UNIVERSIDADE FEDERAL DE LAVRAS

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THE ROLE OF MASSIVE INFRASTRUCTURE PROJECTS ON THE SPREAD OF INVASIVE NON-NATIVE SPECIES AND ITS EFFECTS ON SEMI-ARID REGENERATION

LAVRAS – MG
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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração Ecologia e Conservação de Recursos em Paisagens Fragmentadas e Agrossistemas, para a obtenção do título de Mestre.

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THE ROLE OF MASSIVE INFRASTRUCTURE PROJECTS ON THE SPREAD OF INVASIVE NON-NATIVE SPECIES AND ITS EFFECTS ON SEMI-ARID REGENERATION

O PAPEL DE GRANDES PROJETOS DE INFRAESTRUTURA NA DISSEMINAÇÃO DE ESPÉCIES EXÓTICAS INVASORAS E SEUS EFEITOS NA REGENERAÇÃO DE ÁREAS DE SEMIÁRIDO

Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração Ecologia e Conservação de Recursos em Paisagens Fragmentadas e Agrossistemas, para a obtenção do título de Mestre.

APROVADA em 28 de junho de 2019.
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2019

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“A ciência nunca resolve um problema

sem criar pelo menos outros dez”

(George Bernard Shaw)

RESUMO

Megaprojetos de infraestrutura (MPI) estão se tornando mais comuns em todo o mundo para atender às necessidades de uma população humana crescente. Há evidências que tais infraestruturas facilitam invasões biológicas. A implantação de MPI envolve numerosas formas e mecanismos de transformação do uso da terra, como a abertura de estradas de acesso, desmatamento e intensa movimentação de terras, pessoas e maquinário que degradam o habitat e criam oportunidades para a colonização de espécies exóticas. Essa degradação pode levar ao estabelecimento de espécies exóticas invasoras, uma vez que estas frequentemente têm uma capacidade superior de colonizar locais perturbados e afetar negativamente a regeneração natural. Utilizamos um dos maiores MPI em implantação no Brasil (Projeto de Integração do rio São Francisco - PISF) para avaliar a relação entre a transformação do uso da terra imposta por esses empreendimentos e o estabelecimento e dispersão de espécies exóticas. Avaliamos se o PISF atuou como uma rota de dispersão para espécies exóticas e quais espécies exóticas podem ter se beneficiado do PISF para naturalização e invasão. Além disso, avaliamos os efeitos das principais espécies exóticas invasoras encontradas na regeneração da vegetação da área de estudo e testamos se a riqueza de espécies de locais invadidos difere entre seus respectivos invasores. Os resultados confirmam o PISF como uma rota de dispersão de espécies exóticas. Nos monitoramentos foram registradas 21 espécies de plantas exóticas na área de implantação (AI) do PISF, estabelecidas em vários habitats artificiais e naturais e amplamente distribuídas pela área de estudo. Onze anos após o total desmatamento da AI, 92,28% de sua extensão (383.88 km) possuem populações de plantas exóticas. *Calotropis procera*, *Nicotiana glauca* e *Prosopis juliflora* foram as espécies exóticas mais amplamente distribuídas no PISF. A relação entre as transformações do uso da terra e a ampla distribuição das espécies exóticas invasoras no PISF evidencia que megaprojetos de infraestrutura podem ser corredores para a dispersão de espécies exóticas. Locais invadidos apresentaram riqueza de espécies vegetais significativamente menor do que a comunidade nativa adjacente, e existem diferenças na riqueza de espécies vegetais entre os locais dominados por cada espécie exótica invasora. A invasão por espécies exóticas foi a principal causa da diferença entre comunidades invadidas e não invadidas. A identidade da espécie invasora apenas minoritariamente explica essa diferença. Além disso, áreas invadidas por *C. procera* tiveram diferenças significativas em relação àquelas dominadas pelas outras duas invasoras. Em contraste, *N. glauca* e *P. juliflora* não diferiram entre si. A maior riqueza média e absoluta em locais dominados por *C. procera* indica maior tolerância à coocorrência de espécies nativas.

PALAVRAS-CHAVE: Espécies invasoras. Distúrbio antropogênico. Invasão biológica. Conservação. Impacto ambiental. Plantas exóticas. Riqueza de espécies.

ABSTRACT

Massive infrastructure projects (MIP) are becoming more common around the world to meet the needs of a growing human population. There is evidence of such structures facilitating biological invasions. The implementation of MIP involves numerous forms and mechanisms of land-use transformation, such as opening of access roads, deforestation, and intense movement of land, people and machinery that degrades the habitat and creates opportunities for colonization of new species. This degradation could lead to the establishment of invasive non-native species, considering they often have the ability to colonize disturbed sites, and to negatively affect natural regeneration. In this study, we used one of the largest MIP under development in Brazil (Projeto de Integração do rio São Francisco - PISF) to assess the relationship between land-use transformation imposed by MIP and the establishment and spread of non-native species. We determined if PISF acted as a dispersal route for non-native species and which non-native species may be benefiting from PISF to proliferate. Further, we verified the effects of the main invaders on the plant regeneration of the study area, and tested if the plant richness of the invaded sites differed among invaders. Our results confirmed PISF as a route for the dispersal of non-native species. Monitoring surveys recorded 21 non-native plant species in PISF's deployment area (DA). Species were established in several artificial and natural habitats, and widespread across most of the study area. Eleven years after the DA was completely deforested, 92.3% of its extension had non-native plant populations. *Calotropis procera*, *Nicotiana glauca*, and *Prosopis juliflora* were the most relevant non-native species in PISF. The relationship between land-use transformations and the widespread distribution of invasive species demonstrate that MIP can act as corridors for the spread of these species. We found that invaded sites presented significantly lower plant richness than non-invaded sites and there were differences in richness among invasive species. The invasion of non-native species was the main factor for the difference between invaded and non-invaded communities. The identity of the invasive species explained only a small part of this difference. Also, *C. procera* showed significant differences in relation to both of other invaders. In contrast, *N. glauca* and *P. juliflora* did not differ each other. The highest mean and absolute richness in sites dominated by *C. procera* indicates greater tolerance to co-occurrence of native species.

KEYWORDS: Invasive species. Anthropogenic disturbance. Biological invasion.
Environmental impact. Non-native plants. Species richness.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

Invasões biológicas representam uma grande ameaça tanto à biodiversidade quanto às atividades humanas (SIMBERLOFF et al., 2013). As redes de comércio globais tornam o mundo mais conectado através do transporte de cargas e pessoas. Essa conectividade é uma das principais responsáveis por derrubar barreiras biogeográficas e ampliar a distribuição de espécies invasoras no planeta (CAPINHA et al., 2015; CHAPMAN et al., 2017). Quando uma espécie é introduzida em uma área fora de sua distribuição original, com auxílio (intencional ou não) de atividades humanas, é chamada de espécie exótica (RICHARDSON et al., 2000). Uma vez que a espécie coloniza o local de introdução e se dispersa, produzindo populações autossustentáveis também em áreas mais distantes, ela se torna uma espécie invasora (BLACKBURN et al., 2011; RICHARDSON et al., 2000) e pode causar efeitos socioeconômicos e ambientais negativos.

Por isso, o Plano Estratégico para Biodiversidade (2011-2020) da Convenção sobre a Diversidade Biológica (CDB) traz 20 metas que incluem ações para tentar reduzir a perda de biodiversidade no planeta até 2020 (CDB, 2014a). As espécies exóticas invasoras são especificamente citadas na Meta 09: “Até 2020, as espécies exóticas invasoras e as rotas de introdução/dispersão serão identificadas e priorizadas, as espécies prioritárias serão controladas ou erradicadas, e existem medidas para gerenciar os caminhos para evitar sua introdução e estabelecimento”. Atualmente, a CDB reconhece seis categorias de rotas para introdução de espécies exóticas, das quais duas estão ligadas à dispersão destas no ambiente: “corredores” (introdução não intencional via infraestruturas humanas ligando regiões não conectadas anteriormente) e “natural” (dispersão natural de espécies exóticas introduzidas por atividades humanas) (CDB, 2014b; HULME, P. E. et al., 2008).

Grandes obras de infraestrutura (posteriormente denominadas MIP “Massive Infrastructure Projects”) como rodovias, ferrovias, pontes, túneis, canais, estruturas para suprimento de água e energia, são essenciais para o efetivo desenvolvimento econômico de regiões, países e continentes. Porém elas têm sido causas importantes de introdução e disseminação de espécies exóticas e invasoras ao redor do mundo (ESSL et al., 2015). Existem evidências de que este tipo de empreendimento facilita o estabelecimento e atua como corredor para a dispersão de espécies exóticas (BERGQUIST et al., 2007; HULME, PHILIP E., 2009; LIU et al., 2019; VON DER LIPPE; KOWARIK, 2007). A implantação de

MIP envolve inúmeras formas e mecanismos de transformação no uso da terra, como abertura de estradas, supressão vegetal e intensa movimentação de solo, pessoas e maquinário. Ao contrário da dispersão natural clássica, que ocorre gradualmente, a instalação destas estruturas abre uma grande área com habitats potencialmente adequados, que podem ser colonizados rapidamente (WILSON et al., 2009). Tais processos fornecem mecanismos de transporte para sementes e outras partes reprodutivas das plantas através do deslocamento de solo, na lama dos pneus e na turbulência causada pelo trânsito de veículos (DAVIES; SHELEY, 2007; GELBARD; BELNAP, 2003; VON DER LIPPE; KOWARIK, 2007).

No entanto, essas estruturas também são vulneráveis aos impactos provocados por espécies invasoras, que podem causar danos estruturais e até comprometer o uso e serviços prestados por elas (BOOY et al., 2017). Somente para o ano de 2010, em uma estimativa conservadora, espécies invasoras tiveram um custo de aproximadamente R$ 840 milhões em danos diretos à infraestrutura no Reino Unido, estes custos são direcionados à prevenção, controle, erradicação das espécies e perdas econômicas por mau funcionamento do empreendimento (BOOY et al., 2017). Além de prejuízos econômicos, espécies invasoras podem ser responsáveis por impactos ambientais como redução da abundância e diversidade, alteração de processos ecossistêmicos como a ciclagem de nutrientes (VILÀ et al., 2011), diminuição da regeneração natural de espécies nativas (FLORY; CLAY, 2010), entre outros.

A crescente demanda humana por materiais e serviços estimula a instalação de MIP ao redor do planeta. Diversos exemplos são encontrados na maioria dos continentes, como: túneis para conectar ilhas isoladas (p.ex., Túnel do Canal, no Reino Unido; Túnel Seikan, no Japão); transferência de água entre bacias hidrográficas (p. ex., Projeto San Juan-Chama, nos EUA; Projeto de Água das Terras Altas de Lesoto, no sudeste africano (tradução livre)); canais de navegação (p. ex., Canal do Panamá, na América Central, Canal de Suez, no Egito); redes de comércio (p. ex., Iniciativa Cinturão Rodoviário entre a China, Eurásia e Europa), desenvolvimento energético (p. ex., Bacias de Williston e Wyoming, EUA). No Brasil, um dos maiores empreendimentos de infraestrutura atualmente em implantação/operação é o Projeto de Integração do Rio São Francisco com as Bacias do Nordeste Setentrional (PISF). O PISF é um empreendimento de transferência de água entre bacias hidrográficas, totalmente inserido no bioma Caatinga. Basicamente, é composto por dois eixos independentes (Leste e Norte) que compreendem nossa área de estudo. Cada eixo contém uma série de estações de bombeamento, canais de concreto, túneis, aquedutos e reservatórios. Nosso estudo utilizou as margens dos canais - locais mais afetados pelas obras – para verificar se o PISF age como rota de dispersão para espécies exóticas e a relação entre as mudanças no uso da terra impostas pelo projeto e o estabelecimento dessas espécies (Capítulo 1).

Além disso, para a instalação do PISF, a vegetação natural foi totalmente suprimida nos locais de obra. Por se tratar de uma região semiárida (ANDRADE et al., 2017) o crescimento e o recrutamento de novas plantas são geralmente mais lentos (PRIOR et al., 2011). Em adição, danos causados em ambientes naturais aumentam a disponibilidade de recursos e criam oportunidade para a colonização de novas espécies (DAVIS; GRIME; THOMPSON, 2000). Com isso, plantas de crescimento rápido e alta eficiência no uso dos recursos, como as espécies exóticas invasoras (FUNK; VITOUSEK, 2007; GRAEBNER; CALLAWAY; MONTESINOS, 2012; MATZEK, 2011; ZENNI; CUNHA; SENA, 2016) são mais prováveis de colonizarem habitats pós distúrbio (CATFORD et al., 2012). O nível de impacto de cada espécie invasora pode variar de acordo com as características individuais (HEJDA; PYŠEK; JAROŠÍK, 2009). Para verificar o efeito da invasão de plantas na regeneração em áreas de semiárido verificamos a diversidade de áreas dominadas por três espécies exóticas invasoras (Calotropis procera, Nicotiana glauca e Prosopis juliflora) e da comunidade nativa adjacente a elas, também, comparamos a riqueza de áreas dominadas por cada uma das espécies selecionadas para o estudo (Capítulo 2).

2 CONSIDERAÇÕES FINAIS

O processo de instalação de megaprojetos de infraestrutura (MPI) impõe mudanças no uso do solo através de diversos mecanismos, como supressão da vegetação, abertura de estradas de acesso, movimentação de terra, máquinas, pessoas e equipamentos, trânsito intenso de veículos e criação de locais de despejo de rejeitos. Estas mudanças criam novos habitats e novas oportunidades para colonização de espécies diferentes da flora nativa da região. Portanto, os MPI atuam como facilitador do estabelecimento de espécies exóticas e como rotas para dispersão destas no ambiente. Espécies de plantas exóticas invasoras geralmente aproveitam os recursos disponíveis de forma mais eficiente do que as nativas. Assim, a combinação entre as alterações provocadas por MPI e características intrínsecas de espécies invasoras aumenta o risco de invasões biológicas.

Além disso, identificamos que o nível de intervenção das obras no ambiente pode influenciar no aumento ou retração da distribuição das espécies na área. Durante a fase de instalação do empreendimento, os mesmos processos que facilitam o estabelecimento das espécies exóticas podem funcionar como barreiras à expansão destas nas áreas de implantação das obras. As populações já estabelecidas criam uma alta pressão de propágulos para colonização de novas áreas modificadas pela construção. Essa pressão é periodicamente aliviada por serviços de manutenção das estruturas, manejo ambiental e pela constante movimentação de solo que suprimem e/ou soterram as populações. No entanto, na fase de operação dos empreendimentos, quando o nível de intervenção no ambiente é drasticamente reduzido, as espécies exóticas ficam livres para relançar propágulos para áreas ainda não colonizadas e germinar os bancos de sementes que estavam dormentes no solo.

As espécies de plantas invasoras bem estabelecidas no ambiente modificado podem atrapalhar a regeneração natural por espécies nativas. Constatamos que a riqueza de espécies em locais com invasão é significativamente menor quando comparada com áreas próximas de vegetação nativa, considerando uma situação de número de indivíduos semelhante entre as duas áreas. Também verificamos que a identidade da espécie invasora importa para a regeneração natural. Ou seja, algumas espécies invasoras podem ser mais tolerantes a coocorrência de espécies nativas, enquanto outras são mais restritivas e permitem que menos espécies ocorram em conjunto. Nestes casos, é maior a possibilidade de monodominância pela espécie invasora.

