraded forests, and in a protected part of the Caatinga, officially an ecological station since 2012. In addition to the specified land-use classes, we included distance to the nearest house or road, grazing pressure, vegetation cover in terms of the normalized difference vegetation index (NDVI), and kernel density as indicators of the intensity of anthropogenic disturbance. In particular, we hypothesized that (1) the biometry of the individuals is influenced by the land-use types; (2) young individuals are more frequent and the number of seeds on the soil surface is higher in less disturbed areas; and (3) the inverted-J size-class distribution that indicates sufficient recruitment will be found exclusively in the less disturbed areas. Our results are important for characterizing the protection status of *S. tuberosa* populations in the area. Based on the study, we developed targeted conservation measures and discussed these with different stakeholder groups (farmers, conservation agencies) in the area.

MATERIALS AND METHODS

Study area – The study area includes the municipalities of Petrolândia [with three villages: Comunidade Soares (08º53´S, 38º13´W), Apolônio Sales (08º57´S, 38º14´W) and Icó Mandantes (08º49´S, 38º23´W)], Itacuruba (08º47´S, 38º40´W), Inajá (08º56´S, 37º58´W), Tacaratu (09º05´S, 38º05´W), and Floresta (08º30´S, 38º26´W), Pernambuco state, Brazil. All of the municipalities are located in the Itaparica microregion, except Inajá, which is bordered by Tacaratu and Floresta. They are part of the Caatinga region of northeastern Brazil, with the main vegetation type being SDTF. The climate type is BSh semiarid Brazil, characterized as warm and dry (Alvares, Stape, Sentelhas, Gonçalves, & Sparovek, 2013), with a pronounced dry season interrupted by a rainy season between November and April. In our study area, the average annual temperature is 28°C and the rainfall averages from 300 to 1200 mm per year, with a prolonged dry season of up to 10 months (Assis, Souza, & Sobral, 2015).

Dam construction and subsequent flooding resulted in a loss of arable land, and irrigation farming was promoted to compensate the resettled people and to reduce the traditionally high poverty in this semiarid region (Camelo Filho, 2005). However, not all people have benefited; even more than 30 years since the construction of the reservoir, there is great competition among local farmers for irrigable land. In areas with no irrigation facilities, smallholders rely on livestock farming, primarily with goats owing to their tolerance of the semiarid conditions, as well as on natural resources such as timber or other wood products (Ferraz, Albuquerque, & Meunier, 2006; L. L. Santos, Ramos, Silva, Sales, & Albuquerque, 2009). Due to lack of proper land management, pressure by goats and the extraction of natural resources, the study area suffers from anthropogenic disturbance at different levels and intensities. It is within this mosaic of anthropogenic disturbance and regeneration that *S. tuberosa* grows as an emergent tree in dry forest vegetation or as a solitary tree in fields, pastures, or near houses.

Sampling design and data collection – Data collection was conducted between March 2014 and March 2015, during the rainy season. Considering each tree as a sampling unit, we selected 80 adult *S. tuberosa* individuals with a stem diameter at soil level (dsl) > 5 cm. Density of trees was extremely low in the study area. We therefore used the information of local people to find a sufficient number of trees. For each tree, we measured canopy diameter, height, and dsl; the GPS coordinates of all sampling units were recorded using a Garmin eTrex 20 hand-held GPS receiver. Allometric equations were used to estimate each tree's aboveground biomass (Luoga, Witkowski, & Balkwill, 2002; Ouédraogo, Bondé, Boussim, & Linstädter, 2015). Beneath the canopy of each study tree, we counted the seeds on the soil surface in four squares of 50 × 50 cm to estimate the number of seeds per square meter (seeds.m^{-2}). Recruitment success was evaluated by counting *S. tuberosa* seedlings within a circle 20 m in diameter around each tree.

Land-use types – We classified the land use around each tree into four categories: (1) Protected Caatinga by law (PC): The only area of near-natural Caatinga vegetation protected by law was Serra da Canoa, which officially became an ecological station in 2012 (State decree nº 38.133/2012). Compared with the other land-use types, PC showed a higher biodiversity (Shannon-Wiener diversity index: 0.57, $p > 0.05$; data not shown), with native woody vegetation cover around 70%, greatest distance to the nearest house, and lower density of houses surrounding the trees, which indicates less pressure from collection of the fruits and others useful parts of the plant. Despite an overall good legal conservation status, there is still uncontrolled open access to natural resources within the area, especially during the dry season, due to minimal support from institutions or government. Local farmers allow goats to graze on this land, and the pressure from these domesticated animals can be high. Despite this high grazing pressure, we chose this area as our “control,” as the overall intensity of anthropogenic disturbance was lower (see description below).

(2) Degraded Caatinga (DC): This land-use type was mainly located in rural areas where the land was used for agricultural and pasture purposes. The vegetation cover was 45%, and pioneer Caatinga tree species such as *Cenostigma pyramidale* (Tul.) Gagnon & G.P.Lewis and *Aspidosperma pyrifolium* Mart. were predominant in this area. Thus, the diversity index was lower than in PC (Shannon-Wiener diversity index: 0.29, $p > 0.05$; data not shown). This land-use type was also characterized by proximity to houses and villages, and the trees were easily accessible by local people. Residents reported that, due to human pressure, large native mammals have disappeared. On the other hand, goat presence remained high.

(3) Agricultural areas (AGR): Agricultural areas were those with irrigated farming schemes where monocultures were cultivated and livestock and goats were almost completely absent (for more information, see Cierjacks, Pommeranz, Schulz, & Almeida-Cortez 2016). Most of these areas were cleared approximately 30 years ago, after the dam construction. There was no woody plant diversity, and vegetation cover by native trees was less than 10%. In general, farmers preserved *S. tuberosa* individuals inside the cropland because of the fruits and the shade the trees provide (Araújo, Castro, Amorim, & Albuquerque, 2012). As individuals of *S. tuberosa* were in private areas, fruit collection was normally restricted to the landowner’s family despite the proximity and density of houses.

(4) Abandoned areas (ABN): These areas had previously been used as cropland but were abandoned between 5 and 25 years ago. The vegetation cover was less than 30%, characterized by scattered shrubs and small trees and mainly exposed soil. The Shannon-Wiener diversity index was 0.07 ($p > 0.05$; data not shown). Individuals of *S. tuberosa* in these areas were more subject to overexploitation due to the proximity and density of houses surrounding the trees as well as to goat grazing.

Predictors of disturbance – In addition to the classification of land-use types, we included other metrics of anthropogenic disturbance in our models, since their influence on the communities and plant populations in the Caatinga has already been documented (Martorell & Peters, 2005, 2008; Ribeiro Neto, Tabarelli, & Leal, 2016; Rito, Arroyo-Rodríguez, Queiroz, Leal, & Tabarelli, 2017; Zunzunegui, Esquivias, Oppo, & Gallego-Fernández, 2012). We used the following predictors: distance of tree to the nearest road (*road*), distance of tree to the nearest house (*house*), the number of goat droppings per square meter under the canopy (*goat*), normalized difference of vegetation index (*ndvi*), and kernel density estimation (*kernel*) as an estimate of the density of houses around each tree.

To measure the distance of each tree to the nearest road and house, we gathered spatial information from LANDSAT 8 satellite imagery (median spatial resolution) mapped in QGIS software version 2.18.3 (http://www.qgis.org/en/site/). We used satellite images from orbit 216/66, Thematic Mapper TM satellite Landsat8, taken during the rainy season of 2015. These images are freely available through the Earth Engine Evapotranspiration Flux tool (EEFlux, *https://eeflux-level1.appspot.com*)—a web-based tool that operates on the Google Earth Engine system based on METRIC (Mapping Evapotranspiration at high Resolution with Internalized Calibration) (Allen et al., 2015).

Almost all forests are grazed to some extent by goats along with cattle and sheep (Tiessen, Feller, Sampaio, & Garin, 1998), but in the Caatinga the grazing by goats is most common. Grazing intensity can be quantified using different methods (e.g. livestock faeces, weighing of faeces or assessing trampling of paths) and, as Cierjacks and Hensen (2004) reported a significant correlation between animal loads and the amount of animal faeces, in this study, we assessed grazing intensity by counting goat droppings. Thus, beneath the canopy of each tree, we counted the goat droppings in four squares of 50 × 50 cm to estimate the number of droppings per square meter.

The tool of EEFlux includes the data layer “NDVI (Normalized Difference Vegetation Index)” which is computed from the visible red and near-infrared bands using at-surface reflectance computed based on Tasumi et al. (2008). For our study, we defined a circular buffer of 130 m in radius around the position of each tree. NDVI estimation within the buffer was carried out for a square inscribed inside the 130-m circle. For an image “I” in this square, we have a matrix of aij values of pixels, where a is a cell of the matrix at the position i (row) and j (column). Supposing that pixel size $\varepsilon = 30$ m, the resulting parameters were $i = 3$, $j = 3$ and $n = i*j = 9$ pixels. To gather the information for the buffer at a single point, we had the metric $\mu \pm \delta$, where: $\mu = \frac{((\sum_{i=1}^{3} \sum_{j=1}^{3} aij\ )}{n}$ and $\delta = \sqrt{\frac{(\sum_{i=1}^{3} \sum_{j=1}^{3} (aij - \mu\ )^2}{(n-1)}}$, μ is the NDVI mean value, and δ is the standard deviation.

For kernel density estimation, we used the tool “Kernel map” in QGIS software and adopted the same methodology as for calculating the NDVI per tree. In our analysis, the use of high-spatial-resolution satellite imagery ($\varepsilon < 1$ m) was extremely important to reduce error rates by providing spectral reflectance values at a finer spatial resolution.

To estimate the intensity of anthropogenic disturbance in each land-use type, we scored each predictor variable as 1 (low disturbance), 2 (intermediate disturbance), or 3 (high disturbance) and summed up the scored values to obtain the intensity. Thus, our disturbance index ranges from 4 (lowest level of disturbance) to 12 (highest level of disturbance; maximum sum for the disturbance measures).

Data and statistical analysis –To determine which predictor variables should be used in our models, we performed a principal component analysis (PCA) with the *stats* package for R (R Core Team 2016). As “road” and “house” were collinear, we choose “house” to perform all other analyses.

Generalized linear models (GLM) were used to test the impact of land-use types, distance to the nearest house, pressure by goats, NDVI, and density of houses on canopy diameter, height, stem diameter, biomass of *S. tuberosa* trees, as well as on numbers of seeds and seedlings. We used the gamma error distribution for canopy, height, and stem diameter and the Poisson error distribution for seeds. As there was overdispersion for biomass and seedlings, we used the Bayesian generalized linear models for these response variables, with gamma and Poisson error distribution, respectively. We constructed 19 models for each response variable, including isolated and additive effects, using the *AICcmodavg* package for R (R Core Team 2016). We computed the Akaike’s information criterion corrected for small samples (AICc) for each model as a measure of the goodness of fit (Johnson & Omland, 2004; Venables & Ripley, 1999). Among the resulting models of each type, the GLM with the lowest AIC_C was chosen.