Esses resultados trazem fundamentos importantes para subsidiar a legislação ambiental entorno destes empreendimentos. Com isso, recomendamos que a possibilidade de invasões biológicas oriundas ou facilitadas por MPIs devem constar nas avaliações de risco ambiental das diferentes fases destes projetos em todo o mundo. Medidas de prevenção à introdução e estabelecimento de espécies exóticas são indicadas a compor a fase planejamento dos projetos, enquanto o constante monitoramento, controle e manejo das espécies, assim como esforços de restauração ecológica ativa devem estar previstos durante a instalação e operação dos empreendimentos.

REFERÊNCIAS

ANDRADE, E. M. *et al.* Water as Capital and Its Uses in the Caatinga. In: DA SILVA, J. M. C.; LEAL, I. R.; TABARELLI, M. (Org.). ***Caatinga: The Largest Tropical Dry Forest Region in South America***. Cham: Springer International Publishing, 2017. p. 281–302.

BERGQUIST, E. *et al.* Invasive species and coal bed methane development in the Powder

River Basin, **Wyoming.** ***Environmental Monitoring and Assessment***, v. 128, p. 381–394, 2007.

BLACKBURN, T. M. *et al.* A proposed unified framework for biological invasions. ***Trends in Ecology and Evolution***, v. 26, n. 7, p. 333–339, 2011.

BOOY, O. *et al.* Impact of Biological Invasions on Infrastructure. ***Impact of Biological Invasions on Ecosystem Services***. Cham: Springer International Publishing, 2017. p. 235–247.

CAPINHA, C. *et al.* The dispersal of alien species redefines biogeography in the Anthropocene. ***Science***, v. 348, p. 1–5, 2015.

CATFORD, J. A. *et al.* The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. ***Perspectives in Plant Ecology, Evolution and Systematics***, v. 14, n. 3, p. 231–241, 2012.

CDB. *Global Biodiversity Outlook 4*. Montréal: **Secretariat of the Convention on Biological Diversity**, 2014a.

CDB. Pathways of Introduction of Invasive Species, Their Prioritization and Management. *UNEP/CBD/SBSTTA/18/9/Add.1*. Montréal: **Secretariat of the Convention on Biological Diversity**, 2014b.

CHAPMAN, D. *et al.* Global trade networks determine the distribution of invasive non-native species. ***Global Ecology and Biogeography***, v. 26, n. 8, p. 907–917, 2017.

DAVIES, K. W.; SHELEY, R. L. A Conceptual Framework for Preventing the Spatial Dispersal of Invasive Plants. ***Weed Science***, v. 55, p. 178–184, 2007.

DAVIS, M. A.; GRIME, J. P.; THOMPSON, K. Fluctuating resources in plant communities: A general theory of invasibility. ***Journal of Ecology***, v. 88, n. 3, p. 528–534, 2000.

ESSL, F. *et al.* Crossing Frontiers in Tackling Pathways of Biological Invasions. ***BioScience***, v. 65, n. 8, p. 769–782, 2015.

FLORY, S. L.; CLAY, K.. Non-native grass invasion suppresses forest succession. ***Oecologia***, v. 164, n. 4, p. 1029–1038, 2010.

FUNK, J. L.; VITOUSEK, P. M. Resource-use efficiency and plant invasion in low-resource systems. ***Nature***, v. 446, n. 7139, p. 1079–1081, 2007.

GELBARD, J. L; BELNAP, J. Roads as Conduits for Exotic Plant Invasions in a Semiarid Landscape. ***Conservation Biology***, v. 17, n. 2, p. 420–432, 2003.

GRAEBNER, R. C.; CALLAWAY, R. M.; MONTESINOS, D. Invasive species grows faster, competes better, and shows greater evolution toward increased seed size and growth than exotic non-invasive congeners. ***Plant Ecology***, v. 213, n. 4, p. 545–553, 2012.

HEJDA, M.; PYŠEK, P.; JAROŠÍK, V. Impact of invasive plants on the species richness, diversity and composition of invaded communities. ***Journal of Ecology***, v. 97, n. 3, p. 393–403, 2009.

HULME, P. E. *et al.* Grasping at the routes of biological invasions: A framework for integrating pathways into policy. ***Journal of Applied Ecology***, v. 45, n. 2, p. 403–414, 2008.

HULME, P. E. Trade, transport and trouble: Managing invasive species pathways in an era of globalization. ***Journal of Applied Ecology***, v. 46, n. 1, p. 10–18, 2009.

LIU, X. *et al.* Risks of biological invasion on the Belt and Road. ***Current Biology***, v. 29, p. 1–7, 2019.

MATZEK, V. Superior performance and nutrient-use efficiency of invasive plants over non-invasive congeners in a resource-limited environment. ***Biological Invasions***, v. 13, n. 12, p. 3005–3014, 2011.

PRIOR, L. D. *et al.* Population structures of the widespread Australian conifer Callitris columellaris are a bio-indicator of continental environmental change. ***Forest Ecology and Management***, v. 262, n. 2, p. 252–262, 2011.

RICHARDSON, D. M. *et al.* Naturalization and invasion of alien plants : concepts and definitions. ***Diversity and Distributions***, v. 6, p. 93–107, 2000.

SIMBERLOFF, D. *et al.* Impacts of biological invasions: What's what and the way forward. ***Trends in Ecology and Evolution***, v. 28, n. 1, p. 58–66, 2013.

VILÀ, M. *et al.* Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. ***Ecology Letters***, v. 14, n. 7, p. 702–708, 2011.

VON DER LIPPE, M.; KOWARIK, I. Long-distance dispersal of plants by vehicles as a driver of plant invasions. ***Conservation Biology***, v. 21, n. 4, p. 986–996, 2007.

WILSON, J. R.U. *et al.* Something in the way you move: dispersal pathways affect invasion success. ***Trends in Ecology and Evolution***, v. 24, n. 3, p. 136–144, 2009.

ZENNI, R. D.; CUNHA, W. L.; SENA, G. Rapid increase in growth and productivity can aid invasions by a non-native tree. ***AoB Plants***, v. 8, p. plw048, 2016.

SEGUNDA PARTE – MANUSCRITOS

MANUSCRITO 1

MASSIVE INFRASTRUCTURE PROJECTS AS PATHWAYS FOR THE SPREAD OF INVASIVE NON-NATIVE SPECIES – THE CASE STUDY OF THE INTEGRATION OF THE SÃO FRANCISCO RIVER PROJECT

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Highlights

- MIP are a pathway for the spread of non-native plants in natural environments
- 92.3% of the PISF extension was occupied by non-native plant populations
- Reduced human intervention tend to increase the presence of non-native plants after invasion
- 21 non-native plant species (eight invasive) were recorded in the PISF
- Long-term monitoring, control and active restoration are recommended

Abstract

Massive infrastructure projects (MIP) are becoming more common around the world to meet the needs of a growing human population. There is evidence of such structures facilitating biological invasions. However, direct effects of MIP on the spread of invasive species are still unclear. Here we used the largest MIP under development in Brazil (PISF) to assess the relationship between MIP and spread of non-native species. Between 2015 and 2018, 86 sampling points were monitored along the entire extension of PISF where non-native plant presences were recorded. Additionally, we drove along the 416 km of the study area to determine invasion status for each non-native population. Our results confirmed PISF as a route for dispersal of non-native species. Monitoring surveys recorded 21 non-native plant species on PISF's deployment area (DA), established in several artificial and natural habitats, widespread for almost whole study area. Eleven years after DA was completely deforested, 92.3% of its extension had non-native plant populations. *Calotropis procera*, *Nicotiana glauca* and *Prosopis juliflora* were the most relevant non-native species on PISF. Relationship between land-use transformations and widespread distribution of invasive species evidences that MIP can act as a corridor for spread of this species. Continuous monitoring, control of invasive species and active restoration of invaded sites are recommended for all MIP.

Keywords

Biological invasion, non-native species, anthropogenic disturbance, conservation, invasive spread, non-native plants

Introduction

Increasing rates of biological invasions on the planet are closely related to the intensification of human activities (Hulme, 2009). Many significant effects on native species have been associated with the introduction and invasion of non-native species, such as changes in behavior patterns, genetic composition, richness and abundance, phylogenetic and taxonomic diversity, trophic networks, ecosystem productivity, and nutrient cycling (Brooks et al., 2004; Kenis et al., 2009; Pyšek et al., 2012; Ricciardi et al., 2013; Suarez and Tsutsui, 2008; Vilà et al., 2011; Winter et al., 2009). It is possible that, throughout the world, there are no ecosystems not invaded by some non-native species (Van Kleunen et al., 2010; Wardle et al., 2011).

Non-native species tend to become invasive when there is high propagule pressure (i.e. number, frequency and genetic variability of propagules) (Simberloff, 2009), when introduced species are adapted to the introduction site (Zenni et al., 2016, 2014) and/or when the recipient environment presents low biotic resistance (Fridley et al., 2007; Levine et al., 2004). Propagule pressure, establishment and abundance of non-native species are closely linked to human activities (Hulme, 2009; Vilà and Pujadas, 2001; Zimmermann et al., 2014). Establishment and spread of introduced species are strongly related to changes in patterns of land use (Hobbs, 2000).

One of these changes is caused by the development of massive infrastructure projects (MIP). These projects are built all around the world to meet the rising needs of a growing human population, such as tunnels to connect isolated islands (i.e. Channel tunnel, United Kingdom; Seikan tunnel, Japan), interbasin water transfers (i.e. Lesotho Highlands Water Project, Southern Africa; San Juan-Chama Project, USA), canal navigation (i.e. Suez and Panama Canals, Egypt and Panama, respectively), trade network (i.e. Belt and Road Initiative, China) and energy development (i.e. Williston and Wyoming Basins, USA) and presents evidences of these structures facilitating biological invasions (Bergquist et al., 2007; Hulme, 2015; Liu et al., 2019; Preston, 2015). In fact, although there is evidence of this facilitation, the direct effect of MIP on the spread of invasive species is still uncertain (Hulme, 2015) and just few studies have been addressed to respond to this issue (i.e. Bergquist et al., 2007; Nielsen et al., 2011; Preston, 2015; von der Lippe and Kowarik, 2007).

The implementation of MIP involves numerous forms and mechanisms of land-use transformation, such as opening of access roads, deforestation, and intense movement of land, people and machinery that create new habitats on its deployment area. Increased presence and abundance of non-native plant species have been associated with this type of human infrastructure (Preston, 2015), which provides a transport mechanism for seeds and plants parts on tires/mud and air turbulence by passing vehicles (Davies and Sheley, 2007; Gelbard and Belnap, 2003; von der Lippe and Kowarik, 2007). As a result, MIP can act as a pathway facilitating the introduction and dispersal of non-native species in natural environments.

In Brazil, one of the largest MIP currently under development is the Integration of the São Francisco River Project (PISF). PISF is a water basin transfer that aims at facilitating human access to freshwater in one of the driest regions of the country; it is fully inserted in the Caatinga biome, the Brazilian steppe savannah. This ecological region covers approximately 10% of the Brazilian territory (IBGE, 2004), considered as a seasonally dry tropical forest (SDTF) (Pennington et al., 2009), where rainfall regime averages 700 mm/year and most of the precipitation occurs in a single month (Queiroz et al., 2017). The Caatinga presents high biological and environmental richness and about 23% of its flora is endemic (Queiroz et al., 2017). It is estimated that only 54% of the original Caatinga remains, and despite of this scenario, only 7.5% is within protected areas being one of the least protected biomes in Brazil (ICMBio, 2018). In the whole Caatinga, 205 non-native plant species have been identified so far (Almeida et al., 2014), 155 of which were naturalized (Zenni, 2015) and 20 were considered invasive (Almeida et al., 2014).

Despite of the low level of environmental protection, high biological diversity, robust occurrence records of non-native species, and the existence of important vectors for the species introduction (i.e. PISF and the Transnordestina railway), Caatinga is the object of only 5% of the studies on biological invasions in Brazil (Frehse et al., 2016). Furthermore, there are no studies in Brazil related to the introduction of non-native species via terrestrial MIP (Frehse et al., 2016).

Therefore, there is currently a unique opportunity to study processes of colonization of non-native and invasive non-native species in time to elaborate and propose measures for prevention and mitigation of possible ecological impacts caused by invasive non-native species that benefit from MIP to proliferate. Here, we aimed at assessing (i) if PISF acted as a dispersal route for non-native species, (ii) which non-native species may be benefiting from PISF, (iii) the relationship between land-use transformation imposed by MIP and establishment of non-native species, and (iv) the effects of different levels of anthropogenic intervention on the spread of non-native species.

Material and methods

Study area

PISF is a linear infrastructure project composed of two independent canals, East and North (Fig. 1). Each canal contains a series of pumping stations, concrete canals, tunnels, aqueducts, and dams in which the water flows by pumps and gravity. Currently, the canals cross the States of Pernambuco (PE), Ceará (CE) and Paraíba (PB), in northeast Brazil. For both canals, water is initially pumped from the São Francisco River. The North extends from the São Francisco River in Cabrobó (PE) for 260 km to Cajazeiras (PB), while the East canal extends from the São Francisco River in Floresta (PE) for 217 km to Monteiro (PB).

Our study area corresponds to the stretches of canals where there have been interventions until 2018, which extends 211 km from the São Francisco River for the North canal and 205 km from the São Francisco River for the East canal. Our sampling is delimited by the Deployment Area (DA) of the canals, which corresponds to a marginal strip 100 m wide on each side of the canal over its entire length and the edge of some structures as dams and pumping stations. Together, the study area totals 416 km in length and 83.2 km^2 in area. DA was initially cleared of vegetation prior to the construction of the canal in 2007 (ANA, 2009), and its limits are on one side the edge of the canal and on the other side the exact starting point of native vegetation.

In December 2018, after eleven years, the Brazilian government announced the end of the major structural work on the canals. From the second half of 2017 until the second half of 2018 the East canal operated in the structural testing phase. After an environmental parameters assessment (i.e. water quality, fauna and flora conservation and water supply) the stretch corresponding to the East canal received the Operation License from IBAMA (Instituto Brasileiro de Meio Ambiente e Recursos Naturais Renováveis), the Brazilian environmental licensing agency, in the second half of 2018. Currently, there are only occasional interventions in the DA for maintenance, repairs in the structures and others services throughout the canals. Thus, the intensity of intervention by people and machinery was dramatically reduced in the stretches of canal included in our study.