Data on dsl were categorized into seven diameter size classes of 24 cm intervals (0–24, 25–49, etc.) to check the diameter size-class distribution (SCD, e.g. Kleinschroth, Schöning, Kung’u, Kowarik, & Cierjacks, 2013; Wesche et al., 2008). All individuals with a dsl larger than

145 cm were grouped into a single class. Fischer's exact test was used to test if the SCD differed among the four land-use types. Further, SCDs were plotted on a graph to allow visual comparison.

Population dynamics was inferred by analyzing the slope of a linear regression of SCD parameters. We calculated ordinary least-squares regression (OLS) with the SCD midpoint (mi) treated as the independent variable, and the average number of individuals in each SCD (Ni) as the dependent variable. In order to obtain straight line plots (Obiri, Lawes, & Mukolwe, 2002), Ni was transformed into ln(Ni + 1) since some size classes had zero individuals. Consequently, the regression was performed between ln(Ni + 1) and ln(mi). The interpretation of the SCD slopes was based on Obiri et al. (2002). Negative slopes indicate good recruitment, with more individuals in smaller size classes than in larger size classes; flat slopes indicate equal numbers of individuals in small and large size classes; and positive slopes indicate poor recruitment with more trees found in larger than in smaller size classes (Lykke, 1998; Mwavu & Witkowski, 2009; Obiri et al., 2002).

To measure the degree of deviation from the monotonic decline expected in undisturbed populations, we calculated the permutation index (PI), developed by Wiegand et al. (2000). A monotonically declining population is expected to have a PI = 0, whereas a population with a discontinuous SCD would have a PI > 0. All the analyses regarding population dynamics were performed using *vegan* package for R (R Core Team 2016).

RESULTS

After classification of the land-use type at the position of each tree, we obtained different tree numbers in each category. The number of individuals was highest in degraded areas (33), followed by abandoned areas (17), and agricultural and protected areas (both with 15). Overall, biometry of *S. tuberosa* was characterized by a small height of < 6 m, a broad canopy of about 10 m, mean diameters around 50 cm, and an average biomass of 536 kg (Table 1). The number of seeds was 136 per m^2, and the average number of seedlings was > 1. Only two response variables showed significant differences across the land-use types: trees in PC had a bigger canopy, and the number of seedlings was higher in AGR. The anthropogenic disturbance intensity varied from 5.61 (PC) to 9.45 (ABN), and although the intensity was not statistically different for ABN and DC, we chose to maintain the land-use classifications (Table 2).

Influence of land-use type on biometry of *Spondias tuberosa*

All of the best-fit models showed land-use type as a predictor for all biometric response variables except height and dsl. According to our model, canopy diameter was significantly bigger in PC and DC compared to AGR, with ABN showing intermediate values. Moreover, canopy diameter increased with greater distance to nearest house and with higher NDVI (Fig. 1). Also, tree height was slightly but not significantly bigger in PC and responded positively to NDVI (Fig. 2). In addition, grazing pressure was significantly positively correlated with tree height. Biomass of *S. tuberosa* was significantly higher in PC and ABN than in DC (Fig. 3). The best-fit model for dsl included both “landuse” and “goats”, but nevertheless neither was significantly related (data not shown).

Influence of land-use type on the regeneration of *Spondias tuberosa*

Young individuals, i.e., those not yet of reproductive age, were completely absent in our study area. Hence, we considered seeds per square meter (seeds.m^{-2}) and number of seedlings to analyze the regeneration status. Both seeds.m^{-2} and seedlings showed significant differences according the land-use type (Fig. 4, 5). Seeds.m^{-2} were significantly higher in AGR and DC compared to PC and ABN. Furthermore, the distance to the nearest house showed a significant negative effect, and grazing pressure and NDVI showed significant positive effects on seeds.m^{-2} (Fig. 4). Seedlings were mostly observed in AGR. In contrast to seeds.m^{-2}, the number of seedlings significantly declined with higher goat incidence and increased with higher kernel density and NDVI (Fig. 5).

Influence of land-use type on the population dynamics of *Spondias tuberosa*

The shape of the SCD of *S. tuberosa* populations did not differ among the four land-use types (Kolmogorov-Smirnov test, $p > 0.05$). For all types, regression showed positive but not significant slopes with close to equal numbers of plants in small and large size classes, indicating poor recruitment (Table 2). Most trees were in the 97–120 cm dsl size class (Fig. 6). The PI was fairly similar for the different land-use types as well as for the whole population (Table 3).

DISCUSSION

This paper is the first to relate the population status of an economically important Caatinga species to land use. The biometric data of *S. tuberosa* in our study area revealed mean values similar to those presented by Santos (1997). However, while those authors stated that the differences in edaphoclimatic and geographic distances did not affect the phenotypic differentiation of the species, we found that canopy was influenced by land-use type. Despite this, the population seems to be responding robustly to the current environmental conditions in terms of tree-level attributes. Per-tree biomass of *S. tuberosa* is a newly modeled attribute, which so far has not been published in other studies. In comparison with others tree species from SDTFs such as *Anadenanthera macrocarpa*, *Myracrodruon urundeuva*, and *Schinopsis glabra* with trunk diameter of 30 cm (according to Silva & Sampaio, 2008), *S. tuberosa* shows a higher biomass of about 500 kg per tree. This highlights its potential for carbon sequestration in addition to the array of other services the species provides to society.

Influence of land-use type on the biometry of *Spondias tuberosa*

In accordance with our first hypothesis, land use affected the biometrics of adult individuals. Protected Caatinga showed the tallest trees with the broadest canopies, which was also reflected in the highest biomass values. Further, the predictor variable of the best-fitted models with the greatest effect on the biometry of *S. tuberosa* individuals was NDVI, with a positive impact on canopy diameter and tree height. As the highest value of NDVI was measured in protected areas, this finding supports the results on land-use classes as does the positive correlation of canopy diameter and distance to the next house. Our results are in agreement with those of Salvatierra et al. (2017), who demonstrated that vegetation in deforested areas is less productive and less sensitive to rainfall than in non-deforested areas.

Influence of land-use type on the regeneration of *Spondias tuberosa*

The regeneration of *S. tuberosa* responded differently to land use than did its biometry. Regeneration was more pronounced in agricultural areas than in other types of land use. All predictor variables of the best models had significant effects on seeds. The distance to the nearest house showed a negative effect on seeds.m^{-2}. This could be caused by the greater collection of fruits by the local people, so the fruits never rots and drops its seeds. Although the houses were farther away from the trees and as people surrounding the area depend on the natural resources, they have access to the trees for the collection of the fruits. The pressure induced by goats also affected the seeds.m^{-2}, however, in a positive way. Considering the intense solar irradiance and the high temperature in this SDTF, shade trees such as *S. tuberosa* play a role as shelters for the animals. Thus animals, including goats, feed on the fruits and then ruminate and defecate the seeds under the canopy of the tree, promoting a high number of seeds.m^{-2}.

NDVI had a positive effect on seeds.m^{-2}, with agricultural areas and protected Caatinga showing a high NDVI (Table 2). Degraded and abandoned areas presented a clearly lower NDVI due to deforestation, resulting in greater soil exposure. Consequently, NDVI and the soil surface temperature are directly related. In general, seeds of tropical and subtropical species germinate in a temperature range between 20 and 30ºC. In a survey of Caatinga plants (Souza, Macêdo, & Silva, 2015), only a few species were able to germinate at temperatures above 35°C. Although *S. tuberosa* was not tested in this survey, it seems probable that this species requires lower germination temperatures. In *S. tuberosa*, the seed is enclosed into a thick endocarp, which impedes the desiccation of the embryo but also hinders the entry of water for germination. This adaptation to the semiarid climate likely makes *S. tuberosa* particularly vulnerable to elevated soil temperature.

All predictor variables of the best models also showed significant effects on seedlings. A plausible explanation for the stark difference in the number of seedlings across land-use types is the abundance of water present in the irrigated agricultural areas, which may compensate for the increasingly scarce and inconsistent rainfall, as foreseen for arid and semi-arid regions due to climate change (C. D. Allen et al., 2010; IPCC, 2013; K. Allen et al., 2017). Furthermore, the complete exclusion of goats is a crucial factor for the establishment of seedlings. Thus, due to the abundant regeneration in agricultural areas, we found a positive impact of density of houses on seedlings. On the other hand, pressure by goats had a negative effect on the seedling number. As goat browsing is ubiquitous across the entire study area, except for the fenced-off irrigated areas, our data provide evidence for the detrimental effect of these animals on species regeneration in natural areas. Our results support those of others regarding the absence of seedlings in their natural environment, owing, for example, to overexploitation, deforestation, irregularity of rainfall in the region, difficulties in seed germination (Araújo, Santos, Cavalcante, & Rezende, 2001; Costa, Bruno, Souza, & Lima, 2001; Souza et al., 2005), or damage to seeds and seedlings by insects and mammals (Cavalcanti et al., 2009).

The fact that we found *S. tuberosa* seedlings mostly in agricultural areas highlights the dependence of this species on human action. As landowners often remove weeds using herbicides, much of the potential regeneration of *S. tuberosa* may be regularly destroyed. In informal conversations with residents, only a few people stated that they noticed and protected the seedlings that occasionally appeared on their land. Consequently, conservation of the species seems to require improved awareness through campaigns that broaden the view from the adult trees to the sensitive seedling stage.

Influence of land-use type on the population dynamics of *Spondias tuberosa*

The extremely low seedling numbers, particularly in natural environments, indicated poor recruitment irrespective of land use. Thus, our third hypothesis was refuted. None of the size-class distributions showed the inverted-J-shaped pattern typical of abundant tree recruitment. In addition, the PIs for the populations in the different land uses were higher than zero, which further confirms low recruitment. Tree size-class distributions have been shown to be a reliable tool for predicting species responses to environmental and human influences (Kleinschroth et al., 2013; Wesche et al., 2008). The deviation from the J-shaped pattern is usually a cause for concern. However, a flat slope for the SCD of trees in tropical dry forests is relatively common and has already been reported in several works (Apgaua et al., 2015; Lykke, 1998; McLaren, McDonald, Hall, & Healey, 2005). For *S. tuberosa*, the total absence of young individuals, i.e., those that are not yet in the reproductive phase, has already been reported in other studies. Our detailed study involving different life stages from seeds and seedlings to young and adult trees provides novel insights into the effects of different land-use options and possibilities for improving the conservation of this threatened species, although it is not officially on the Red List of Threatened Species (Mertens, Germer, Siqueira Filho, & Sauerborn, 2017).

CONCLUSION

Our findings highlight the critical status of *S. tuberosa* and provide further evidence of the threats facing a typical Caatinga trees species with high economic and cultural value. We found taller and broader trees outside agricultural areas with the largest trees being present in the protected Caatinga and on abandoned land. However, tree size did not translate to greater regeneration success. Both seeds and seedling establishment were most pronounced within the highly artificial irrigated sites established after dam construction. Irrigation and livestock exclusion were likely the most important factors promoting tree regeneration in agricultural areas. Due to deficient seedling conservation in agricultural habitats and goat presence in all other land-use types, differences in the population dynamics of *S. tuberosa* among land-use classes were not detectable.