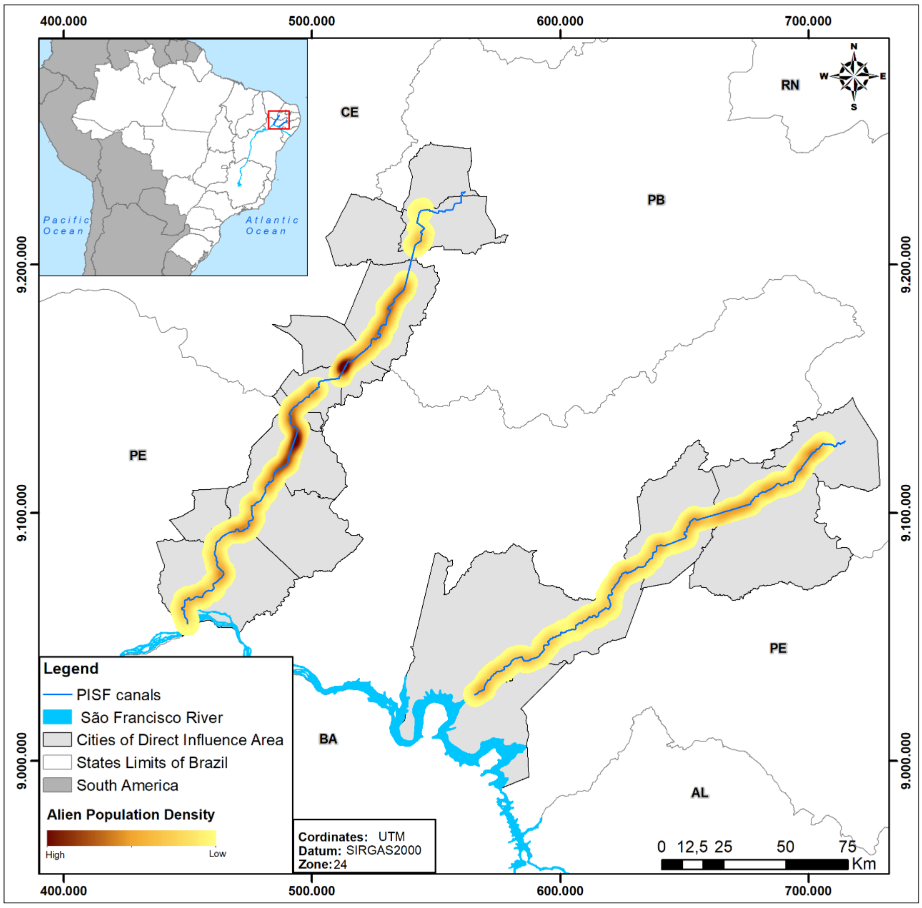

Figure 1. Kernel Map showing the non-native populations density at PISF-DA. Darker areas are the ones with greatest non-native density populations. Cities of Direct Influence Area are those that contain stretches of the canals within its boundaries. To date, PISF interventions go through the Brazilian States of Ceará (CE), Paraíba (PB) and Pernambuco (PE).

Non-native plant presence

Since 2015, we conducted monitoring surveys twice a year in the DA to identify and record the presence of non-native species along the canals. Here, we report the results from six surveys undertaken on May-June/2015, February-March/2016, September-October/2016, January/2017, May/2017, and May-June/2018. To assess the non-native plant colonization along the DA we first established sampling points every 5 km from the São Francisco River until the end of the existing canal (211 and 205 km away depending on the canal). We had 44 sampling points on the North canal and 42 sampling points on the East canal. The sampling points were adjacent to the edge of the canal. The sampling points were pre-selected using PISF's geographical information system. The geographic coordinates of each point were uploaded to a handheld GPS unit which was used to locate the sampling site. At each sampling point we split the visual field into four 90°quadrants and all non-native species visible on each quadrant were recorded. There were no minimum or maximum distances from the sampling point for species to be included. The species had to be visible from the sampling point and had to be located inside the DA (e.g. not in the native Caatinga outside DA). Species not identified in the field were collected for identification by botanists of the NEMA team at UNIVASF.

To assess if the non-native species' presence and distribution were related to the PISF canals' infrastructure, we built two linear models for each non-native species found using different subsets of the data. The number of sampling points on which the species were found was the dependent variable and the surveys were the independent variable. The first set of models used only data from the first five surveys, when there was intense human and machinery movement throughout the DA, and a second set of models used data from all surveys. The last survey was performed after the heavy construction work on a large part of the study area had ended. Next, we calculated the differences between slopes ($\Delta\beta$) from the first and the second set of models for each species to evaluate changes in occurrence trends per species with and without heavy human intervention. Finally, we did a Chow test between the two linear models built for each species to verify if the models were statistically different. Significant relationships at $\alpha = 0.05$ with positive slopes ($\Delta\beta > 0$) indicate that with less human intervention, species tend to increase their presence, whereas significant relationships at $\alpha = 0.05$ with negative slopes ($\Delta\beta < 0$) indicate that with less human intervention, species tend to reduce their presence along the canals. Only species recorded during three or more surveys were used in the assessment.

Non-native species population status

To determine if non-native species present along the PISF were casual, naturalized, or invasive (*sensu* Blackburn et al., 2011; Richardson et al., 2000), we drove along the 416 km of the study area stopping every time a population of a non-native plant species was found inside the DA. Sections above tunnels were not sampled owing to the lack of access. Also, grasses were excluded from the invasion status assessment owing to their absence or difficulty of detection during the dry months of the year. At each population, we recorded its linear extension along the canal using a handheld GPS marking where each population started and ended, we counted the number of plants, and counted the number of plants producing flowers and/or fruits. We considered that two populations were different if the gap between plants were greater than 500 m.

Each population was classified as casual, naturalized or invasive following the criteria established by Richardson et al., 2000. Populations with one to 10 reproductive individuals and spread distance below 100 m were considered casuals; Populations with 11 to 100 reproductive individuals were considered naturalized. Assuming that the DA was totally deforested at the beginning of the construction, populations that achieved more than 100 m of spread and had more than 100 reproductive individuals were classified as invasive. Data used for the invasion status reported here were collected in June, 2018.

To show the distribution of the populations and the occupation intensity of non-native plant populations along the PISF we built a Kernel Density Map (Fig. 1). This map is an estimation and shows the intensity of a phenomenon in a region. In this case, Kernel density was calculated using polylines representing the extent of each population within the Deployment Area, considering for each one a different weight according to its invasion status (casual populations weighed = 1, naturalized weighed = 2 and invasive weighed = 3). This intensity is calculated from the number of polylines (populations) and the product of the polylines size (in meters) with the weight assigned to it. Thus, darker areas of the map are the ones with most populations, being balanced by their invasion status. We used a 200 m cell size (to match the size of the DA) and a 5,000 m radius size (corresponding to the size of the DAA), the unit was "Square Map Units", once our data are categorical. Kernel density estimation was made with ArcMap 10.2 (ESRI) using the Kernel Density tool.

Results

We recorded a total of 21 non-native plant species, distributed in 19 genera and 10 families (Appendix 1). The most representative family was Poaceae with 10 species (47% of the species), and other families were all represented by one or two species. *Azadirachta indica*, *Cryptostegia grandiflora*, and *Urochloa mollis* occurred only in the North canal, whereas *Eragrostis ciliaris* occurred only in the East canal. Life forms of non-native species varied among grasses (57%), shrubs (24%), trees (14%) and liana (5%). Eleven species were found locally as isolated plants or in very low numbers. Two species were found to had naturalized populations and eight species had invasive populations. Only 7.7% of the assessed area was free of non-native and invasive plant populations. Because of this, PISF can be considered a pathway for the spread of non-native species.

Non-native plant presence

The most widespread species along the PISF canals were *Prosopis juliflora*, *Nicotiana glauca,* and *Calotropis procera*. Throughout the surveys, these species were present on average in 62% (54±4 sampling points), 59% (51±7 sampling points) and 47% (40±7 sampling points) of the sampling points, respectively. The number of records per sampled point ranged from zero to 12 species with an average of four species per point in both canals. In the last survey (May-June/2018) *Dactyloctenium aegyptium* (Poaceae) had a sudden increase in distribution, being recorded in 74 out of the 86 sampling points (86%). Before that, *D. aegyptium* was rarely detected (28 ± 28 sampling points). This is the largest number of records for a single survey in our historical series. Seven species were recorded in all surveys (*Calotropis procera*, *Dactyloctenium aegyptium, Melinis repens*, *Momordica charantia*, *Nicotiana glauca*, *Prosopis juliflora*, and *Ricinus communis*). Grasses showed greater variation in number of sampling points through the surveys than shrubs and trees (Fig. 2). The comparisons of pre- and post-heavy construction intervention did not show statistically differences between the two linear models for all but one species ($p > 0.05$). *Momordica charantia* showed a negative trend ($\Delta\beta = - 0.043$). Also, *Eragrostis tenella* was the species that showed the greatest spread after heavy construction interventions ceased ($\Delta\beta = 4.628$) (Appendix 1). Five species were recorded for the first time during the last survey (May/2018), when intervention levels in the PISF were reduced: *Echinochloa colona* (Poaceae, two sampling points in East canal and 10 sampling points in North canal), *Eragrostis ciliaris* (Poaceae, five sampling points in East canal), *Urochloa mollis* (Poaceae, five sampling points in North canal), *Azadirachta indica* (Meliaceae, one sampling point in North canal), and *Mangifera indica* (Anacardiaceae, one sampling point in North canal).

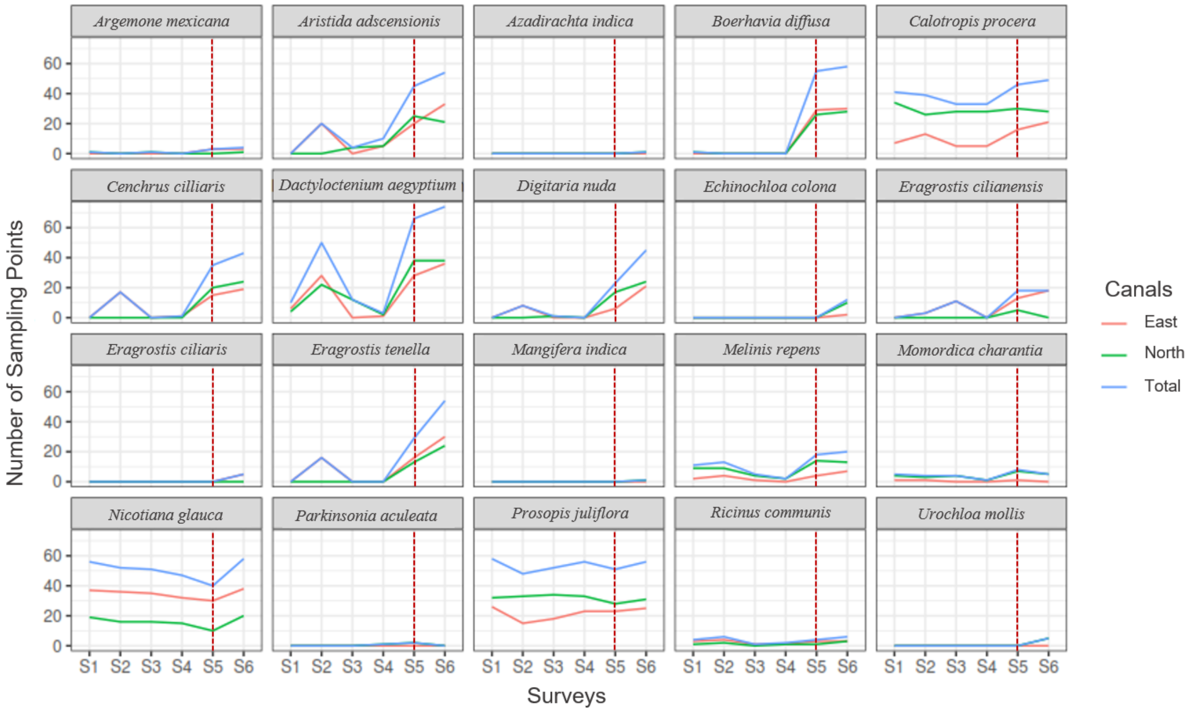

Figure 2. Number of sampling points that the species were recorded in each survey (S1, S2, S3, S4, S5 and S6), for the East and North canals and total record. The red dash marks the periods with high (S1, S2, S3, S4, S5) and low (S6) anthropogenic intervention on the environment.

Table 1. Linear models of non-native species distribution considering two temporal intervals (2015-2017: higher intervention level (S1 to S5); and 2015-2019: higher and lower intervention levels (S1 to S6) and the difference between them (Delta (Δ)). Chow Test: Calculated F values greater than Tabulated F values indicates that models are significantly different each other.

Species	Linear Models			Chow Test	
	Slope		Delta (Δ)	Calculated F	Tabulated F
	S1 to S5	S1 to S6			
Prosopis juliflora	-0.600	0.085	0.685	0.266	5.117
Nicotiana glauca	-3.700	-0.857	2.843	2.890	5.117
Calotropis procera	0.400	1.742	1.342	0.471	5.117
Dactyloctenium aegyptium	6.500	10.250	3.750	0.183	5.117
Aristida adscensionis	8.000	10.020	2.020	0.219	5.117
Boerhavia diffusa	10.800	12.850	2.050	0.123	5.117
Eragrostis tenella	4.200	8.828	4.628	1.043	5.117
Cenchrus ciliaris	5.400	7.714	2.314	0.276	5.117
Digitaria sanguinalis	3.800	7.685	3.885	1.336	5.117
Melinis repens	0.300	1.628	1.328	0.360	5.117
Eragrostis cilianensis	3.300	3.542	0.242	0.016	5.117
Momordica charantia	0.300	0.257	-0.043	0.003	5.117
Ricinus communis	-0.400	0.142	0.542	0.644	5.117
Argemone mexicana	0.400	0.657	0.257	0.476	5.117

Non-native species population status

The extension of the PISF canals occupied by non-native species was equivalent to 92.3% of the sampled area (Figure 1). The species with the highest occupancy and the largest mean population size were *N. glauca*, *P. juliflora* and *C. procera* (Appendix 1).

We found a total of 294 populations of non-native species, of which 153 were casual, 64 were naturalized and 77 were invading. The species with the highest number of populations were also *Prosopis juliflora*, *Nicotiana glauca* and *Calotropis procera*. Despite having population extending over smaller areas, *Momordica charantia* and *Ricinus communis* also presented a number of populations above the average of all other species: 39 and 53 non-native populations, respectively (Appendix 1).

Discussion

Our study presented evidences that mega infrastructure projects can act as a pathway for establishment and spread of non-native species. Our results highlight the presence of 21 non-native species on the deployment area of the largest MIP of Brazil and about 92% of infrastructure area occupied by non-native species' populations. The massive occupation and widespread distribution of invasive species along the disturbed area indicate that the land transformation imposed by PISF facilitates the establishment of non-native species and reinforce the evidences that MIP act as a corridor for spread of these species. Also, we found a tendency that once an area was disturbed and non-native species had established, lower levels of human intervention tend to increase the spread of non-native species to new regions.

Most of the species recorded by this study are well-known non-natives for the Caatinga (Almeida et al., 2014), but it is the first time that the species *Argemone mexicana* was found invading in the biome. Four new species had the first record for PISF-DAA: *Digitaria nuda*, *Eragrostis ciliaris*, *Urochloa mollis* and *Parkinsonia aculeata* (Fabricante and Siqueira-Filho, 2012). The most representative family (Poaceae) was the same as in other six arid regions in Africa, America and Europe (Sanz Elorza et al., 2010).