Overall, our study provides further evidence that *S. tuberosa* as well as with other Caatinga species is threatened by current land uses, which involve free roaming livestock in forests (Cierjacks, Pommeranz, Schulz, & Almeida-Cortez 2016). On the other hand, the species may be easily promoted by creating safe sites for germination and establishment by fencing off *S. tuberosa* individuals in remaining forests and the cessation (or at least the reduction) of agricultural practices around trees in agricultural areas. Our study hence highlights the relevance of land-use science, in particular in complex situations such as reservoir construction, for better counteracting species extinction caused by certain management practices.

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FIGURE CAPTIONS

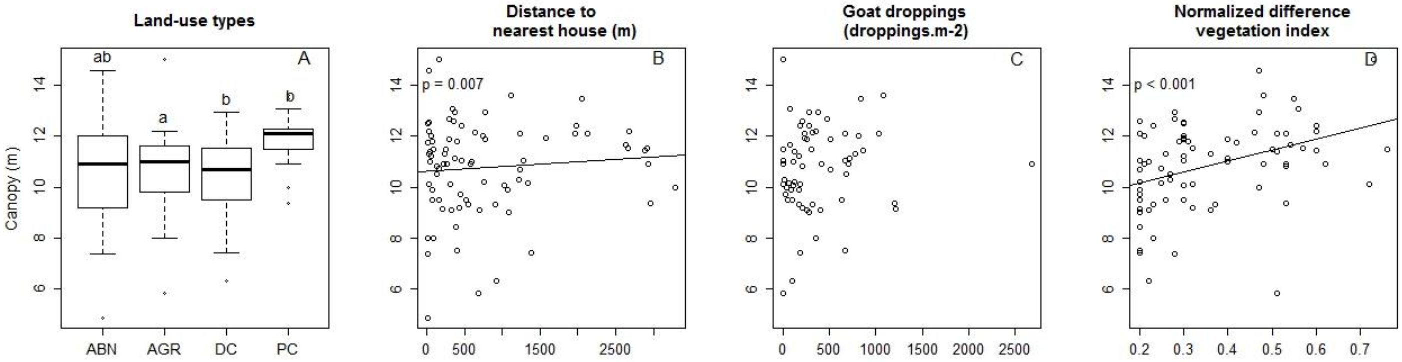

Figure 1. Impact of land-use type (A), distance to the nearest house (B), pressure by goats (C), and vegetation cover (D) on canopy diameter of *Spondias tuberosa* Arr. (Anacardiaceae). Model: Canopy ~ landuse + houses + goat + ndvi. Small letters in (A) indicate significant differences among land-use types. For the other predictor variables, the p-value shows the significance.

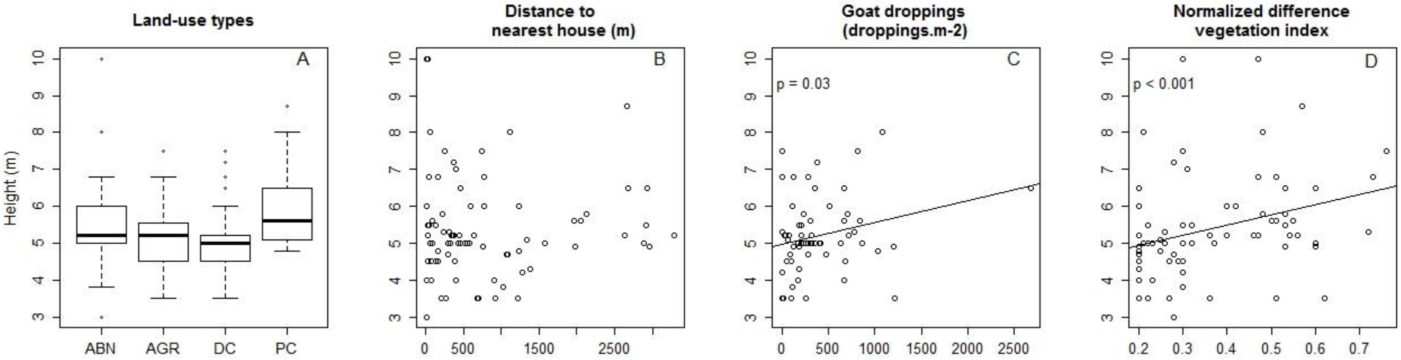

Figure 2. Impact of land-use type (A), distance to the nearest house (B), pressure by goats (C), and vegetation cover (D) on height of *Spondias tuberosa* Arr. (Anacardiaceae). Model: Height ~ landuse + houses + goat + ndvi. Small letters in (A) indicate significant differences among land-use types. For the other predictor variables, the p-value shows the significance.

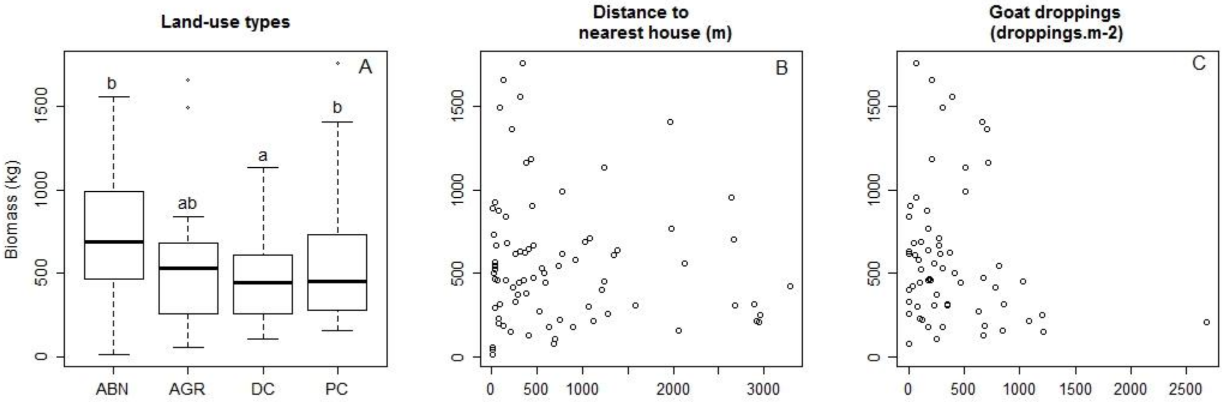

Figure 3. Impact of land-use type (A), distance to the nearest house (B), and pressure by goats (C) on biomass of *Spondias tuberosa* Arr. (Anacardiaceae). Model: Biomass ~ landuse + houses + goat. Small letters in (A) indicate significant differences among land-use classes. For the other predictor variables, the p-value shows the significance.

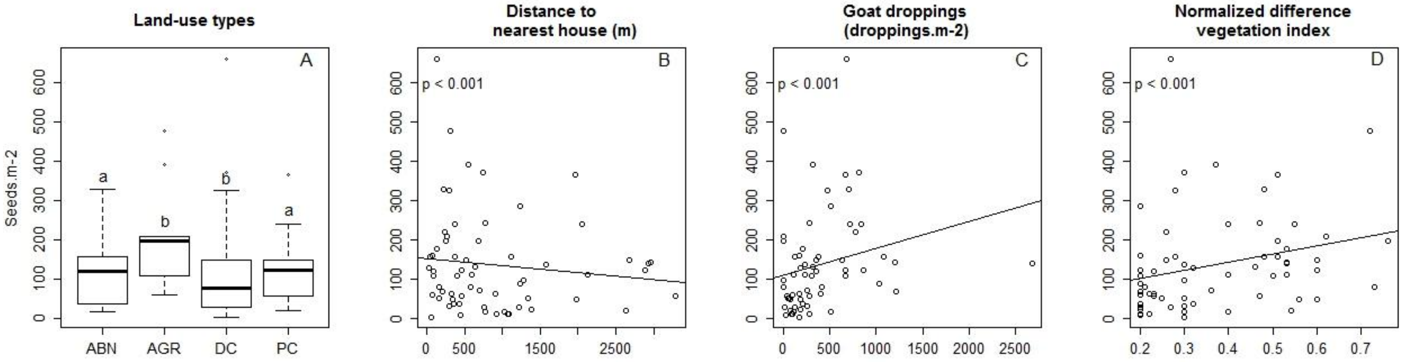

Figure 4. Impact of land-use type (A), distance to the nearest house (B), pressure by goats (C), and vegetation cover (D) on seeds of *Spondias tuberosa* Arr. (Anacardiaceae). Model: Seeds ~ landuse + houses + goat + ndvi. Small letters in (A) indicate significant differences among land-use types. For the other predictor variables, the p-value shows the significance.

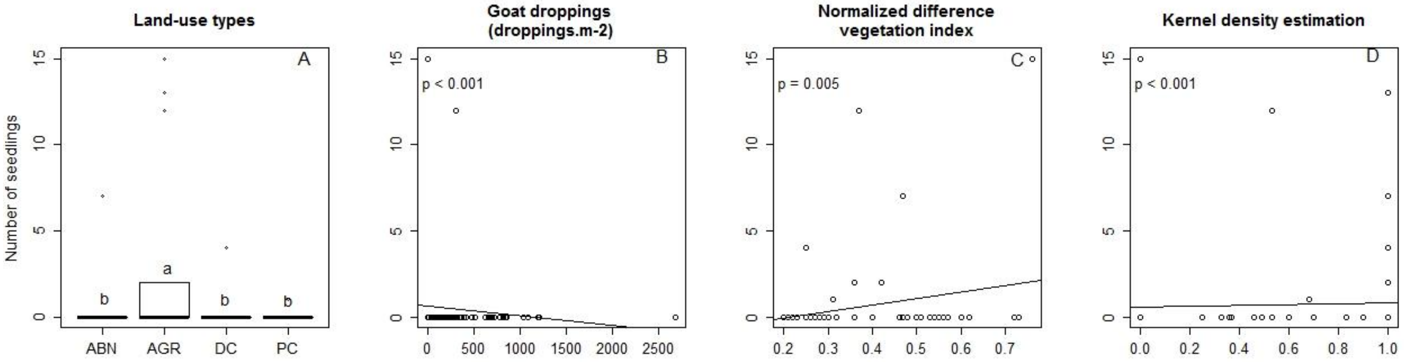

Figure 5. Impact of land-use type (A), pressure by goats (B), vegetation cover (C), and density of houses (D) on seedlings of *Spondias tuberosa* Arr. (Anacardiaceae). Model: Seedlings ~ landuse + goat + ndvi + kernel. Small letters in (A) indicate significant differences among land-use types. For the other predictor variables, the p-value shows the significance.

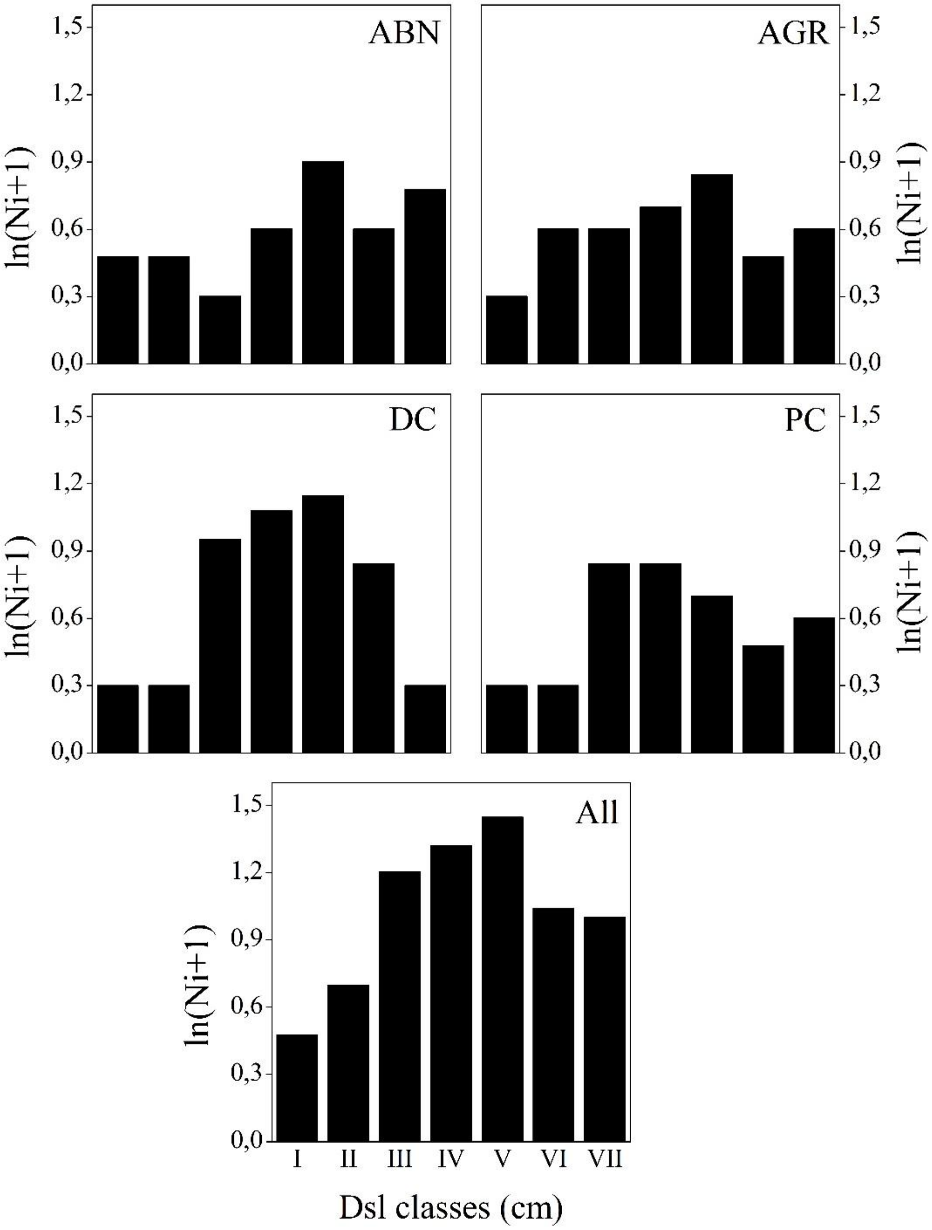

Figure 6. Size-class distributions (dsl in 24-cm intervals) for each land-use type. ABN: abandoned areas, AGR: agricultural areas, DC: degraded Caatinga, PC: protected Caatinga since 2012, All: whole population.

TABLES

Table 1. Descriptive statistics (mean ± SD) of response variables of *Spondias tuberosa* (Anacardiaceae) in four land-use types in a seasonally dry tropical forest.

Land-use type*	**N**	**Canopy diameter (m)**	**Height (m)**	**Diameter (cm)**	**Biomass (kg)**	**Seeds (nº.m^{-2})**	**Seedlings (nº around trees)**
ABN	17	10.4 ± 2.3	5.6 ± 2.0	55.4 ± 20.9	745.2 ± 435.3	118.2 ± 99.7	0.41 ± 1.6
AGR	15	10.7 ± 2.0	5.1 ± 1.1	49.9 ± 19.6	583.4 ± 466.2	210.2 ± 139.2	2.93 ± 5.4
DC	33	10.4 ± 1.6	4.9 ± 1.0	46.8 ± 11.6	440.6 ± 234.1	124.0 ± 140.1	0.12 ± 0.6
PC	15	11.8 ± 1.1	5.9 ± 1.1	48.2 ± 18.7	606.9 ± 463.9	129.8 ± 91.8	0.06 ± 0.2
All	80	10.7 ± 1.8	5.3 ± 1.37	49.5 ± 16.9	536.2 ± 388.7	136.5 ± 125.9	0.70 ± 2.6

*ABN: abandoned areas; AGR: agricultural areas; DC: degraded Caatinga; PC: protected Caatinga since 2012.

Table 2. Descriptive statistics (mean ± SD) of predictor variables and intensity of disturbance in four land-use types in a seasonally dry tropical forest.

Land-use type*	N	House (m)	Goat (droppings.m^{-2})	NDVI	Kernel	Intensity of disturbance
ABN	17	227.4 ± 295.5	330.9 ± 223.3	0.26 ± 0.07	0.87 ± 0.3	9.45
AGR	15	179.3 ± 202.3	101.8 ± 135.3	0.47 ± 0.1	0.79 ± 0.3	7.44
DC	33	735.1 ± 572.2	337.7 ± 293.4	0.32 ± 0.1	0.48 ± 0.4	8.30
PC	15	2085.0 ± 932.6	713.8 ± 726.0	0.50 ± 0.1	0.04 ± 0.1	5.61
Overall	80	776.1 ± 877.5	380.4 ± 434.2	0.36 ± 0.15	0.54 ± 0.46	7.82

*ABN: abandoned areas; AGR: agricultural areas; DC: degraded Caatinga; PC: protected Caatinga since 2012.

Table 3. Slope regression (diameter at soil level versus number of individuals) and permutation index (PI) for the different land-use types and for all individuals of *Spondias tuberosa* (Anacardiaceae) in four land-use types in a seasonally dry tropical forest.

Land-use type*	**Slope**	**SE slope**	**R^2**	**p-value**	**PI**
ABN	0.29	0.19	0.18	0.18	20
AGR	0.27	0.15	0.26	0.13	17
DC	0.46	0.39	0.05	0.29	17
PC	0.33	0.22	0.17	0.19	20
All	0.66	0.26	0.47	0.05	20

*ABN: abandoned areas; AGR: agricultural areas; DC: degraded Caatinga; PC: protected Caatinga since 2012.

4.2 ARTIGO 2 – DOES LAND USE INFLUENCE THE GENETIC DIVERSITY OF *Spondias tuberosa* ARR. IN CAATINGA?

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ABSTRACT

Spondias tuberosa Arr. Câm. is an endemic fruit bearing tree in Caatinga, a seasonally dry tropical forest in Northeastern of Brazil. This species has been threatened by the decrease of population size as well as the low natural recruitment of young individuals due the anthropogenic disturbance. We performed a molecular analysis to investigate the influence of four land-use types on the genetic diversity of *S. tuberosa*. We used two molecular markers: (i) seven SSRs and (ii) polymorphic AFLPs. *S. tuberosa* showed overall low genetic diversity due to biparental inbreeding and a low genetic differentiation between the land-use types. This low differentiation is a consequence of the high gene flow, which show patterns of one connected population. The Bayesian analysis showed two gene pools, however, the protected area is formed by a predominant gene pool different from the others land-use types, once this area have a high number of private alleles. Our study highlights the importance to safeguard the currently existing genetic base in the species by increasing conservation areas as well as the control in areas destined to Caatinga's conservation that already exist.

Key-words: AFLP, genetic diversity, land-use type, Seasonally tropical dry forest, SSR, Spondias tuberosa.

INTRODUCTION

Seasonally tropical dry forests (STDF) are one of the most threatened ecosystems in the world (Miles et al. 2006) but conservation efforts have so far been insufficient (Espírito-Santo et al. 2006). The Caatinga is one of the largest STDF located in Northeastern Brazil characterized by a mosaic of phytophysiognomies (Santos et al. 2011; Albuquerque et al. 2012) and by its biodiversity, with high levels of both species richness and endemism (Giullieti et al. 2002; Rocha et al. 2004). However, these ecosystems are endangered by agricultural practices and pasture expansion, which are currently the main drivers of landscape transformation (Espírito-Santo et al. 2009).

Several studies have reported the negative influence of anthropogenic disturbance on genetic diversity of species (Collevatti et al. 2001; Lamont et al. 2003; Baldauf et al. 2013). In particular, habitat fragmentation proved to be one of the main causes of biodiversity loss due to the drastic effects of the reduction and isolation of populations. In the short term, genetic diversity in populations is reduced by genetic bottleneck effects, especially by lower proportions of polymorphic loci and a reduction in the number of alleles per locus expected within the fragments (McGarigal and Cushman 2002; Fahrig 2003). In the long run, a reduction in heterozygosity can result in the accumulation of deleterious recessive alleles or in a lower adaptive capacity to environmental or climate changes, thereby reducing the fitness of the species (Young et al. 1996; Lowe et al. 2005).

Genetic diversity is a prerequisite for evolutionary change and its maintenance plays a fundamental role for the long-term survival of threatened species. Consequently, it is important to understand the structure, evolutionary relations, taxonomy and biogeography of the species for future application strategies and management plans conserve and protect taxa (Milligan et al. 1994). For rare species, knowledge about the structure, dynamics and relations of genetic variability within and among populations supports the development of efficient conservation genetic resources strategies, which may support the establishment of genotypes for germplasm banks. Further, several studies demonstrated that ecosystem function is effected by genetic diversity within species (Maddox and Root 1987; Cahill et al. 2005; Wise 2007; Karley et al. 2008). This holds particularly for useful species, whose function translate directly to ecosystem services. The level of genetic diversity in populations highly depends on the mating system, the evolutionary history of a species and their populations, and on the level of environmental heterogeneity.

Neutral molecular markers, such as microsatellite markers, also known as simple sequence repeat (SSR) markers, and amplified fragment length polymorphisms (AFLPs) are valuable tools to investigate processes on a relatively small spatial scale, allowing genetic diversity evaluation and the interpretation of evolutionary processes (Caixeta et al. 2006; Latta 2006). In particular, the use of SSR markers has become increasingly common due to its accessibility and efficiency. Microsatellites markers are codominant and multi-allelic markers and their high mutation rates make them particularly useful to study rapid responses of genetic variation to landscape change (Wang 2011). In comparison, dominant markers such as AFLPs are multi-locus markers that are described to be less informative than microsatellite markers. Nonetheless, they derive their statistical power from their sheer number (Sunnucks 2000; Mariette et al. 2002; Belaj et al. 2003). Overall, both methods have advantages for analyzing population genetics of species and may therefore be combined.