Some species recorded here are globally recognized as invasive, such as *Calotropis procera*, *Nicotiana glauca*, *Parkinsonia aculaeta*, *Prosopis* sp. and *Ricinus communis* (Richardson and Rejmánek, 2011). Because of their large number of records, persistence in the disturbed area and populational status, the species *C. procera*, *N. glauca* and *P. juliflora* are the most relevant non-native species in PISF. Further, our field observations indicate these species are sympatric at some stretches, form wide mono-dominant stands and invade several types of habitat in the disturbed area, such as steep slopes, “dump” areas and rocky outcrops, which facilitates their spread along the entirety of the PISF extension. Also, there are populations of these three species both in dry and humid areas.

Nicotiana glauca is a shrub native to Argentina and Bolivia (Goodspeed, 1954 in (Fabricante et al., 2015)) and recorded in several arid zones in the world (Sanz Elorza et al., 2010). Some traits favor their status as a successful invader in the Caatinga such as abundant production of fruits and seeds that germinate with high efficiency (Fabricante et al., 2015), persistent soil seed bank (DiTomaso et al., 2013) easily recovering populations after flooding events (Florentine et al., 2006), and toxicity for humans (Steenkamp et al., 2002) and other animals (Panter et al., 2000).

Calotropis procera is a perennial shrub native to southwestern Asia and Africa (Brandes, 2005) and widespread in Brazil (Zenni and Ziller, 2011) and other regions on the world (Farahat et al., 2015). The fast growth and early flowering and fructification (Andrade et al., 2005) associated with high tolerance for edaphic and climatic conditions (Oliveira et al., 2009), enables *C. procera* to establish and spread in disturbed sites like the study area, which could be related with the success in invading the Caatinga ecosystem.

Prosopis juliflora is a tree native to southern North America, Central America and northern South America (Paciecznik et al., 2001), introduced in the Caatinga in 1942 as forage for pasture animals (Azevedo et al, 1982). It is a fast growing species, has wide ecological amplitude tolerant to arid conditions and different types of soils, usually found in areas where water and soil fertility are limiting factors (Paciecznik et al., 2001). Previous studies have demonstrated the influence of *P. juliflora* on declines of species diversity and species richness owing to increased mortality and reduced growth of native species in invaded areas (Nascimento et al., 2014; Pegado et al., 2006).

We believe that the variation in number of sampling points that each species was recorded may have been influenced by the different construction phases, whose greater intensity leads to the burial of many populations due to soil deposition. In addition, the dry seasons favor the disappearance of grasses, which are dormant or hard to detect (Balachowski et al., 2016). Another finding was the variation in the distribution of non-native species due to different anthropogenic intervention levels. The great number of non-native populations on the canal tends to generate a high propagule pressure into new cleared areas. This pressure is periodically relieved due to the maintenance of the physical structures and environmental management of the project that clear and/or buries these populations. This way, human intervention acts as a barrier to populations expansions. In post disturbed scenario, without this barrier, the non-native species are free to re-launch the seeds to new areas and germinate the seed bank buried in places where native species were hardly detected, such as the “dump” areas and steep slopes. These new habitats created by the construction work presents a cause of concern to native flora once these areas are a repository of non-native species and can function as permanent source of propagules to the surrounding areas occupied by Caatinga vegetation.

The capacity of invasive species to establish and invade a particular site is often attributed to a better ability to compete for resources and/or to a greater performance of invasive species in resource use (Gioria and Osborne, 2014). Additionally, to a superior capacity in resources acquisition, invasive species usually reduce resource availability for co-occurring native species (Gioria and Osborne, 2014). Despite of lower competitive capacity, biotic resistance by the native community can help contain the abundance of established invaders (Levine et al., 2004). However, the construction process may contribute to diminish the effects of local biotic resistance by inputting disturbances that difficult the native species to occupy the new areas cleared. Besides of competition and biotic resistance, propagules pressure plays an important role in invasion success (Simberloff, 2009). Eschtruth and Battles (2009) argue that the interaction between propagule pressure and disturbance can represent the main driver of its success. Therefore, the combination of MIP environmental effects and the intrinsic characteristics of non-native species increase the risk of biological invasion.

Given the worldwide distribution of non-native species (Pyšek et al., 2017), its negative socioeconomic and environmental impact (Pimentel et al., 2005; Pyšek et al., 2012) and the growth of human population resulting in more MIP all around the world (Hulme, 2015; Liu et al., 2019), we strongly suggest that non-native species monitoring and management should be part of all large-scale construction projects. Furthermore, we identified that immediately after construction work done is probably the critical stage to spread of invasive species. Thus, monitoring and control of invasive species, followed by active ecological restoration efforts (Gaertner et al., 2012) must be done right after the construction has ended to avoid the continuous spread to susceptible areas.

References

Almeida, W.R., Lopes, A. V., Tabarelli, M., Leal, I.R., 2014. The non-native flora of Brazilian Caatinga: deliberate introductions expand the contingent of potential invaders. Biol. Invasions 17, 51–56. https://doi.org/10.1007/s10530-014-0738-6

ANA, 2009. Relatório de Fiscalização do andamento do cumprimento das condicionantes estabelecidas na Resolução ANA no 411, de 26/09/2005, e nos compromissos assumidos pelo Ministério de Minas e Energia. Agência Nac. Águas 1–7.

Andrade, M.V.M., Silva, D.S., Andrade, A.P., Medeiros, A.N., Pinto, M. do S. de C., 2005. Fenologia de Calotropis procera Ait R . BR., em função do sistema e da densidade de plantio. Arch. Zootec. 54, 631–634.

Azevedo, G.F., 1982. Como e porque a algarobeira foi introduzida no Nordeste, in: Fonseca, F.C.E., Mota, A.P.B., Azêvedo, C.F., Trindade, I., Cruz, J.F., Brito, R.A.L. (Eds.), Simpósio Brasileiro Sobre Algaroba 1. EMPARN (Empresa Agropecuária do Rio Grande do Norte), Natal, pp. 300–306.

Balachowski, J.A., Bristiel, P.M., Volaire, F.A., 2016. Summer dormancy, drought survival and functional resource acquisition strategies in California perennial grasses. Ann. Bot. 118, 357–368. https://doi.org/10.1093/aob/mcw109

Bergquist, E., Evangelista, P., Stohlgren, T.J., Alley, N., 2007. Invasive species and coal bed methane development in the Powder River Basin, Wyoming. Environ. Monit. Assess. 128, 381–394. https://doi.org/10.1007/s10661-006-9321-7

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U., Richardson, D.M., 2011. A proposed unified framework for biological invasions. Trends Ecol. Evol. 26, 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Brandes, D., 2005. Calotropis procera on Fuerteventura. Germany.

Brooks, M.L., D’Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of Invasive Non-native Plants on Fire Regimes. Bioscience 54, 677–688.

Cepan, 2009. Contextualização Sobre Espécies Exóticas Invasoras, Dossiê Pernambuco. Centro de Pesquisas Ambientais do Nordeste, Recife.

Davies, K.W., Sheley, R.L., 2007. A Conceptual Framework for Preventing the Spatial Dispersal of Invasive Plants. Weed Sci. 55, 178–184. https://doi.org/10.1614/WS-06-161.1

DiTomaso, J.M., Kyser, G.B., Oneto, S.R., Wilson, R.G., Orloff, S.B., Anderson, L.W., Wright, S.D., Roncoroni, J.A., Miller, T.L., Prather, T.S., Ransom, C., Beck, K.G., Duncan, C., Wilson, K.A., Mann, J.J., 2013. Weed control in natural areas in the Western United States. Weed Research and Information Center, University of California.

Eschtruth, A.K., Battles, J.J., 2009. Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. Ecol. Monogr. 79, 265–280.

Fabricante, J.R., Castro, R.A., Araújo, K.C.T., Siqueira-Filho, J.A., 2015. Atributos ecológicos da bioinvasora nicotiana glauca Graham (Solanaceae) e avaliação da susceptibilidade de sua ocorrência no Brasil. Cienc. Florest. 25, 959–967. https://doi.org/10.5902/1980509820650

Fabricante, J.R., Siqueira-Filho, J.A., 2012. Exotic and Invasive Plants of the Caatingas of the São Francisco River, in: Flora of the Caatingas of the São Francisco River. Andrea Jakobsson, Rio de Janeiro, pp. 366–393. https://doi.org/10.1016/B978-0-08-029966-2.50005-5

Farahat, E., Galal, T., El-Midany, M., Hassan, L., 2015. Effect of urban habitat heterogeneity on functional traits plasticity of the invasive species Calotropis procera (Aiton) W.T. Aiton. Rend. Lincei. Sci. Fis. e Nat. 26, 193–201. https://doi.org/10.1007/s12210-015-0408-3

Flora do Brasil 2020, 2018. Flora do Brasil 2020 [WWW Document]. Jard. Botânico do Rio Janeiro. URL http://floradobrasil.jbrj.gov.br (accessed 8.17.18).

Florentine, S.K., Westbrooke, M.E., Gosney, K., Ambrose, G., O'Keefe, M., 2006. The arid land invasive weed Nicotiana glauca R. Graham (Solanaceae): Population and soil seed bank dynamics, seed germination patterns and seedling response to flood and drought. J. Arid Environ. 66, 218–230. https://doi.org/10.1016/j.jaridenv.2005.10.017

Frehse, F. de A., Braga, R.R., Nocera, G.A., Vitule, J.R.S., 2016. Non-native species and invasion biology in a megadiverse country: scientometric analysis and ecological interactions in Brazil. Biol. Invasions 18, 3713–3725. https://doi.org/10.1007/s10530-016-1260-9

Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D., Von Holle, B., 2007. Concepts & Synthesis Emphasizing New Ideas To Stimulate Research in Ecology the Invasion Paradox: Reconciling Pattern and Process in Species Invasions. Ecology 88, 3–17. https://doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2

Gaertner, M., Fisher, J., Sharma, G., Esler, K., 2012. Insights into invasion and restoration ecology: Time to collaborate towards a holistic approach to tackle biological invasions. NeoBiota 12, 57–76. https://doi.org/10.3897/neobiota.12.2123

Gelbard, J.L., Belnap, J., 2003. Roads as Conduits for Exotic Plant Invasions in a Semiarid Landscape. Conserv. Biol. 17, 420–432.

Gioria, M., Osborne, B.A., 2014. Resource competition in plant invasions: emerging patterns and research needs. Front. Plant Sci. 5, 1–21. https://doi.org/10.3389/fpls.2014.00501

Hobbs, Richard J., 2000. Land-use changes and invasions, in: Mooney, H.A., Hobbs, R. J. (Eds.), Invasive Species in a Changing World. Island Press, Washigton DC, pp. 55–64.

Hulme, P.E., 2015. Invasion pathways at a crossroad: Policy and research challenges for managing non-native species introductions. J. Appl. Ecol. 52, 1418–1424. https://doi.org/10.1111/1365-2664.12470

Hulme, P.E., 2009. Trade, transport and trouble: Managing invasive species pathways in an era of globalization. J. Appl. Ecol. 46, 10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

IBGE, 2004. Mapa de Biomas e de Vegetação do Brasil [WWW Document]. Inst. Bras. Geogr. e Estatística. URL https://ww2.ibge.gov.br/home/presidencia/noticias/21052004biomashtml.shtm (accessed

8.16.18).

ICMBio, 2018. Caatinga Biome. Instituto Chico Mendes de Conservação da Biodiversidade. [WWW Document]. URL http://www.mma.gov.br/biomas/caatinga (accessed 8.16.18).

Kenis, M., Auger-Rozenberg, M.A., Roques, A., Timms, L., Péré, C., Cock, M.J.W., Settele, J., Augustin, S., Lopez-Vaamonde, C., 2009. Ecological effects of invasive non-native insects, in: Ecological Impacts of Non-Native Invertebrates and Fungi on Terrestrial Ecosystems. Springer, Dordrecht, pp. 21–45. https://doi.org/10.1007/978-1-4020-9680-8_3

Levine, J.M., Adler, P.B., Yelenik, S.G., 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecol. Lett. 7, 975–989. https://doi.org/10.1111/j.1461-0248.2004.00657.x

Liu, X., Blackburn, T.M., Song, T., Li, X., Huang, C., Li, Y., 2019. Risks of biological invasion on the Belt and Road. Curr. Biol. 29, 1–7. https://doi.org/10.1016/j.cub.2018.12.036

Nascimento, C.E. de S., Tabarelli, M., Silva, C.A.D., Leal, I.R., Tavares, W. de S., Serrão, J.E., Zanuncio, J.C., 2014. The introduced tree Prosopis juliflora is a serious threat to native species of the Brazilian Caatinga vegetation. Sci. Total Environ. 481, 108–113. https://doi.org/10.1016/j.scitotenv.2014.02.019

Nielsen, S.E., Aldridge, C.L., Hanser, S.E., Leu, M., Knick, S.T., 2011. Occurrence of non-native invasive plants: The role of anthropogenic features, in: Aldridge, C.L., Hanser, S.E., Leu, M., Knick, S.T. (Eds.), Sagebrush Ecosystem Conservation and Management: Ecoregional Assessment Tools and Models for the Wyoming Basins. Allen Press, Kansas, pp. 357–386.

Oliveira, S.H.F., Negreiros, D., Fernandes, G.W., Barbosa, N.P.U., Rocha, R., Almeida-Cortez, J.S., 2009. Seedling growth of the invader Calotropis procera in ironstone rupestrian field and seasonally dry forest soils. Neotrop. Biol. Conserv. 4, 69–76. https://doi.org/10.4013/nbc.2009.42.01

Pasiecznik, N.M., Felker, P., Harris, P.J.C., Harsh, L.N., Cruz, G., Tewari, J.C., Cadoret, K., Maldonado, L.J., 2001. The Prosopis juliflora - Prosopis pallida Complex: A Monograph. Coventry, UK. https://doi.org/10.1111/jsap.12202

Panter, K.E., Weinzweig, J., Gardner, D.R., Stegelmeier, B.L., James, L.F., 2000. Comparison of cleft palate induction by Nicotiana glauca in goats and sheep. Teratology 61, 203–210. https://doi.org/10.1002/(SICI)1096-9926(200003)61:3<203::AID-TERA8>3.0.CO;2-I

Pegado, C.M.A., Andrade, L.A., Félix, L.P., Pereira, I.M., 2006. Efeitos da invasão biológica de algaroba: Prosopis juliflora (Sw.) DC. sobre a composição e a estrutura do estrato arbustivo-arbóreo da caatinga no Município de Monteiro, PB, Brasil. Acta Bot. Brasilica 20, 887–898. https://doi.org/10.1590/S0102-33062006000400013

Pennington, R.T., Lavin, M., Oliveira-Filho, A., 2009. Woody Plant Diversity, Evolution, and Ecology in the Tropics: Perspectives from Seasonally Dry Tropical Forests. Annu. Rev. Ecol. Evol. Syst. 40, 437–457. https://doi.org/10.1146/annurev.ecolsys.110308.120327

Pimentel, D., Zuniga, R., Morrison, D., 2005. Update on the environmental and economic costs associated with non-native-invasive species in the United States. Ecol. Econ. 52, 273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Preston, T.M., 2015. Presence and abundance of non-native plant species associated with recent energy development in the Williston Basin. Environ. Monit. Assess. 187, 200, 16pp. https://doi.org/10.1007/s10661-015-4408-7

Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U., Vilà, M., 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. Glob. Chang. Biol. 18, 1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x

Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., Kreft, H., Weigelt, P., Winter, M., Kartesz, J., Nishino, M., Antonova, L.A., Barcelona, J.F., Cabezas, F.J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Dullinger, S., Ebel, A.L., Figueiredo, E., Fuentes, N., Genovesi, P., Groom, Q.J., Henderson, L., Inderjit, Kupriyanov, A., Masciadri, S., Maurel, N., Meerman, J., Morozova, O., Moser, D., Nickrent, D., Nowak, P.M., Pagad, S., Patzelt, A., Pelser, P.B., Seebens, H., Shu, W.S., Thomas, J., Velayos, M., Weber, E., Wieringa, J.J., Baptiste, M.P., Van Kleunen, M., 2017. Naturalized non-native flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. Preslia 89, 203–274. https://doi.org/10.23855/preslia.2017.203

Queiroz, L.P. de, Cardoso, D., Fernandes, M.F., Moro, M.F., 2017. Diversity and Evolution of Flowering Plants of the Caatinga Domain, in: Silva, J.M.C. da, Leal, I.R., Tabarelli, M. (Eds.), Caatinga: The Largest Tropical Dry Forest Region in South America. Springer, pp. 23–64. https://doi.org/10.1007/978-3-319-68339-3_6

Ricciardi, A., Hoopes, M.F., Marchetti, M.P., Lockwood, J.L., 2013. Progress toward understanding the ecological impacts of non native species. Ecol. Monogr. 83, 263–282.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000. Naturalization and invasion of non-native plants : concepts and definitions. Divers. Distrib. 6, 93–107.