Spondias tuberosa Arr. is an endemic species in Northeastern Brazil (Giulietti et al. 2002), belonging to the Anacardiaceae family. This species is a long-lived and deciduous tree, which blossoms in the end of the dry season. The inflorescence has masculine and hermaphrodite flowers. *S. tuberosa* is an outcrossing species, with high self-incompatibility, and its pollinators are mainly bees and wasps (Nadia et al. 2007; Leite and Machado 2010). Its fruits are consumed by wild and domesticated animals, as well as by the local people, who also use the fruits to produce handcraft and manufactured products for commercial purposes (Borges et al. 2007; Lins Neto et al. 2010; Reis et al. 2010). Despite its ecological, social and economic importance, *S. tuberosa* has suffered from the decrease of population size as well as from the low natural recruitment of young individuals due the anthropogenic disturbance (Oliveira et al. submitted). Owing its ecological and economic importance and its sensitivity to land-use changes, it may represent a model species for analyzing ecological processes in Caatinga SDTFs and the conservation status of related species, in general. We therefore investigated the population genetics of *S. tuberosa* using SSR and AFLPs in relation to land use and geographical distribution in the Caatinga area along the Itaparica revervoir, an area particularly subjected to different land-use types and with a high risk of degradation (Schulz et al. 2017). We hypothesized that 1) genetic diversity of *S. tuberosa* located in the São Francisco sub-region are influenced by the land-use types, and 2) that individuals located in the less disturbed area (furthest from the houses) present greater genetic diversity.

MATERIAL AND METHODS

Study area and land-use types

The Caatinga is a mosaic of physiognomies, environment types and floristic groups, constituting the main phytogeographical domain of the Northeastern region in Brazil (Veloso et al. 2002; Moro et al. 2016). The climate is semi-arid with a pronounced dry season interrupted by a rainy season between November and April and an average of temperature at 25 ºC. The amount of annual rainfall ranges from 250 to 1500 mm (Ab'Saber 1974; Reis 1976; Sampaio 1995, 1996), though it is very heterogeneous and varies considerably between consecutive years and across the territory. The study area comprises seven municipalities surrounding the Itaparica reservoir (Fig. 1), in the sub-medium basin of the São Francisco River, one out of nine reservoirs used for flood regulation and hydroelectric power generation (Romano and Garcia 1999). In this area, the average rainfall ranges from 300 to 1200 mm and the dry season can prolong from seven to ten months (Assis et al. 2015).

We collected young and healthy leaves and cambium samples of 89 trees of *S. tuberosa* with a minimum distance of 200 m between each tree to avoid clonal relation among individuals. The samples were stored in silica gel and each individual was georeferenced using GPS (Garmin: eTrex® 20). We classified the land use around each *S. tuberosa* tree based on four categories, described as follows:

(1) Protected Caatinga by law (PC): This area is an ecological station since 2012 (State decree nº 38.133/2012) and is the only area with near-natural Caatinga protected by law, known as *Serra da Canoa*. Compared to the others land-use types, PC has a higher plant biodiversity (Schulz et al. submitted), longest distance to the nearest housings and lower density of houses surrounding the trees (Oliveira et al. submitted).

(2) Degraded Caatinga (DC): This land-use type was mainly located in rural areas with agricultural and pasture purposes. The vegetation is characterized by pioneer Caatinga tree species such as *Cenostigma pyramidale* (Tul.) L. P. Queiroz and *Aspidosperma pyrifolium* Mart. The proximity to houses makes it easy to local people to access *S. tuberosa* trees.

(3) Agricultural areas (AGR): Areas within irrigated farming schemes where monocultures (e.g. banana, guava and coconut) are cultivated, and higher animals are most commonly absent (Cierjacks et al. 2016). Most of these areas were cleared approximately 30 years ago. In general, farmers preserve *S. tuberosa* individuals inside the cropland to provide its fruits and the shade the trees (Araújo et al. 2012). Due to the proximity and density of houses, fruit collection of *S. tuberosa* is restricted to the landowner's family.

(4) Abandoned areas (ABN): These areas had previously been used as cropland but were abandoned 5 to 25 years ago. They are characterized by scattered shrubs and small trees and mainly exposed soil. Individuals of *S. tuberosa* in these areas were more subject to overexploitation due to their proximity to localities and the density of houses surrounding the trees, as well as goat grazing.

Plant material and DNA extraction

As some studies report differences in quality of DNA from different tissues (Donini et al. 1997; Lin and Walker 1997), we tested if these differences were consistent also for *S. tuberosa*. Based on the quality control by agarose gel electrophoresis and optical density estimation with a NanoPhotometer™ (Implen GmbH, Munich, Germany), cambium samples were chosen for population genetic screening (unpublished data). We extracted total genomic DNA with the "InnuPREP Plant DNA Kit" (Analytik Jena AG, Jena, Germany), following the protocol of the manufacturer with modifications described in Rohwer and Rudolph (2005).

SSRs and AFLPs analysis

Individuals were genotyped at seven microsatellite loci; five of which (U1, TUB74, TUB75, TUB77 and TUB78) were developed for *S. tuberosa* (Almeida et al., unpublished) and two (Spo8 and Spo14) for *S. radkolferi* (Aguilar-Barajas et al. 2014), the latter successfully cross-amplifying in *S. tuberosa*. The SSR loci were amplified following the protocol of Aguilar-Barajas et al. (2014), with an annealing temperature at 60 ºC. The PCR was conducted in a T-professional (Biometra GmbH, Göttingen, Germany) thermocycler.

The AFLP protocol based on Vos et al. (1995). High quality genomic DNA was digested by two restriction endonucleases (EcoRI and MseI), pre-amplification was performed using primer pairs with one additional nucleotide (EcoRI+1/MseI+1), and selective amplification with primer pairs with three additional nucleotides (EcoRI+3/MseI+3). Eighteen primer combinations (data not shown) including those already published for population analyses of *S. tuberosa* (Santos et al. 2008, 2011a) were evaluated with cambium samples, and two primer combinations were finally selected that expressed a clear and highly informative genetic pattern. The two successive restrictions steps, ligation, pre-amplification and the selective amplification were also conducted in thermocyclers T-professional (Biometra GmbH, Göttingen, Germany).

Selected SSR and AFLP *primers* were fluorescently labeled (6-FAM and HEX) to detect PCR products with a 3500xL Genetic Analyzer (Thermofisher Scientific Inc., Waltham, USA). GeneScan™ 500 LIZ® (AppliedBiosystems, Carlsbad, USA) was used as internal standard. The sizes of the PCR products in the electropherograms were calculated with the Genemapper® software (AppliedBiosystems, Carlsbad, USA). Each individual was analyzed twice and only reproducible fragments were transferred into a data matrix per marker system.

Data analyses

Genetic diversity in SSR and AFLP markers

All sizes of SSRs alleles were coded in base pairs (bp). The occurrence of one peak per sample at a given locus was regarded as homozygous. Loci with more than one PCR product were interpreted as heterozygous. Microsatellite loci were characterized by the number of alleles per locus (N_a), number of effective alleles (N_e), total expected heterozygosity (H_T), expected heterozygosity within populations (H_E), observed heterozygosity (H_O) (Nei 1987), their genetic differentiation by the infinite alleles model (F_{ST}) and inbreeding coefficient (F_{IS}) (Weir and Cockerham 1984). All genetic diversity parameters were estimated with the software GenAlEx 6.5 (Peakall and Smouse 2012) and Fstat version 2.9.3 (Goudet 1995).We calculated the frequencies of null alleles using Cervus v.3.0.3 (Marshall et al. 1998), that estimates the presence of null alleles by analyzing deviations from Hardy-Weinberg equilibrium.

For AFLP markers, we assumed that each amplified fragment (peak) corresponded to a dominant allele of a given locus. Therefore, the amplification products were scored as binary data encoded with the values 1 for presence and 0 for absence of each peak. To describe the different primer combinations for AFLP loci, we calculated the total number of PCR products (TNL), total number of polymorphic loci (TNPL), percentage of polymorphic loci (PPL), number of rare alleles (NRA) and rare loci (RL) using the MS Excel plugin GenAlEx v 6.5software (Peakall and Smouse 2012).

Effects of land-use types on genetic diversity of *S. tuberosa*

Levels of genetic diversity within land-use types were described in SSR data by the number of effective alleles (N_e), allelic richness (Rs), gene diversity (Gd), observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient in populations (F_{IS}) and number of migrants (N_m) for overall population. We computated these parameters also using the software GenAlEx 6.5 (Peakall and Smouse 2012) as well as Fstat version 2.9.3 (Goudet 1995). To characterize the level of genetic diversity within the different land-use types with AFLP data, we calculated the total number of polymorphic loci (TNPL), percentage of polymorphic loci (PPL), Nei's genetic diversity index (h), Shannon's information index (I) and the number of private loci (NPrL). These analyses were computed using POPGENE version 1.31 (Yeh et al. 1999).

In order to visualize the genetic differentiation between the individuals of *S. tuberosa* from the four land-use types, we applied a Principal Coordinates Analysis (PCoA) based on genetic similarity (Euclidian and Dice in SSR and AFLP data, respectively) using PAST 3.11 (Hammer et al., 2001). The degree of relationship between the individuals was estimated with a hierarchical cluster analysis based on the Neighbor Joining method (Saitou and Nei 1987). The visualization of relationship was an unrooted dendrogram with proportional branch lengths. The likelihood of-each branching was evaluated with 10,000 bootstrap repetitions and Euclidean and Dice distance algorithms in the software PAST 3.11 (Hammer et al. 2001).

Genetic distances between populations were compared to geographical distances. With a Mantel test significances (1,000 permutations) were estimated with the software AIS (Alleles in Space) 1.0 (Miller 2005). Additionally, we computed the distribution of molecular variation within one hierarchical level as measured by Analysis of Molecular Variance (AMOVA) and the pairwise F_{ST} with GenAlEx 6.5 (Peakall and Smouse 2012). For SSR, F_{ST} was calcutated assuming an infinite allele model (IAM).

To verify if all sampled individuals comprise a single gene pool or if they belong to different demes or populations, a Bayesian analysis of population structure was carried out with the software STRUCTURE 2.2 (Pritchard et al. 2000). We estimated best K with 10 replicates for each K value (1 - 10). Each run consisted of a burn-in period of 500,000 with 700,000

MCMC replications after burn-in. To infer the most likely number of clusters (K), the method of Evanno et al. (2005) was employed, based upon the ad hoc measure of ΔK, from the online software STRUCTURE Harvester Web v0.6.94 (Earl and VonHoldt 2012).

RESULTS

Genetic diversity in SSR and AFLP markers

The null allele frequencies of the SSRs were high for the loci TUB77 and TUB78, with 20 and 73%, respectively. However, comparing the data with and without these two loci no significant difference in most of parameters was found. Thus, we retained the set of seven loci for genotyping all individuals. The discrimination power for each locus based on H_E parameters ranged from 0.232 to 0.685. Detailed data are shown in Table 1.

In the AFLP analysis, the marker with the primer combination EcoAAA/MseCTG exhibited 181 loci and the marker EcoAAA/MseAGT 188 loci, some of which had to be excluded during conflation of both markers, hence, the combined data matrix had a total number of 360 loci. The AFLP marker EcoAAA/MseCTG revealed a polymorphism rate of 94% and the EcoAAA/MseAGT 84%. Overall, the loci of the combined 1/0 matrix showed a polymorphism rate of 90% (Table 2).

Effects of land-use types on genetic diversity of *S. tuberosa*

The number of effective alleles in SSR data of the different land-use types was very similar. Though not significant, individuals of PC had a slightly higher average of alleles at all SSR loci. The average number of effective alleles in populations of all land-use types was lower than the average number of alleles per locus, indicating a large amount of low-frequency alleles. As shown in Table 3, the average H_E was 0.437, ranging from 0.407 in AGR to 0.455 in DC. H_O values between populations ranged from 0.238 to 0.275 in AGR and DC, respectively. The F_{IS} values ranged from 0.398 to 0.505 in DC and PC, respectively.

In the AFLP analyses the total number of polymorphic loci ranged from 147 in ABN to 227 in DC, corresponding 40.27% and 62.19%, respectively. The Nei's genetic diversity index was 0.117 in ABN, AGR and DC, and 0.137 in PC, with an average value of 0.122. The Shannon diversity index varied from 0.182, in ABN, to 0.219 in PC. The number of private loci also was higher in PC (33), followed by DC (21), AGR (11) and ABN (8) (Table 3).

Both PCoA analyses with SSR and AFLP markers did not produce any distinct land use clusters (Fig. 2a and 2b), though a differentiation of individuals from the PC is visible especially in the PCoA analyses of the AFLP data (Fig. 2b). However, two clearly separated clusters were generated in the neighbor-joining dendrogram, which were supported with a bootstrap value of 100 (Fig. 3). These results also were confirmed by the very low percentage of variation between the land-use types with 1 and 5% for SSR and AFLP markers, respectively (Tables 4 and 5). Despite the significant values of pairwise F_{ST}, the genetic distance matrices obtained for both markers indicated the low genetic differentiation of *S. tuberosa* between the land-use types, which values were 0.049 and 0.046 for SSR and AFLP loci, respectively (Table 6). However, in AFLP pairwise F_{ST}, PC showed a moderate level of differentiation from the others land-use types, confirming the grouping of PC individuals shown in the PCoA.

The Mantel test revealed a significant positive correlation between genetic and geographic distances (SSR: $r = 0.20$, $p < 0.001$; AFLP: $r = 0.24$, $p < 0.001$). However, also a significantly positive value was found between individuals from PC and DC in the Mantel test of the four land-use types in both SSR and AFLP data (Table 7).

The population structure analysis with Bayesian clustering methods of STRUCTURE, allowed us to distinguish two gene pools for both markers ($K = 2$) (Fig. 4). Individuals in ABN, AGR and DC presented higher percentage of red gene pool (> 68%), while in PC the green gene pool was dominant (60%).

DISCUSSION

Several studies already have reported about influences of land-use change on biodiversity of ecosystems around the entire world. However, there is still a deficit for those that focus on how land-use changes reduce genetic diversity in plant species, especially in seasonally tropical dry forests. Thus, our work highlights the status of the genetic diversity of *S. tuberosa*, an endemic and intensely used tree in the Caatinga.

Genetic diversity in SSR and AFLP markers

The present study detected low levels of genetic diversity in the seven SSR loci that were evaluated. The detected levels of genetic diversity using SSR markers were lower than the values reported for other Caatinga species. An average of 2.9 alleles was estimated for the whole set of individuals in the present study. Whereas López-Roberts et al. (2016) found a low average of 3.2 alleles per locus in for *Senna spectabilis* var. *excelsa* (Fabaceae), Caetano et al. (2008) reported a much higher average number of 18.8 alleles per locus for *Astronium urundeuva* (Anacardiaceae), with a range from 4 to 33 alleles. The number of alleles per locus the endemic palm tree *Syagrus coronata* (Arecaceae) ranged from 5 to 10, with an average of 9.8 (Simplicio et al. 2017). Regarding the observed and expected heterozygosity, *S. tuberosa* also presented lower values in comparison with the species mentioned above. Further, the observed heterozygosity in the present study was lower than expected, which indicates a heterozygotes deficit. This excess of homozygotes may be attributed to biparental inbreeding since *S. tuberosa* is an outcrossing and self-incompatible species.

To support our results and to verify whether the trends for different analyses were similar with both marker systems, we additionally carried out AFLP analysis based on capillary electrophoresis techniques. We detected a large number of polymorphic loci (323 AFLPs) with two primer combinations. The number of polymorphic characters was much higher than reported in literature for *S. tuberosa*, with 171 polymorphic loci in comparison with the 14 primer combinations in Santos et al. (2008) and six polymorphic loci in Santos et al. (2011) obtained with the primer combination EcoAAA/MseCTG. The success of this high level of polymorphism may be due the use of an automatic sequencer, the optimized protocol or the different tissues used. According to Bonin et al. (2007), 200 markers in AFLP data is a good starting point for measuring genetic variation and differentiation. Accordingly, the larger number of AFLP polymorphic bands than the above mentioned indicates a high level of reliability for our results have.

Effects of land-use types on genetic diversity of *S. tuberosa*

In this present study, land-use change clearly influenced the genetic diversity of *S. tuberosa*. We found significant differences among land-use types in the analyses with AFLP markers. The same trend was observed for SSR markers, despite the differences were not significant. The average genetic diversity of *S. tuberosa* was overall low compared to other frequent Caatinga species (to mention works with SSR and AFLP). While *S. tuberosa* had an average H_E of 0.437, *S. mombin*, showed an H_E of 0.545, also with SSR markers (Silva et al. 2009). In natural populations of *S. tuberosa*, Santos et al. (2008) reported an average of Nei's genetic diversity (*h*) with AFLP markers of 0.313, whereas in our study *h* was 0.122. Presumably, the difference between the results presented in our work and Santos et al. (2008) can be related to large geographic distribution of *S. tuberosa* in semi-arid region and the fact that different generations can be found at a particular time due to the tree's long live span, leading to the sampling of multi-aged populations.

The low genetic diversity found in *S. tuberosa* in all land-use types may be due to the moderate level of inbreeding, as evidenced by F_{IS}. *S. tuberosa* is an outcrossing and self-incompatible species (Leite 2006; Nadia et al. 2007), with a high synchronous flowering during the dry season, which is favoring a high within plant and patch residence time of pollinators. Besides that, in degraded areas, the population size and density is reduced, and this can lead to high levels of inbreeding.

Domestication is also a process that can reduce genetic diversity. Miller and Schaal (2005) assessed management effects on the genetic variability in populations of *S. purpurea*. They conclude that the process of domestication reduced the degree of genetic variation observed in cultivated varieties as compared to wild populations. However, the authors found that species-rich home-gardens often serve as species diversity reservoirs. In accordance, Lins Neto et al. (2013) found that individuals *S. tuberosa* growing in yards showed pronounced morphological and genetic differences. Our results clearly differ from those found by Lins-Neto et al. (2013) as individuals of *S. tuberosa* in disturbed areas had particularly low levels of genetic diversity.

Our results clearly differentiated PC from the other land-use types. The Mantel test provided statistical evidence for the relationship of geographic and genetic distances with the weak but significant correlation. This was also significant when analyzing PC and DC alone. Thus, the high number of private alleles found in PC in both marker systems implies that this area preserves a high genetic diversity, presumably related to another gene pool that may be important for the fitness of the species in the study area. PC also showed higher levels of genetic diversity which caused the differentiation in PCoA with AFLP data. Bayesian analysis, PCoA and dendrogram results indicated that two mixed population groups exist with one gene pool prevailing in PC and the other on being more frequent in the remaining land uses. In addition, in both used markers PC presented the green gene pool as predominant, while in the others land-use types the predominant is the red gene pool. This result also confirm PC as an important source of genetic diversity.

The differentiation between land-use types may be considered low, albeit we found significant values among land uses. Low genetic differentiation may be caused by the high number of migrants N_m (> 6.0), which implies sufficient gene flows and a low degree of genetic isolation(Oliveira et al. 2002). According to Hartl and Clark (1997), $N_m < 1.0$ indicates genetic isolation, whereas N_m values greater than 1.0 are sufficient to avoid the random loss of alleles within population. In contrast, N_m greater than four indicates homogenization of alleles within the population which seems to be the case in our study species. As *S. tuberosa* is a long-lived tree, N_m comprises both current and historic migration. Still, the actual number of *S. tuberosa* individuals seems to be relict of a few large populations with high gene flow amongst each other, which nowadays shows a lower density of individuals than in the past. This may explain the overall low genetic diversity along with low genetic differentiation.

Implications of this study for *Spondias tuberosa* conservation

Knowledge about population genetics is a key issue for understanding microevolutionary processes in plant populations and supporting or developing appropriate use and conservation strategies (Lengkeek et al. 2006). Our study provides further evidence to the apparently contradictory idea that many tree species seems to be robust to anthropic disturbance because they maintain high levels of genetic connectivity by pollen dispersal (Bacles and Jump 2011); at the same time, many species show increased biparental inbreeding in these disturbed habitats (Vranckx et al. 2012). The mating between close relatives in consequence of the high levels of inbreeding may play an important role in determining the genetic structure of these populations (Weir 1996).

The establishment of a conservation plan for *S. tuberosa* is urgent, especially to avoid further genetic losses and ensure the long-term viability of subsequent generations of all populations. The findings of this study clearly indicate that PC in Serra da Canoa is a hot spot of genetic diversity in the study area and therefore should be a priority area for conservation. *In situ* genetic reserves should be as large as possible to minimize problems of genetic drift and consequent depression of genetic variability that can be expected in small reserves (Leite 2005).

Although, the area with the greatest genetic diversity is already officially protected, there still exists overexploitation of natural resources due to the lack of efficient control. Consequently, a complementary strategy of *ex situ* conservation, such as the establishment of a living gene bank possibly integrated into participatory breeding programs, is recommendable to avoid future genetic losses of this important tree species.

CONCLUSION

Both molecular markers revealed comparable trends showing the advantage of employing both types of markers for studying the genetic diversity of *S. tuberosa*. Low levels of genetic diversity observed in *S. tuberosa* might be due to the moderate level of biparental inbreeding. The fact that individuals in PC present private alleles, as well as a different gene pool from the others land-use types, shows the importance of the areas destined to the preservation of the Caatinga and, thus, of the maintenance of the genetic diversity. The weak genetic structure and the high levels of historical gene flow detected among land-use types would suggest that the studied populations of *S. tuberosa* behave practically as a homogeneous genetic unit in that area of São Francisco River. Our study will guide in conservation, breeding strategies and general management (seed collection, seed distribution and afforestation activities) of this important species of Caatinga. In addition, our results show that the increase of protected areas will ensure the survival of *S. tuberosa* species and at the same time contribute to the preservation of the threatened Brazilian SDTF remnants.

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TABLES

Table 1. Diversity indexes and differentiation parameters for the polymorphic SSR loci in *Spondias tuberosa*.

Locus	N_a	N_e	H_O	H_E	H_T	F_{ST}	F_{IS}
U1	5	2.978	0.399	0.685	0.940	0.011	0.382*
Spo 8	2	1.284	0.217	0.233	0.231	-0.010	0.054
Spo 14	4	2.837	0.566	0.683	0.681	-0.006	0.194
TUB 74	2	1.292	0.168	0.232	0.243	0.041	0.219
TUB 75	2	1.439	0.240	0.300	0.311	0.029	0.232
TUB 77	3	1.883	0.107	0.507	0.508	-0.001	0.803*
TUB 78	3	2.056	0.052	0.520	0.535	0.019	0.843*
Overall	2.964	1.972	0.250	0.451	0.457	0.009	0.430

N_a: number of alleles; N_e: number of effective alleles; H_O: observed heterozigosity; H_E: expected heterozygosity within populations; H_T: total expected heterozygosity; F_{ST}: genetic differentiation coefficients between populations; F_{IS}: inbreeding coefficient; *significant deviations from HWE.