Richardson, D.M., Rejmánek, M., 2011. Trees and shrubs as invasive non-native species - a global review. Divers. Distrib. 17, 788–809. https://doi.org/10.1111/j.1472-4642.2011.00782.x

Sanz Elorza, M., Bernardo, F.G., Oliván, A.S., Iglesias, L.P.G., 2010. Invasiveness of non-native vascular plants in six arid zones of Europe, Africa and America. Lazaroa 31, 109–126. https://doi.org/10.5209/rev

Simberloff, D., 2009. The Role of Propagule Pressure in Biological Invasions. Annu. Rev. Ecol. Evol. Syst. 40, 81–102. https://doi.org/10.1146/annurev.ecolsys.110308.120304

Steenkamp, P.A., Van Heerden, F.R., Van Wyk, B.E., 2002. Accidental fatal poisoning by Nicotiana glauca: Identification of anabasine by high performance liquid chromatography/photodiode array/mass spectrometry. Forensic Sci. Int. 127, 208–217. https://doi.org/10.1016/S0379-0738(02)00123-8

Suarez, A. V., Tsutsui, N.D., 2008. The evolutionary consequences of biological invasions. Mol. Ecol. 17, 351–360. https://doi.org/10.1111/j.1365-294X.2007.03456.x

Van Kleunen, M., Weber, E., Fischer, M., 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol. Lett. 13, 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P., 2011. Ecological impacts of invasive non-native plants: A meta-analysis of their effects on species, communities and ecosystems. Ecol. Lett. 14, 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Vilà, M., Pujadas, J., 2001. Land-use and socio-economic correlates of plant invasions in European and North African countries. Biol. Conserv. 100, 397–401. https://doi.org/10.1016/S0006-3207(01)00047-7

von der Lippe, M., Kowarik, I., 2007. Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conserv. Biol. 21, 986–996. https://doi.org/10.1111/j.1523-1739.2007.00722.x

Wardle, D.A., Bardgett, R.D., Callaway, R.M., Van der Putten, W.H., 2011. Terrestrial ecosystem responses to species gains and losses. Science (80-.). 332, 1273–1277. https://doi.org/10.1126/science.1197479

Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Hejda, M., Hulme, P.E., Arianoutsou, M., Basnou, C., Delipetrou, P., Didziulis, V., Lambdon, P.W., Pergl, J., Pyšek, P., Roy, D.B., Kühn, I., 2009. Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. Proc. Natl. Acad. Sci. United States Am. 106, 21721–21725.

Zenni, R.D., 2015. The naturalized flora of Brazil: A step towards identifying future invasive non-native species. Rodriguesia 66, 1137–1144. https://doi.org/10.1590/2175-7860201566413

Zenni, R.D., Bailey, J.K., Simberloff, D., 2014. Rapid evolution and range expansion of an invasive plant are driven by provenance-environment interactions. Ecol. Lett. 17, 727–735. https://doi.org/10.1111/ele.12278

Zenni, R.D., Cunha, W.L., Sena, G., 2016. Rapid increase in growth and productivity can aid invasions by a non-native tree. AoB Plants 8, plw048. https://doi.org/10.1093/aobpla/plw048

Zenni, R.D., Ziller, S.R., 2011. An overview of invasive plants in Brazil. Rev. Bras. Botânica 34, 431–446. https://doi.org/10.1590/S0100-84042011000300016

Zimmermann, H., Brandt, P., Fischer, J., Welk, E., von Wehrden, H., 2014. The Human Release Hypothesis for biological invasions: human activity as a determinant of the abundance of invasive plant species. F1000Research 3, 109. https://doi.org/10.12688/f1000research.4008

Appendix 1. List of non-native plant species recorded in the PISF-DA. Species are arranged alphabetically according to its respective family. The following information is given for each species: Family, species names, life forms, populational invasion status (Casual, Naturalized and Invasive), Occupancy Measures with Numbers of populations with more than 100 m of extent, the largest population in extension, total extension in both canals, mean extension, the standard deviation of extension and the proportion (%) occupied for each species in both canals. Δβ showing the tendency of growth or reduction of spread after heavy construction has ended. The final invasion status the PISF-DA. A species was considered invasive if it had, at least, one population within the pre-established parameters. Grasses and the species *Boerhavia diffusa* were excluded from the invasion status assessment owing to their absence or hard detection during the dry months of the year. Species valid names and its respective authors were obtained with Flora do Brasil 2020.

Families/Species	Life form	Populations			Occupancy Measures						Slope	Status
		Casual	Naturalized	Invasive	Number of Populations (>100m)	Largest Population (m)	Total Extension (m)	Mean Extension (m)	SD Extension	% Occupancy	Δβ	
Apocynaceae												
Calotropis procera (Aiton) W.T. Aiton	Shrub	30	5	15	30	29,201	153,379	3,068	± 6,896	36.88	1.342	Invasive
Cryptostegia grandiflora R.Br.	Shrub	4	0	1	1	159	159	32	± 71	0.04	-	Invasive
Anacardiaceae												
Mangifera indica L.	Tree	3	1	0	0	-	-	-	-	-	-	Naturalized
Cucurbitaceae												
Momordica charantia L.	Liana	13	17	9	14	13,500	36,495	936	± 2,374	8.77	-0.043	Invasive
Euphorbiaceae												
Ricinus communis L.	Shrub	36	13	4	14	2,801	10,564	199	± 524	2.54	0.542	Invasive
Fabaceae												
Parkinsonia aculeata L.	Tree	16	1	1	2	694	1,328	63	± 199	0.32	-	Invasive
Prosopis juliflora (Sw.) DC.	Tree	26	10	25	44	38,995	255,090	4,181	± 6,997	61.33	0.685	Invasive
Meliaceae												
Azadirachta indica A. Juss.	Shrub	8	2	0	1	164	164	16	± 52	0.04	-	Naturalized
Nyctaginaceae												
Boerhavia diffusa L.	Grass	-	-	-	-	-	-	-	-	-	2.050	-
Papaveraceae												
Argemone mexicana L.	Grass	2	4	1	2	897	1,066	152	± 334	0.26	0.257	Invasive
Poaceae												

Aristida adscensionis L.	Grass	-	-	-	-	-	-	-	-	-	2.020	-
Cenchrus ciliaris L.	Grass	-	-	-	-	-	-	-	-	-	2.314	-
Dactyloctenium aegyptium (L.) Willd	Grass	-	-	-	-	-	-	-	-	-	3.750	-
Digitaria nuda (L.) Scop.	Grass	-	-	-	-	-	-	-	-	-	3.885	-
Echinochloa colona (L.) Link	Grass	-	-	-	-	-	-	-	-	-	-	-
Eragrostis cilianensis (All) VignoloexJanch.	Grass	-	-	-	-	-	-	-	-	-	0.242	-
Eragrostis ciliaris (L.) R.Br.	Grass	-	-	-	-	-	-	-	-	-	-	-
Eragrostis tenella (L.) P.Beauv. ex Roem. &Schult.	Grass	-	-	-	-	-	-	-	-	-	4.628	-
Melinis repens (Willd.) Zizka	Grass	-	-	-	-	-	-	-	-	-	1.328	-
Urochloa mollis (Sw.) Morrone&Zuloaga	Grass	-	-	-	-	-	-		-	-	-	-
Solanaceae												
Nicotiana glauca Graham	Shrub	15	11	21	38	28,782	285,966	4,766	± 7,925	63.81	2.843	Invasive

MANUSCRITO 2

EFFECTS OF PLANT INVASION ON THE REGENERATION OF SEMI-ARID AREAS

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Abstract

Natural regeneration of disturbed sites can be negatively affected by plant invasions. Consequently, regenerating areas dominated by invasive species tend to present less diversity than native ones. Also, individual invaders may have different levels of impact at community scale. To test these hypotheses, we selected ten sites dominated by the three invaders most widespread (*Calotropis procera*, *Nicotiana glauca* and *Prosopis juliflora*) in the study area and compared the richness of invaded and non-invaded sites and whether this originates from the identity of the invasive species. In addition, we used pairwise comparisons to test if the species richness of invaded sites differed according to the identity of the invaders. We found that invaded sites presented significantly lower plant richness than non-invaded sites and that there were differences in species richness among communities dominated by different invaders. The invasion of non-native species was the main cause for the difference between invaded and non-invaded communities (R^2= 0.55). The identity of the invasive species explained only a small part of the variation in plant communities across invaded sites (R^2= 0.3). *C. procera* showed significant differences in relation to both of the other invaders (*C. procera* vs *N. glauca*: F= 6.77, p= 0.009, and *C. procera* vs *P. juliflora*: F= 5.84, p= 0.016). In contrast, *N. glauca* and *P. juliflora* did not differ between each other (F= 1.1, p= 0.319). The highest mean and absolute richness in sites dominated by *C. procera* (18±2.08 species), compared with sites invaded by *N. glauca* (10±2.5 species) and *P. juliflora* (9±7 species), suggest greater tolerance to co-occurrence of native species.

Keywords

Plant invasion; non-native plants, regeneration, disturbance, semiarid, arid environments

Introduction

Natural disturbances are major forces in the successional dynamics of plant communities (Hubbell et al. 1999). Several factors are known to affect the regeneration of sites in early successional stage, such as resource competition, seed dispersal and predation, and seedling survival (Gill and Marks 1991; Myster 1993; Berkowitz et al. 1995; Ostfeld et al. 1997). However, unlike those factors that naturally affect regeneration, anthropogenic disturbances may facilitate the emergence of invasive species (Gorchov and Trisel 2003; Rudgers et al. 2007; Moles et al. 2012; Jauni et al. 2015). Invasive species are more likely to colonize habitats after disturbances (Catford et al. 2012), once they use the available resources more efficiently than natives (Matzek 2011). In early successional stages, invasive species can directly and/or indirectly affect the regeneration of native species (Meiners 2007; Flory and Clay 2010). Also, studies assessing the impact of more than one invasive species indicate that the impact on diversity in invaded sites differs among individual invaders (Hejda et al. 2009; Kuebbing and Nuñez 2016). This difference can be related to intrinsic characteristics of the invader and the type of the invaded community (Hejda et al. 2009).

Vegetation recovery in arid/semi-arid zones is influenced by a combination of factors including long periods of drought, with unusually wet years, and fire regimes (Read 1995; Nano and Clarke 2011). Although fire had been less destructive in arid zones than temperate or tropical regions, when it does occur, the local mortality is very high (Prior et al. 2011). Perennial invasive species may facilitate the occurrence of fire in dry habitats, even in fire-free regions, by maintaining an abundant inflammable biomass (D’Antonio et al. 2000; Rahlao et al. 2009). Arid zones present slow growth and recruitment (Prior et al. 2011), which may favor the establishment of fast growing species, such as invasive species (Graebner et al. 2012; Zenni et al. 2016). The introduction of non-native herbivores also contributes to difficult the regeneration of semi-arid regions (Auld and Keith 2009) reducing the establishment of seedlings (Briggs et al. 2008).

Our study was developed within the Caatinga biome, a seasonal tropical dry forest (STDF) (Pennington et al. 2009), the rainfall averages 700 mm annually that may precipitate in a single month (Andrade et al. 2017), and harbors the richest STDF in terms of flowering plants in the New World (Queiroz et al. 2017). Caatinga has faced several types of habitat degradation, since slash-and-burn agriculture, overgrazing by livestock and introduction of non-native species for farming-based activities (Leal et al. 2005; Almeida et al. 2014;

Nascimento et al. 2014). Thereby, the conservation of Caatinga have been receiving more attention in the last few years (Leal et al. 2005; Ribeiro et al. 2015; Queiroz et al. 2017). However, despite the efforts to increase scientific knowledge of non-native invasive species in Caatinga (Andrade et al. 2005, Andrade et al. 2009, 2010; Almeida et al. 2014; Nascimento et al. 2014), the effects of biological invasions on native diversity needs to be better understood.

The traits that favor successful invasion of non-native species are well-known (Flory and Clay 2010; Van Kleunen et al. 2010; Dawson et al. 2011; Matzek 2011), but the effects of plant invasion on diversity of regenerating sites remain poorly studied. In addition, only few studies aiming at the relationship between the richness of non-native and native species were developed in tropical regions (Peng et al. 2019). Our study evaluated the effects of three globally distributed invasive species comparing the diversity of the regenerating communities under invaded and non-invaded conditions in a semiarid tropical region. This comparison can provide valuable information on the management of invasive species and the nature conservation (Hejda et al. 2009).

In order to assess the effects of plant invasion on the species richness of regenerating semiarid areas we aimed at verifying (i) if the species richness of the regenerated areas dominated by invasive species differ from the richness found in neighboring native vegetation and, if so, whether this originates from the identity of the invasive species, and (ii) if the species richness of invaded sites differ between the dominating invasive species. We hypothesized that sites dominated by invasive species present less species richness than non-invaded, independent of the identity of the invasive species and that the richness of the invaded sites differs between invasive species.