Table 2. Descriptive statistics about the different primer combinations for AFLP loci in *Spondias tuberosa*.

Primer combinations	TNL	TNPL	PPL (%)	NRA	RL
E-AAA/ M-CTG	181	171	94	79	43
E-AAA/ M-AGT	188	158	84	66	35
E-AAA/M-CTG + E-AAA/M-AGT	360	323	90	126	35

TNL: total number of loci; TNPL: total number of polymorphic loci; PPL: percentage of polymorphic loci; NRA: number of rare alleles; RL: rare loci.

Table 3. Genetic diversity in *Spondias tuberosa* with microsatellites (SSRs) and amplified fragment length polymorphisms (AFLPs).

Land-use types	**SSR**								**AFLP**					
	N	**N_e**	**Rs**	**Gd**	**H_O**	**H_E**	**F_{IS}**	**N_m**	**N**	**TNPL**	**PPL**	***h***	***I***	**NPrL**
ABN	18	2.027	2.863	0.451	0.241	0.448	0.458		8	147	40.27	0.117	0.182	8
AGR	17	1.822	2.740	0.412	0.238	0.407	0.422		17	173	47.40	0.117	0.187	11
DC	40	2.011	2.929	0.457	0.275	0.455	0.398		39	227	62.19	0.117	0.192	21
PC	14	2.029	3.086	0.487	0.245	0.438	0.505		14	211	57.81	0.137*	0.219	33
Mean		1.962	2.921	0.452	0.250	0.437	0.445	6.119		189.5	51.92	0.122	0.195	18.25

ABN: abandoned areas; AGR: agricultural areas; DC: degraded Caatinga; PC: preserved Caatinga; N: total number of analyzed samples; N_e: number of effective alleles; Rs: allelic richness; Gd: gene diversity; H_O: observed heterozigosity; H_E: expected heterozigosity; F_{IS}: inbreeding coefficient in populations; N_m: number of migrants; TNPL: total number of polymorphic loci; PPL: percentage of polymorphic loci; *h*: Nei's genetic diversity index; *I*: Shannon's information index; NPrL: number of private loci.

Table 4. Analysis of molecular variance (AMOVA) using SSR data.

Source of variation	**d.f.**	**SS**	**Est. var.**	**%**
Among population	3	9.978	0.011	1%
Among individuals	82	238.004	1.038	55%
Within individuals	86	71.000	0.826	44%
Total	171	318.983	1.875	100%

Table 5. Analysis of molecular variance (AMOVA) using AFLP data.

Source of variation	**d.f.**	**SS**	**Est. var.**	**%**
Among population	3	260.635	2.408	5%
Within population	77	3279.336	50.451	95%
Total	80	3539.971	52.859	100%

Table 6. Pairwise F_{ST} among land-use types based on the SSR and AFLP markers.

Land-use types	**ABN**	**AGR**	**DC**	**PC**
ABN	**-**	0.000	**0.033**	**0.081**
AGR	0.005	**-**	**0.018**	**0.076**
DC	0.000	0.000	**-**	**0.065**
PC	**0.028**	**0.033**	0.016	**-**

ABN: abandoned areas; AGR: agricultural areas; DC: degraded Caatinga; PC: preserved Caatinga. Values at upper right position refer to AFLP markers and values at bottom left refer to SSR markers. Significant F_{ST} values are in bold ($p < 0.05$).

Table 7. Mantel test between genetic and geographical distances in four land-use types.

Land-use type*	SSR	AFLP
ABN	r = - 0.04	r = - 0.23
AGR	r = 0.03	r = - 0.06
DC	**r = 0.23**	**r = 0.20**
PC	**r = 0.23**	**r = 0.47**
All	**r = 0.20**	**r = 0.24**

*ABN: abandoned areas; AGR: agricultural areas; DC: degraded Caatinga; PC: preserved Caatinga. Significant values are in bold ($p < 0.001$).

FIGURE LEGENDS

Figure 1. Sampling sites of *Spondias tuberosa* Arr. in Pernambuco State, Brazil.

Figure 2. Scatter plot of the first two PCoA axes based on SSR (a) and AFLP (b) data showing the relationship of individuals from four land-use types of *Spondias tuberosa*. The first and the second coordinates in SSR data accounted for 12.64 and 11.82% of the variation, respectively. For AFLP data, the first and the second coordinates accounted for 14.1 and 7.5%, respectively. Light blue: abandoned areas (ABN); dark blue: agricultural areas (AGR); red: degraded Caatinga (DC); green: protected Caatinga (PC).

Figure 3. Neighbor-joining tree of the four land-use types of *Spondias tuberosa* based on Euclidian distance of SSR (a) and AFLP (b) data (bootstrap of 1,000 replicates). Light blue: abandoned areas (ABN); dark blue: agricultural areas (AGR); red: degraded Caatinga (DC); green: protected Caatinga (PC).

Figure 4. Results of STRUCTURE (Pritchard et al., 2000) analyses based on SSR (a) and AFLP (b) data. K = 2 are shown. Each individual is represented by a single vertical line broken into K-colored segments with lengths proportional to each of the K-inferred clusters. ABN: abandoned areas; AGR: agricultural areas; DC: degraded Caatinga; PC: protected Caatinga. The black lines separe the land-use types.


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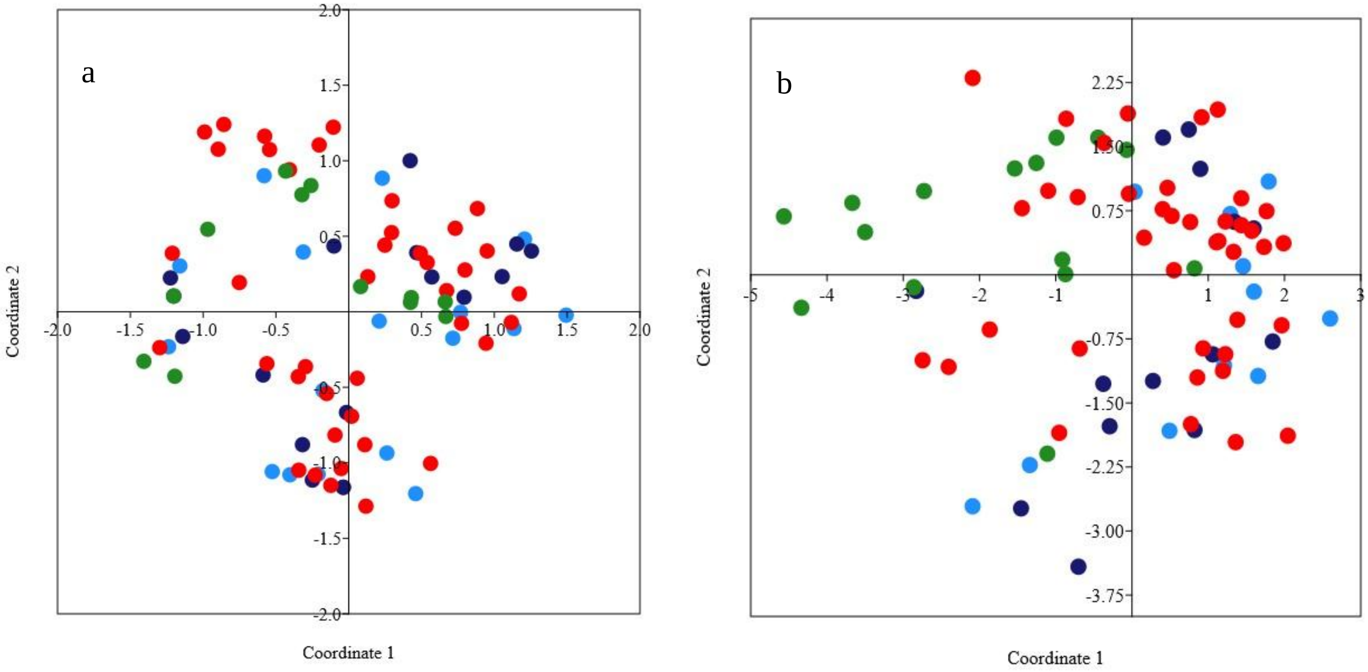
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Figure 2.

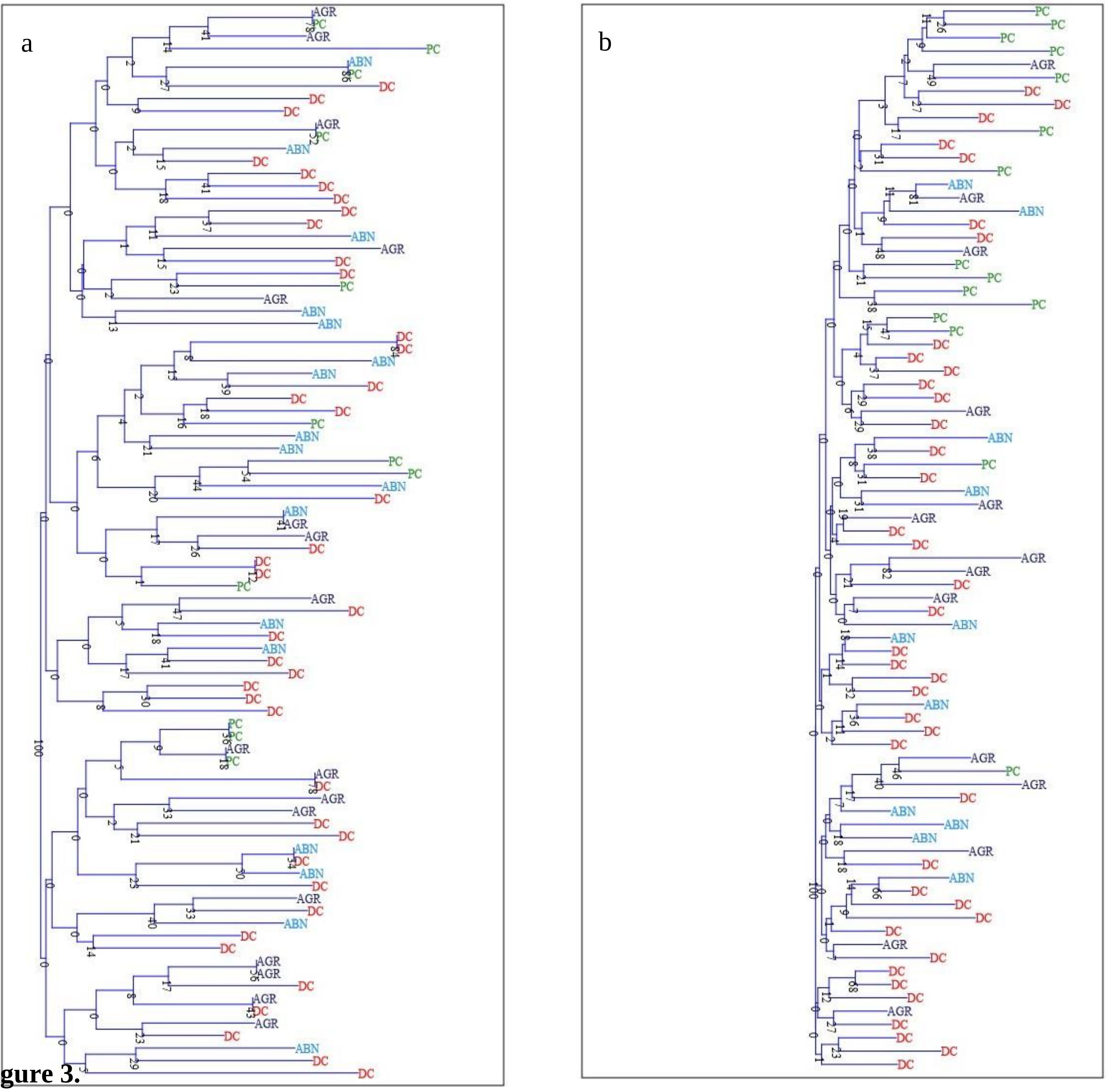
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Figure 3.