Material and Methods

Study site

This study was conducted at the Deployment Area (DA) of the Integration of the São Francisco River Project (PISF) and its neighboring area. PISF is a water basin transfer basically composed by two independent concrete canals and structures responsible for the water transport. Each canal contains a series of pumping stations, concrete canals, tunnels, aqueducts, and dams in which the water flows by pumps and gravity. Together, the canals extend linearly trough 477 km within Caatinga boundaries. DA corresponds to a marginal strip 100 m wide on each side of the canal over its entire length and the edge of some structures as dams and pumping stations, that was initially cleared of vegetation prior to the construction of the canal in 2007 (ANA, 2009). Since then, the DA had been occupied by several invasive populations, and altered by the constructions process, which include deforestation, ground excavation, underground explosions, debris deposition. In this period, the DA was under different levels of intervention, less or more permissive to natural regeneration depending on the phase of construction. Data collection were done by placing a series of plots within invasive populations, which were mainly on debris disposal areas and steep slopes created to support concrete structures, and within the neighboring native vegetation.

Species Selection

Our selection criteria to select the species on this study were based on populational and ecological aspects of the invaders obtained from monitoring surveys between May/2015 and June/2018 (see Chapter 1 for details). We looked for the species with greatest number of records at the sampling points, greatest number of invasive populations, most widespread occurrence, and that occupied the larger extents in the project’s deployment area.

Currently, PISF has 21 non-native species recorded, eight of which, are considered invasive (Chapter 1). Of these species, three stand out due to their invasion status in the area and, thus, were selected for this study: *Calotropis procera* (Aiton) W.T.Aiton (Apocynaceae), *Nicotiana glauca* Graham (Solanaceae) and *Prosopis juliflora* (Sw.) DC. (Fabaceae). Together, they were responsible for about 80% of invasive populations and 54% of total non-native populations of the PISF. Also, their populations occupied 37% (*C. procera*), 64% (*N. glauca*) and 61% (*P. juliflora*) of DA’s extension, co-occurring at some stretches.

Sampling design

In order to assess the invasive species effects on DA’s ecological succession, sampling points were settled in 10 different sites (populations) of the three invasive species (four populations of *N. glauca*, three populations of *C. procera* and three populations of *P. juliflora*). The sampling points had a minimal extent in which the invasive species was dominant in the community and were settled in sections from 160 m (perpendicular Sampling) to 400 m (Parallel Sampling). In each section, circular plots of 6 m radius (approximately 100m^2) were arranged within DA (invaded plots) and in the neighboring native vegetation (non-invaded plots). In just one case, one individual of an invasive species (*P. juliflora*) was recorded within a non-invaded plot, that could not cause any changes in vegetation structure or species composition. To fit that, two different sampling designs were used: (i) when the entire DA's width was occupied by a specific invasive species six pairs of plots were placed at the sampling point (three in invaded plots and three within neighboring area), the distance between the pair and the next pair were 80 m (Perpendicular Sampling - Figure 1), (ii) when the invasive population was located in only a part of DA, a nine plots transect, parallel to the canal, were established, with regular distances between them (invaded) and three pairs of plots (non-invaded) were placed at the beginning, middle and end of the transect within neighboring native area (Parallel Sampling - Figure 2), the transects varied between 240 m to 400 m in length. At the native vegetation (non-invaded plots), the distance between plots inside the pair was 30 m, for both perpendicular and parallel sampling.

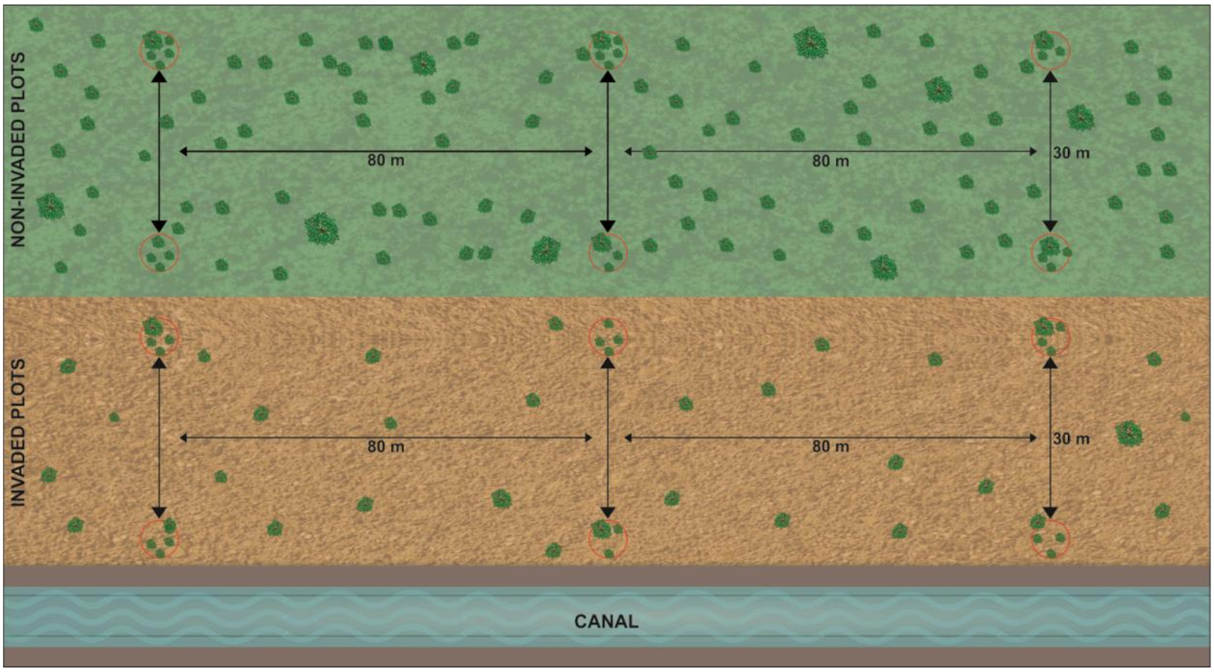

Figure 1. Perpendicular Sampling Scheme to assess the invasion effects on the regeneration of invaded sites. Non-invaded plots were located within native vegetation, represented by the green area. Invaded plots were located at the disturbed area under regeneration, represented by the ground color area. Red circles represent the plots and black lines indicate the distances between plots inside the pair (30 m) and between pairs (80 m).

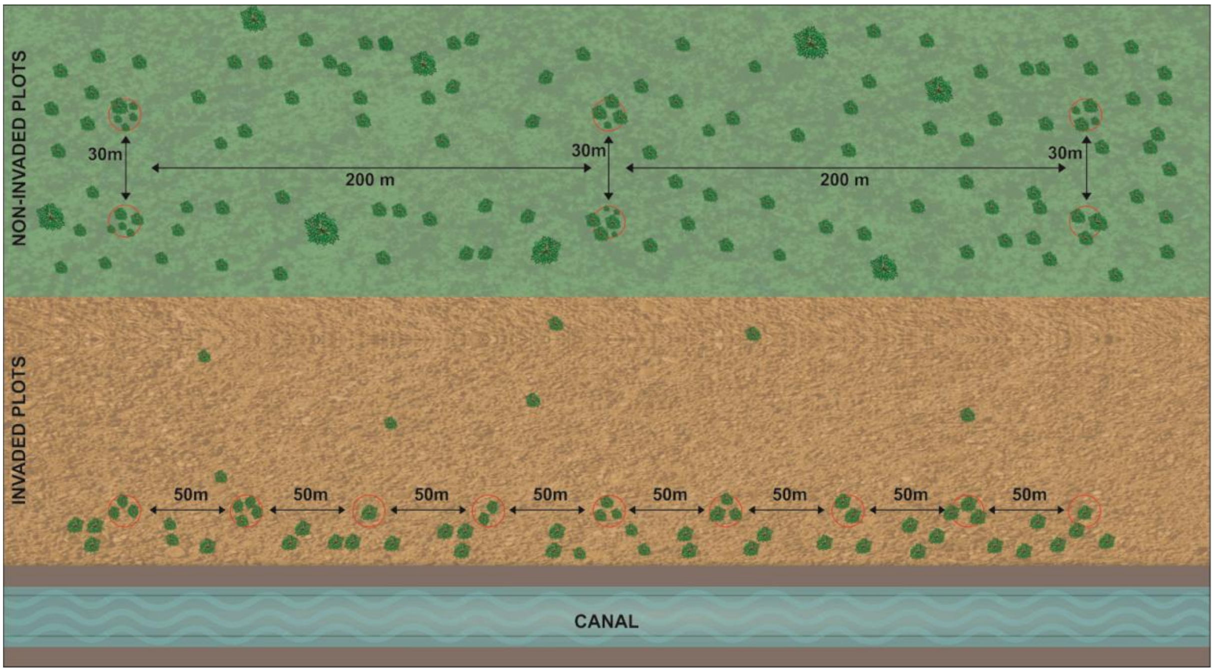

Figure 2. Parallel Sampling Scheme to assess the invasion effects on the regeneration of invaded sites. Non-invaded plots were located within native vegetation, represented by the green area. Invaded plots were located at the disturbed area under regeneration, represented by the ground color area. Red circles represent the plots and black lines indicate the distances between plots of the transect (50 m) (invaded plots), inside the pair (30 m) and between pairs (200 m) (non-invaded plots).

Data Analysis

For each plot, all plant species were recorded (richness, S) and their individuals counted (abundance). Grasses were excluded from the assessment due to absence and difficulty to detection during the sampling season. To verify differences in regeneration between invaded and non-invaded areas we compared the species richness between then. Comparisons of the species richness among areas were made using permutational multivariate analysis of variance (PERMANOVA). Prior to the analysis, an individual-based rarefaction (95% of confidence level) was performed for each plot to account for differences in number of individuals between the invaded and non-invaded areas. The estimated richness values obtained from the rarefaction were used to compare the species richness among the environments. The Bray-Curtis dissimilarity was used as distance measure for PERMANOVA based on species richness.

First, we tested if the species richness of the invaded and non-invaded communities were different and if there were differences between the diversity of the areas dominated by each of the invasive species (*C. procera*, *N. glauca* and *P. juliflora*) using a two-way PERMANOVA using the condition of the plots (invaded or non-invaded) and the invading species as factors with the estimated richness data. The observed difference between species was later checked through pairwise one-way PERMANOVA considering all possible combinations between pairs of species, using data only from the non-invaded plots.

Second, we conducted an Indicator Value (IndVal) test (Dufrêne and Legendre 1997) to verify which native species were associated with sites dominated by each of the invasive species. IndVal is a simple measure to find indicator species for a group of sites. In this method the species relative abundance (specificity) is combined with its relative frequency of occurrence (fidelity) in the various groups of sites (Dufrêne and Legendre 1997) chosen a priori. A good indicator species is the one where most of the individuals are found in a single group and which occurs in all sites of that group. To perform this analysis, we split our 10 sites in three groups relative to each dominant invasive species. Only data from the invaded plots were used for the test.

Results

13,971 plants representing 89 species, distributed in 62 genera and 27 families were registered during this study (Appendix 1). 78 species were identified (at least at genus level) and 11 species remain without identification. The most representative families were Fabaceae (23% of the species), Euphorbiaceae (14%), Malvaceae (13%), Bromeliaceae (6%) and Cactaceae (6%). Other families were represented by a maximum of three species. Life forms of the species found varied among herbs, liana, scandent/vine, shrubs, subshrub, succulent and trees (Appendix 1). Most of the species (n=49) occurred exclusively at non-invaded plots (55%), 11 species occurred exclusively at invaded plots (12%) and 29 species occurred both at invaded and non-invaded plots (33%) (Appendix 1). Among the identified species, six were non-natives for Caatinga (Appendix 1). Two non-native species (*P. juliflora* and *T. procumbens*) were registered within non-invaded plots and four native species (*Tarenaya spinosa*, *Ipomoea asarifolia*, *Ditaxis desertorum* and *Vachelia farnesiana*) occurred exclusively at invaded plots (Appendix 1).

Non-invaded plots presented higher species richness than invaded plots. Rarefied species richness ranged from five to eleven species (median = 7) in non-invaded plots, while in invaded plots it ranged from two to five species (median = 3), removing the outliers (Fig. 3). It was confirmed by the Two-way PERMANOVA results. There was significant difference between species richness of invaded and non-invaded sites owing both the presence/absence of invasion (F= 191.761, p= 0.001) and the identity of the invasive species (F= 5.475, p= 0.003) (Table 1). Additionally, the invasion on the regenerating sites was the factor that most explain differences in species richness between sites ($R^2 = 0.55$) (Table 1).

Table 1. Results of two-way non-parametric permutational multivariate analysis of variance (PERMANOVA) test for differences in the species richness of plant communities between invaded and non-invaded sites. DF = Degrees of freedom; SS = sums of squares; MS = mean square; Statistical test = F; R^2 = determination coefficient; p = probability value. 999 permutations and $\alpha = 0.05$. Source: Local (Invaded and/or non-invaded plots); Invasive Non-native Species (I.A.S.); Residuals and Total.

Source	DF	SS	MS	F	R^2	P
Local	1	5.116	5.116	191.761	0.55630	**0.001**
I.A.S.	2	0.292	0.146	5.475	0.03176	**0.003**
Residuals	142	3.788	0.0267		0.41194	
Total	145	9.197			1.00000	

Note: Results in boldface are significant at $p < 0.05$.

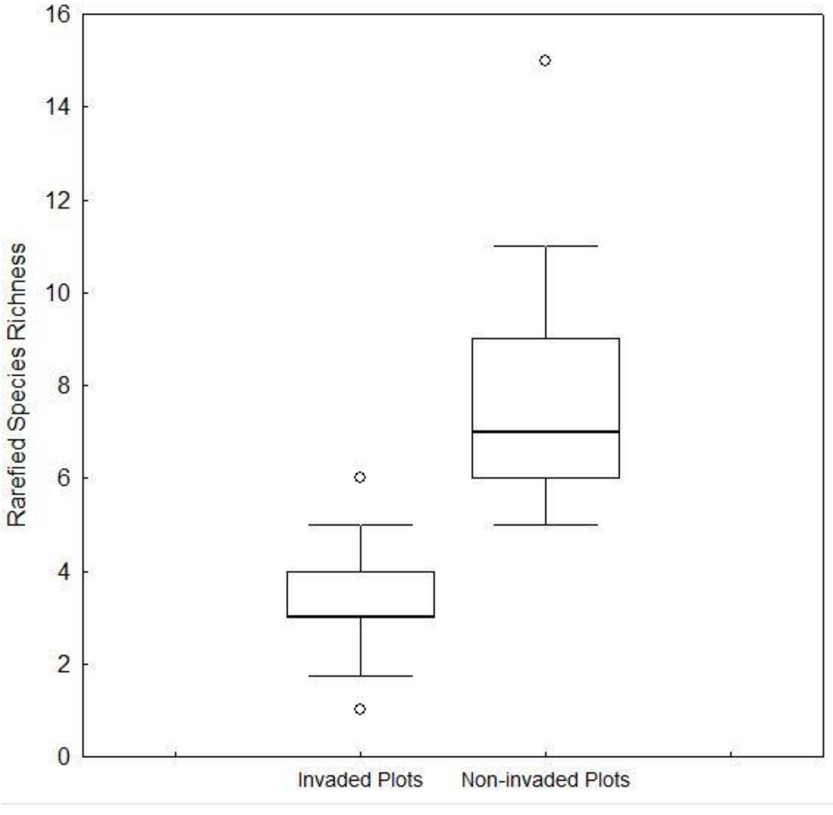

Figure 3. Boxplot of the rarefied species richness in invaded and non-invaded sites. Boxplot are median (bold black line), quartiles (white rectangles), non-outlier range (black lines), and possible outliers (white circles).