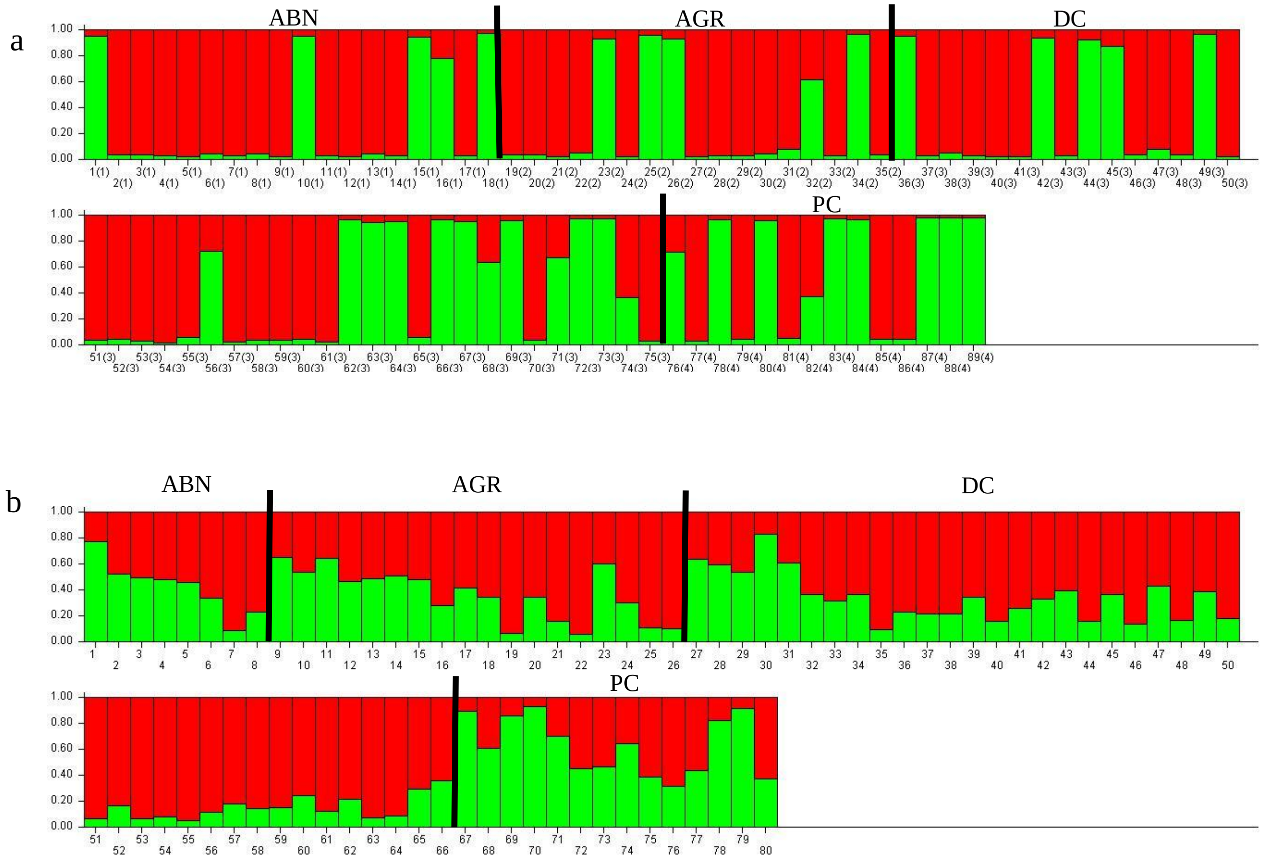
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Figure 4.

5 CONSIDERAÇÕES FINAIS

Efeitos negativos de atividades antrópicas tem sido largamente reportados na literatura. As pesquisas apontam resultados alarmantes com grande perda da biodiversidade, em especial em florestas secas tropicais e áreas de baixa produtividade. Diversos estudos também têm mostrado as respostas de espécies vegetais quanto às mudanças no uso da terra, por exemplo, queda da produção de frutos e declínio populacional. No entanto, nosso estudo é o primeiro que mostra como população de *Spondias tuberosa*, uma árvore frutífera endêmica da Caatinga, respondem às mudancas no uso da terra.

No primeiro artigo estudamos a dinâmica populacional e regeneração natural de *S. tuberosa* em uma área de floresta tropical seca em resposta aos impactos diretos e indiretos resultantes das mudanças no uso da terra. De acordo com nossos resultados, árvores mais altas e mais largas fora das áreas agrícolas, com as maiores árvores presentes na Caatinga protegida e em terras abandonadas. Ambos sementes e estabelecimento de mudas foram mais pronunciados dentro dos locais altamente artificiais irrigados estabelecidos após a construção da barragem. A irrigação e a exclusão de animais foram provavelmente os fatores mais importantes que promoveram a regeneração de árvores em áreas agrícolas. Devido à deficiente conservação de plântulas em habitats agrícolas e presença de caprinos em todos os outros tipos de uso da terra, diferenças na dinâmica populacional de *S. tuberosa* entre as classes de uso da terra não foram detectáveis.

A partir do material vegetal coletado de indivíduos de *S. tuberosa*, análises genéticas foram feitas a fim de verificar a influência dos usos da terra nas populacoes. Nossos resultados do segundo artigo mostraram que a baixa diversidade genética observada em *S. tuberosa* é devido ao nível moderado de endogamia biparental. Além disso, a alta taxa de migrantes observada sugere que as populações estudadas de *S. tuberosa* se comportam praticamente como uma única unidade genética homogênea na região estudada.

No geral, nosso estudo fornece mais evidências de que *S. tuberosa*, assim como outras espécies de Caatinga, está ameaçada pelos atuais usos da terra, que envolvem animais soltos nas florestas. Além disso, nossos resultados fornecem mais evidências para a ideia aparentemente contraditória de que muitas espécies arbóreas são mais resistentes às perturbações antrópicas porque mantêm altos níveis de conectividade genética por dispersão de pólen. No entanto, muitas espécies apresentam aumento da endogamia biparental nestes habitats perturbados. O acasalamento entre parentes próximos em conseqüência dos altos níveis de endogamia pode desempenhar um papel importante na determinação da estrutura genética dessas populações.

O estabelecimento de um plano de conservação para *S. tuberosa* é urgente, especialmente para evitar o declínio populacional e, consequentemente, mais perdas genéticas, além de garantir a viabilidade a longo prazo das gerações subsequentes de todas as populações. Indivíduos de *S. tuberosa* podem ser facilmente promovidos pela criação de locais seguros para germinação e estabelecimento de plântulas por cercamento desses indivíduos em florestas remanescentes, bem como a cessação (ou pelo menos a redução) de práticas agrícolas ao redor de árvores em áreas agrícolas. Embora a área de maior diversidade genética já esteja oficialmente protegida, ainda existe superexploração dos recursos naturais devido à falta de controle eficiente. Consequentemente, uma estratégia complementar de conservação ex situ, como o estabelecimento de um banco genético vivo possivelmente integrado em programas participativos de reprodução, é recomendável para evitar futuras perdas genéticas dessa importante espécie arbórea.

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ANEXO A - NORMAS DOS PERIÓDICOS

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AUTHOR INFORMATION PACK

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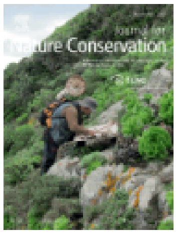

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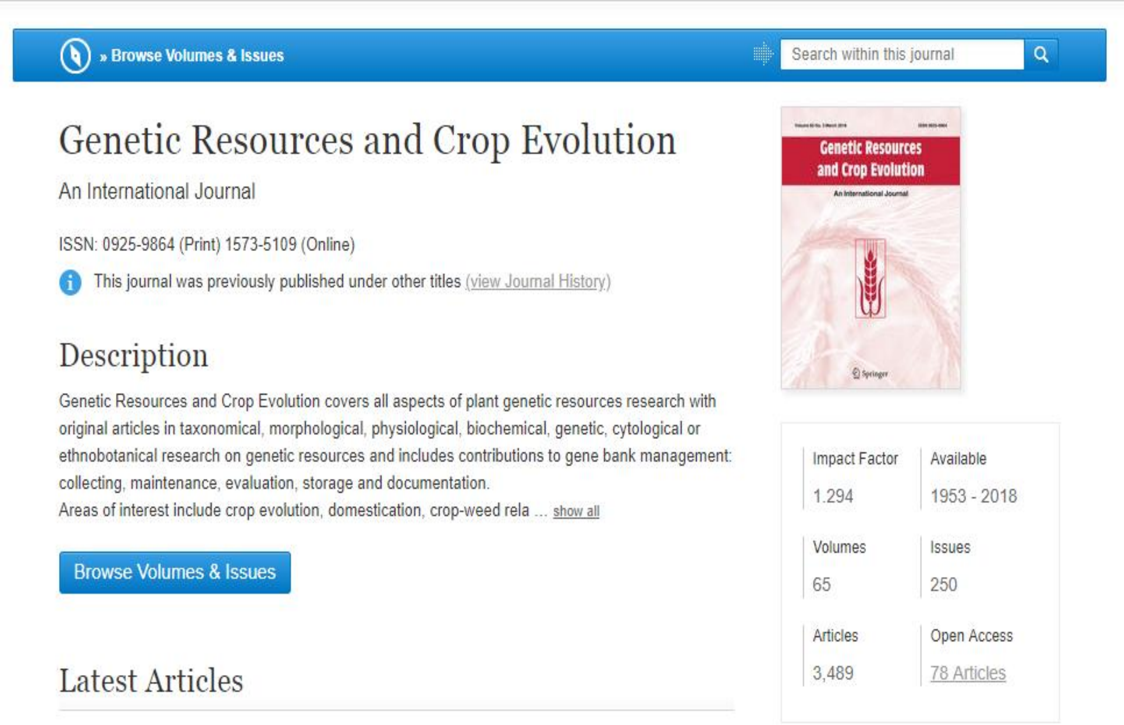

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