Sites invaded by *C. procera* presented significant difference in species richness compared with both of other invaders (*C. procera* vs *N. glauca*: F= 6.77, p= 0.009, and *C. procera* vs *P. juliflora*: F= 5.84, p= 0.016) (Table 2). In contrast, *Nicotiana glauca* and *P. juliflora* were not significant different from each other (F= 1.1, p= 0.319) (Table 2). The highest mean richness of sites invaded by *C. procera* (18±2.08 species) in comparison with sites invaded by *N. glauca* (10±2.5 species) and *P. juliflora* (9±7 species) suggest that *C. procera* allows more species to co-occur in sites dominated by this (Fig. 4).

Table 2. Results of one-way non-parametric permutational multivariate analysis of variance (PERMANOVA) tests for differences between invasive species in the diversity of the invaded communities. DF = Degrees of freedom; SS = sums of squares; MS = mean square; Statistical test = F; R² = determination coefficient; p = probability value. 999 permutations and α = 0.05. Source: Invasive Non-native Species (I.N.S.).

	Pairwise comparisons					
	C. procera vs. *N. glauca*		*C. procera* vs. P. *juliflora*		*N. glauca* vs. *P. juliflora*	
Source	F	P	F	p	F	p
I.N.S.	6.77	**0.009**	5.84	**0.016**	1.1	0.319

Note: Results in boldface are significant at $p < 0.05$.

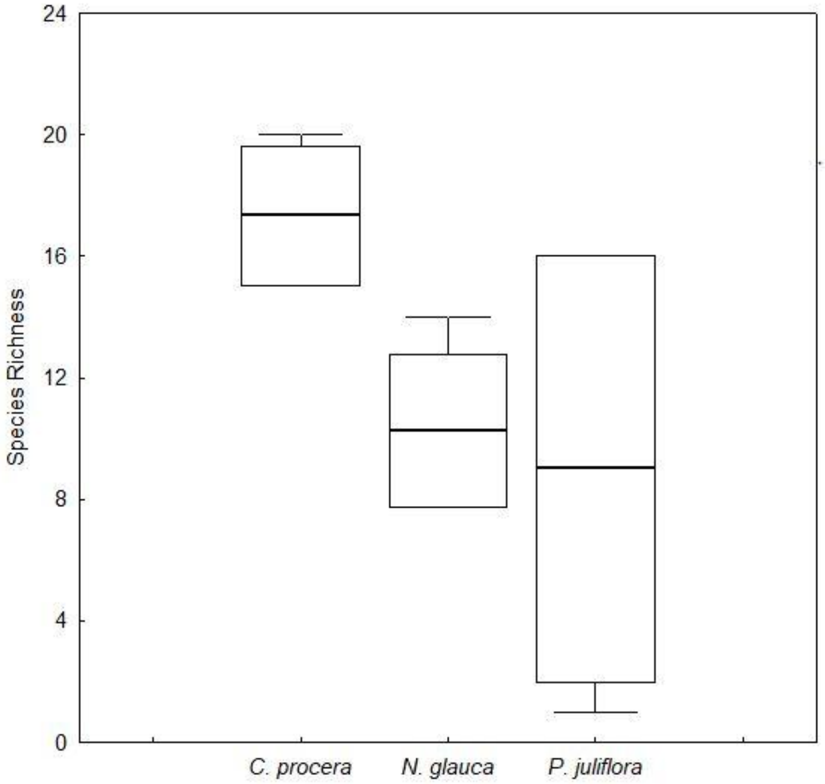

Figure 4. Boxplot of the mean species richness of the invasive species on the study. Boxplot are mean (bold black line), standard deviation (white rectangles), non-outlier range (black lines).

Species association

The IndVal method revealed three significant indicator species for sites invaded by *Calotropis procera* (*Piptadenia stipulacea*: p= 0.018; *Poincianela pyramidalis*: p= 0.018, and *Mimosa arenosa*: p= 0.013), and one significant indicator species for sites invaded by *Calotropis procera* and *Nicotiana glauca* (*Sida sp2*: p= 0.030) (Table 3). No species were disproportionally associated with *P. juliflora* populations. All the species associated with the groups are natives to the Caatinga. Life forms of the indicators varied among herb, shrub, subshrub and tree. All indicator species are related with pioneer and/or early secondary successional stages. IndVal results supported the results of one-way PERMANOVA tests. Sites invaded by *C. procera* were the only that had strongly associated species.

Table 3. Species associated to each invaded site by Indicator Value (IndVal) method. Indicated Groups: Sites invaded by *C. procera* populations (1), Sites invaded by *N. glauca* populations (2), IndVal Index (ranged from 0 to 1), Statistical significance (p< 0.05), values obtained by aleatory permutation procedure. Life form and Origin were checked with *Flora do Brasil* 2020.Ecological Groups: Pioneer (PI), Early Secondary (ES), according to the classification of Gandolfi et al. (1995).

Indicator Species	Indicated Group	IndVal Index	p	Life Form	Origin	Ecological Group
Piptadenia stipulacea	1	1.000	0.018	Shrub	Native	ES
Poincianela pyramidalis	1	1.000	0.018	Shrub, Tree	Native	PI, ES
Mimosa arenosa	1	0.938	0.013	Shrub, Tree	Native	PI, ES
Sida sp2	1 + 2	0.995	0.030	Herb, Shrub, Subshrub	Native	PI

Discussion

Our results support the hypothesis that sites dominated by invasive species present less species richness than neighboring non-invaded sites. Also, the invasion by non-native species in the regeneration sites was the main cause of the difference between invaded and non-invaded communities. The species richness of invaded sites was different depending on the individual dominant invasive species. However, the identity of the invasive species only marginally explained these differences. We found significant differences in plant communities between sites dominated by *N. glauca* and *P. juliflora* from those invaded by *C. procera*. We also found higher mean and absolute species richness in plots invaded by *C. procera*. This result suggests that *C. procera* has a greater tolerance to co-occurrence of native species.

Measuring the effects of invasive species on invaded communities by comparing invaded and non-invaded sites may bring some uncertainty related to other factors that could have influenced the establishment of the existing plant community other than biological invasion (Hejda et al. 2009). In our study, the invaded plots were positioned near the non-invaded areas (paired design), in sites with similar environmental conditions. Also, others effects of disturbance on the habitat were controlled using the rarefaction method for the collected data in order to avoid a potential sampling bias. We believe that possible external factors were successfully controlled once the variation in plant communities was mainly explained by the effect of invasion ($R^2 = 0.55$).

The reduced diversity in invaded areas was already expected, since invasive species generally have superior performance than natives in several traits, such as growth rate, size and fitness (Van Kleunen et al. 2010). In addition, anthropogenic disturbances, such as those found in our study area, tend to favor the increase of the diversity and abundance of non-native species (Jauni et al. 2015). The high resource-use efficiency, even in limited-resource environments (Funk and Vitousek 2007; Matzek 2011) confers to many invasive non-native species a greater ability to colonize disturbed sites compared to native species. Habitats in early successional stages after disturbance are more likely to be colonized by non-native species (Catford et al. 2012) because the damage of these disturbances on the resident community increases resource availability and creates opportunities for colonization of new species (Davis et al. 2000). It is possible that the additive effect of disturbance plus superior performance of non-native species alters the regeneration patterns of the local native community.

Except for Lugo and Helmer (2004), which suggest that exotic-dominated sites can provide suitable regeneration habitats for native species, plant invasion generally has direct or indirect negative effects on regeneration of native species (Reinhart et al. 2005; Meiners 2007; Mascaro et al. 2008; Flory and Clay 2010). Direct effects involve decreased natural regeneration through competition and reduced light availability (Flory and Clay 2010) and indirect effects related to increasing risk of seed predation (Meiners 2007) and incorporation of physical barriers to seedlings establishment (Flory and Clay 2010).

Another effect of invasive species on the regeneration of native communities is on the recruitment of native plants. It is known that non-native species could have negative impact on the growth, survival and fecundity of native seedlings (Gould and Gorchov 2000; Stinson et al. 2006), but evidences showing the mechanisms on how invasive plant species affect native plant recruitment are poorly documented. In contrast, the presence of non-native plant species may have a positive influence on the recruitment of other plants, but this is context-dependent. For example, shade-tolerant plants had greater richness and abundance under the canopy of the non-native shrub *Pyracantha angustifolia* (Rosaceae) than when associated with another native shrub (Tecco et al. 2006).

Papers have been published measuring the effects of a wide range of invaders on species diversity and composition of invaded communities (Hejda and Pyšek 2006; Hulme and Bremner 2006; Hejda and Pysek 2008; Hejda et al. 2009). They indicate that individual invaders have different levels of impact at the community scale. Traits related with species biometrics (height and cover) and the capacity to form mono-dominant stands (Hejda et al. 2009) were among the characteristics for this difference.

Aspects such as seed size and time of invasion seem to be important in minimizing the invasion effects on the regeneration of native species. Flory and Clay (2010) found that small-seeded species, which have less stored resources, were more affected than large-seeded species under the same invader. Also, the contribution of native species on canopy cover after fire events were insignificant in long-invaded sites compared with non-invaded and recently invaded sites (Holmes and Cowling 1997).

Implications for management and restoration

Despite the fact that identity of the invasive species had less explanatory power to the reduced species richness on invaded sites, we found interesting differences among the three invasive species in our study. Sites invaded by *N. glauca* and *P. juliflora* were not significantly different each other, while those invaded by *C. procera* differed of both (Table 2). Although *C. procera* has similar characteristics to the other two invaders in the studied area, such as high production of fruits and seeds (Fabricante et al. 2013) that germinate with high efficiency (Leal et al. 2013) and high tolerance to edaphic and climatic conditions (Oliveira et al. 2009), this difference indicates that *C. procera* are less restrictive to the presence of other native species. Accordingly, the IndVal analysis suggested three native species strongly associated with *C. procera* populations (Table 3). All indicator species are associated with pioneer and/or early secondary successional stages, which suggest that even under invasion by *C. procera* certain level of regeneration is allowed.

The wide distribution of *Nicotiana glauca* and *Prosopis juliflora* in the Caatinga represents serious concern for the conservation of the biome. Both species have high seed production (Shiferaw et al. 2004; Fabricante et al. 2015) with high germination rates (Shiferaw et al. 2004; Ollerton et al. 2012; Fabricante et al. 2015) and form dense and persistent soil seed banks (GISP 2005; DiTomaso et al. 2013). In addition, each species has specificities that make it difficult to restore the sites dominated by them. The high toxicity of *Nicotiana glauca* to humans (Steenkamp et al. 2002) and other animals (Panter et al. 2000) makes its natural biological control unlikely and, therefore, active and frequent management of the species is recommended. Prolonged drought periods, common in the Caatinga (Queiroz et al. 2017), increase adult mortality, but the survivor growth and the soil seed banks of *N. glauca* are easily recovered after flooding events (Florentine et al. 2006). *P. juliflora* has a socioeconomic context that favored its establishment and dispersion in Caatinga. Introduced in Brazil in the 1940s, as forage for livestock (Azevedo et al., 1982), its use was stimulated by the government (Reis 1984) and has become a key resource for the rural population. Also, several studies conducted in the Caatinga, demonstrate that *P. juliflora* has been associated with reduced diversity (Pegado et al. 2006; Andrade et al. 2008, 2009, 2010), increased mortality and inhibition growth of native species (Nascimento et al. 2014).

Restoration and management programs may face financial resources limitation, this case, a priorities planning becomes necessary to efficient use the resources. Considering the intrinsic characteristics of *N. glauca* and *P. juliflora* and its greater negative effect on the regeneration of natural areas, the areas invaded by these species should have a higher priority to receive management efforts. Based on the importance of restoration for the management of non-native plant invasion (Gaertner et al. 2012) we suggest that the management and control of non-native species in the invaded Caatinga areas must be followed by continuous efforts of active restoration. Also, the species *Mimosa arenosa*, *Piptadenia stipulacea* and *Sida* sp. are indicated for the recovery process of areas under *C. procera* invasion.

References

Almeida WR, Lopes A V., Tabarelli M, Leal IR (2014) The non-native flora of Brazilian Caatinga: deliberate introductions expand the contingent of potential invaders. Biol Invasions 17:51–56. doi: 10.1007/s10530-014-0738-6

ANA (2009) Relatório de Fiscalização do andamento do cumprimento das condicionantes estabelecidas na Resolução ANA no 411, de 26/09/2005, e nos compromissos assumidos pelo Ministério de Minas e Energia. Agência Nac Águas 1–7

Andrade EM de, Aquino D do N, Chaves LCG, Lopes FB (2017) Water as Capital and Its Uses in the Caatinga. In: Silva JMC da, Leal IR, Tabarelli M (eds) Caatinga: The Largest Tropical Dry Forest Region in South America. pp 281–302

Andrade LA, Fabricante JR, Oliveira FX (2009) Invasão biológica por Prosopis juliflora (Sw.) DC.: impactos sobre a diversidade e a estrutura do componente arbustivo-arbóreo da caatinga no Estado do Rio Grande do Norte, Brasil. Acta Bot Brasilica 23:935–943. doi: 10.1590/S0102-33062009000400004

Andrade LA, Fabricante JR, Oliveira FX (2010) Impactos da invasão de Prosopis juliflora (sw.) DC. (Fabaceae) sobre o estrato arbustivo-arbóreo em áreas de Caatinga no Estado da Paraíba, Brasil. Acta Sci Biol Sci 32:249–255. doi: 10.4025/actascibiolsci.v32i3.4535

Andrade MVM, Silva DS, Andrade AP, et al (2005) Fenologia de Calotropis procera Ait R . BR., em função do sistema e da densidade de plantio. Arch Zootec 54:631–634

Andrade MVM, Silva DS, Andrade AP, et al (2008) Produtividade e qualidade da flor-de-seda em diferentes densidades e sistemas de plantio. Rev Bras Zootec 37:1–8

Auld TD, Keith DA (2009) Dealing with threats: Integrating science and management. Ecol Manag Restor 10:. doi: 10.1111/j.1442-8903.2009.00447.x

Azevedo GF (1982) Como e porque a algarobeira foi introduzida no Nordeste. In: Fonseca FCE, Mota APB, Azêvedo CF, et al. (eds) Simpósio Brasileiro sobre Algaroba 1, Documentos. EMPARN (Empresa Agropecuária do Rio Grande do Norte), Natal, pp 300–306

Berkowitz AR, Canham CD, Kelly VR (1995) Competation vs. Facilitation of tree Seedling Growth and Survival in Early Successional Communities. Ecology 76:1156–1168

Briggs SV, Taws NM, Seddon JA, Vanzella B (2008) Condition of fenced and unfenced remnant vegetation in inland catchments in south-eastern Australia. Aust J Bot 56:590–599

Catford JA, Daehler CC, Murphy HT, et al (2012) The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. Perspect Plant Ecol Evol Syst 14:231–241. doi: 10.1016/j.ppees.2011.12.002

D’Antonio CM, Timothy Tunison J, Loh RK (2000) Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. Austral Ecol 25:507–522. doi: 10.1111/j.1442-9993.2000.tb00056.x

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: A general theory of invasibility. J Ecol 88:528–534. doi: 10.1046/j.1365-2745.2000.00473.x

Dawson W, Burslem DFRP, Hulme PE (2011) The comparative importance of species traits and introduction characteristics in tropical plant invasions. Divers Distrib 17:1111–1121. doi: 10.1111/j.1472-4642.2011.00796.x

DiTomaso JM, Kyser GB, Oneto SR, et al (2013) Weed control in natural areas in the Western United States. Weed Research and Information Center, University of California

Dufrêne M, Legendre P (1997) Species Assemblages and Indicator Species : The Need for a Flexible Asymmetrical Approach. Ecol Monogr 67:345–366

Fabricante JR, Castro RA, Araújo KCT, Siqueira-Filho JA (2015) Atributos ecológicos da bioinvasora nicotiana glauca Graham (Solanaceae) e avaliação da susceptibilidade de sua ocorrência no Brasil. Cienc Florest 25:959–967. doi: 10.5902/1980509820650

Fabricante JR, Oliveira MNA de, Siqueira-Filho JA (2013) Aspectos da ecologia de Calotropis procera (Apocynaceae) em uma área de Caatinga alterada pelas obras do Projeto de Integração do Rio São Francisco em Mauriti, CE. Rodriguésia 64:647–654

Flora do Brasil 2020 (2018) Flora do Brasil 2020. In: Jard. Botânico do Rio Janeiro. http://floradobrasil.jbrj.gov.br. Accessed 17 Aug 2018

Florentine SK, Westbrooke ME, Gosney K, et al (2006) The arid land invasive weed Nicotiana glauca R. Graham (Solanaceae): Population and soil seed bank dynamics, seed germination patterns and seedling response to flood and drought. J Arid Environ 66:218–

230. doi: 10.1016/j.jaridenv.2005.10.017

Flory SL, Clay K (2010) Non-native grass invasion suppresses forest succession. Oecologia 164:1029–1038. doi: 10.1007/s00442-010-1697-y

Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. Nature 446:1079–1081. doi: 10.1038/nature05719

Gaertner M, Fisher J, Sharma G, Esler K (2012) Insights into invasion and restoration ecology: Time to collaborate towards a holistic approach to tackle biological invasions. NeoBiota 12:57–76. doi: 10.3897/neobiota.12.2123

Gandolfi S, Leitão Filho H de F, Bezerra CL (1995) Levantamento florístico e caráter sucessional das espécies arbustivo-arbóreas de uma floresta mesófila semidecídua no município de Guarulhos, SP. Rev Bras Biol 55:753–767

Gill DS, Marks PL (1991) Tree and Shrub Seedling Colonization of Old Fields in Central New York Author. Ecol Monogr 61:183–205

GISP (2005) América do Sul Invadida: A crescente ameaça das espécies exóticas invasoras. Programa Global de Espécies Invasoras

Gorchov DL, Trisel DE (2003) Competitive effects of the invasive shrub, Lonicera maackii (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. Plant Ecol 166:13–24

Gould AMA, Gorchov DL (2000) Effects of the Exotic Invasive Shrub Lonicera Maackii on the Survival and Fecundity of Three Species of Native Annuals. Am Midl Nat 144:36–50

Graebner RC, Callaway RM, Montesinos D (2012) Invasive species grows faster, competes better, and shows greater evolution toward increased seed size and growth than exotic non-invasive congeners. Plant Ecol 213:545–553. doi: 10.1007/s11258-012-0020-x

Hejda M, Pysek P (2008) Estimating the community-level impact of the riparan non-native species Mimulus guttatus by using a replicated BACI field experiment. Rabitsch, W, F Essl F Kling (Eds) Biol Invasions - from Ecol to Conserv Neobiota 7 7:250–257

Hejda M, Pyšek P (2006) What is the impact of Impatiens glandulifera on species diversity of invaded riparian vegetation? Biol Conserv 132:143–152. doi: 10.1016/j.biocon.2006.03.025

Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. J Ecol 97:393–403. doi: 10.1111/j.1365-2745.2009.01480.x

Holmes PM, Cowling RM (1997) The Effects of Invasion by Acacia saligna on the Guild Structure and Regeneration Capabilities of South African Fynbos Shrublands. J Appl Ecol 34:317. doi: 10.2307/2404879

Hubbell SP, Foster RB, Condit R, et al (1999) Light-Gap Disturbances , Recruitment Limitation , and Tree Diversity in a Neotropical Forest. Science (80-) 283:554–557

Hulme PE, Bremner ET (2006) Assessing the impact of Impatiens glandulifera on riparian habitats: Partitioning diversity components following species removal. J Appl Ecol 43:43–50. doi: 10.1111/j.1365-2664.2005.01102.x

Jauni M, Gripenberg S, Ramula S (2015) Non-native plant species benefit from disturbance: A meta-analysis. Oikos 124:122–129. doi: 10.1111/oik.01416

Kuebbing SE, Nuñez MA (2016) Invasive non-native plants have a granter effect on neighbouring natives than other non-natives. Nat Plants 2:1-7. doi: 10.1038/nplants.2016.134

Leal IR, da Silva JMC, Tabarelli M, Lacher TE (2005) Changing the course of biodiversity conservation in the Caatinga of Northeastern Brazil. Conserv Biol 19:701–706. doi: 10.1111/j.1523-1739.2005.00703.x

Leal LC, Meiado M V., Lopes A V., Leal IR (2013) Germination responses of the invasive Calotropis procera (Ait.) R. Br. (Apocynaceae): Comparisons with seeds from two ecosystems in northeastern Brazil. An Acad Bras Cienc 85:1025–1034. doi: 10.1590/S0001-37652013000300013

Lugo AE, Helmer E (2004) Emerging forests on abandoned land: Puerto Rico’s new forests. For Ecol Manage 190:145–161. doi: 10.1016/j.foreco.2003.09.012

Mascaro J, Becklund KK, Hughes RF, Schnitzer SA (2008) Limited native plant regeneration in novel, exotic-dominated forests on Hawai’i. For Ecol Manage 256:593–606. doi: 10.1016/j.foreco.2008.04.053

Matzek V (2011) Superior performance and nutrient-use efficiency of invasive plants over non-invasive congeners in a resource-limited environment. Biol Invasions 13:3005–

3014. doi: 10.1007/s10530-011-9985-y

Meiners SJ (2007) Apparent competition: An impact of exotic shrub invasion on tree regeneration. Biol Invasions 9:849–855. doi: 10.1007/s10530-006-9086-5

Moles AT, Flores-Moreno H, Bonser SP, et al (2012) Invasions: The trail behind, the path ahead, and a test of a disturbing idea. J Ecol 100:116–127. doi: 10.1111/j.1365-2745.2011.01915.x

Myster RW (1993) Tree Invasion and Establishment in Old Fields at Huteheson Memorial Forest. Bot Rev 59:251–272

Nano CEM, Clarke PJ (2011) How do drought and fire influence the patterns of resprouting in Australian deserts? Plant Ecol 212:2095–2110. doi: 10.1007/s11258-011-9988-x

Nascimento CE de S, Tabarelli M, Silva CAD, et al (2014) The introduced tree Prosopis juliflora is a serious threat to native species of the Brazilian Caatinga vegetation. Sci Total Environ 481:108–113. doi: 10.1016/j.scitotenv.2014.02.019

Oliveira SHF, Negreiros D, Fernandes GW, et al (2009) Seedling growth of the invader Calotropis procera in ironstone rupestrian field and seasonally dry forest soils. Neotrop Biol Conserv 4:69–76. doi: 10.4013/nbc.2009.42.01

Ollerton J, Watts S, Connerty S, et al (2012) Pollination Ecology of the Invasive Tree Tobacco Nicotiana Glauca: Comparisons Across Native and Non-Native Ranges. J Pollinat Ecol 9:85–95. doi: 10.1007/s13592-013-0213-x

Ostfeld RS, Manson RH, Canham CD (1997) Effects of Rodents on Survival of Tree Seeds and Seedlings Invading Old Fields. Ecology 78:1531–1542

Panter KE, Weinzweig J, Gardner DR, et al (2000) Comparison of cleft palate induction by Nicotiana glauca in goats and sheep. Teratology 61:203–210. doi: 10.1002/(SICI)1096-9926(200003)61:3<203::AID-TERA8>3.0.CO;2-I

Pegado CMA, Andrade LA, Félix LP, Pereira IM (2006) Efeitos da invasão biológica de algaroba: Prosopis juliflora (Sw.) DC. sobre a composição e a estrutura do estrato arbustivo-arbóreo da caatinga no Município de Monteiro, PB, Brasil. Acta Bot Brasilica 20:887–898. doi: 10.1590/S0102-33062006000400013

Peng S, Kinlock NL, Gurevitch J, Peng S (2019) Correlation of native and exotic species richness: a global meta-analysis finds no invasion paradox across scales. Ecology 100:1–10. doi: 10.1002/ecy.2552

Pennington RT, Lavin M, Oliveira-Filho A (2009) Woody Plant Diversity, Evolution, and Ecology in the Tropics: Perspectives from Seasonally Dry Tropical Forests. Annu Rev Ecol Evol Syst 40:437–457. doi: 10.1146/annurev.ecolsys.110308.120327

Prior LD, McCaw WL, Grierson PF, et al (2011) Population structures of the widespread Australian conifer Callitris columellaris are a bio-indicator of continental environmental change. For Ecol Manage 262:252–262. doi: 10.1016/j.foreco.2011.03.030

Queiroz LP de, Cardoso D, Fernandes MF, Moro MF (2017) Diversity and Evolution of Flowering Plants of the Caatinga Domain. In: Silva JMC da, Leal IR, Tabarelli M (eds) Caatinga: The Largest Tropical Dry Forest Region in South America. Springer, pp 23–64

Rahlao SJ, Milton SJ, Esler KJ, et al (2009) Effects of invasion of fire-free arid shrublands by a fire-promoting invasive non-native grass (Pennisetum setaceum) in South Africa. Austral Ecol 34:920–928. doi: 10.1111/j.1442-9993.2009.02000.x

Read J (1995) Recruitment Characteristics Of The White Cypress Pine (Callztrzs Glaucophylla) In Arid South Australia. P O Box 150 17:228–40

Reinhart KO, Greene E, Callaway RM (2005) Effects of Acer platanoides Invasion on Understory Plant Communities and Tree Regeneration in the Northern Rocky Mountains. Ecography (Cop) 28:573–582

Reis MS (1984) A política de reflorestamento para o nordeste semi-árido. Edição dos Anais do 1. Seminário sobre potencialidade florestal do semi-árido brasileiro. Silvicultura 10:33–37

Ribeiro EMS, Arroyo-Rodríguez V, Santos BA, et al (2015) Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. J Appl Ecol 52:611–620. doi: 10.1111/1365-2664.12420

Rudgers JA, Holah J, Orr SP, Clay K (2007) Forest succession suppressed by an introduced plant-fungal symbiosis. Ecology 88:18–25

Shiferaw H, Teketay D, Nemomissa S, Assefa F (2004) Some biological characteristics that foster the invasion of Prosopis juliflora (Sw.) DC. at Middle Awash Rift Valley Area, north-eastern Ethiopia. J Arid Environ 58:135–154. doi: 10.1016/j.jaridenv.2003.08.011

Steenkamp PA, Van Heerden FR, Van Wyk BE (2002) Accidental fatal poisoning by Nicotiana glauca: Identification of anabasine by high performance liquid chromatography/photodiode array/mass spectrometry. Forensic Sci Int 127:208–217. doi: 10.1016/S0379-0738(02)00123-8

Stinson KA, Campbell SA, Powell JR, et al (2006) Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. PLoS Biol 4:727–731. doi: 10.1371/journal.pbio.0040140

Tecco PA, Gurvich DE, Díaz S, et al (2006) Positive interaction between invasive plants: The influence of Pyracantha angustifolia on the recruitment of native and exotic woody species. Austral Ecol 31:293–300. doi: 10.1111/j.1442-9993.2006.01557.x

Van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol Lett 13:235–245. doi: 10.1111/j.1461-0248.2009.01418.x

Zenni RD, Lacerda W, Sena G (2016) Evolutionary Dynamics of Tree Invasions Rapid increase in growth and productivity can aid invasions by a non-native tree. AoB Plants 8:1–16. doi: 10.1093/aobpla/plw048

Appendix 1. List of non-native plant species recorded in the study area. Species are arranged alphabetically according to its respective family. The following information is given for each species: Family, species names, origin (native or non-native) and life forms. Species valid names, its respective author, origin and life form were obtained with Flora do Brasil 2020.

Species	Origin	Local	Life form
Amaranthaceae			
Amaranthus sp.		I/N	Herb
Anacardiaceae			
Myracrodruon urundeuva Allemão	Native	I/N	Tree
Schinopsis brasiliensis Engl.	Native	N	Tree
Spondias tuberosa Arruda	Native	N	Shrub, Tree
Apocynaceae			
Aspidosperma pyrifolium Mart. &Zucc.	Native	I/N	Tree
Calotropis procera (Aiton) W.T.Aiton	Non-native	I	Shrub
Asteraceae			
Tridax procumbens L.	Non-native	I/N	Herb
Bignoniaceae			
Handroanthus sp.		N	Shrub, Tree
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore	Native	N	Tree
Boraginaceae			
Cordia oncocalyx (Allemão)	Native	N	Tree
Varronia globosa Jacq.	Native	N	Shrub
Bromeliaceae			
Bromelia laciniosa Mart. ex Schult. & Schult.f.	Native	N	Herb
Neoglaziovia variegata (Arruda) Mez	Native	N	Herb
Tillandsia loliacea Mart. ex Schult. & Schult.f.	Native	N	Herb
Tillandsia recurvata (L.) L.	Native	N	Herb
Tillandsia streptocarpa Baker	Native	N	Herb
Burseraceae			

Commiphora leptophloeos (Mart.) J.B.Gillet	Native	N	Shrub, Tree
Cactaceae			
Cereus jamacaru DC.	Native	N	Succulent, Tree
Melocactus zehntneri (Britton & Rose) Luetzelb.	Native	N	Subshrub, Succulent
Opuntia palmadora Britton& Rose	Native	N	Shrub, Subshrub, Succulent
Pilosocereus gounellei (F.A.C.Weber) Byles & Rowley	Native	I/N	Shrub, Succulent
Tacinga inamoena (K.Schum.) N.P.Taylor & Stuppy	Native	N	Subshrub, Succulent
Capparaceae			
Capparis yco (Mart.) Eichler	Native	N	Shrub
Cynophalla hastata (Jacq.) J.Presl	Native	I/N	Shrub
Cleomaceae			
Tarenaya spinosa (Jacq.) Raf.	Native	I	Herb, Shrub
Combretaceae			
Combretum monetaria Mart.	Native	I/N	Liana, scandent/vine, Shrub, Tree
Combretum sp.		N	Liana, scandent/vine, Shrub, Tree
Convolvulaceae			
Ipomoea asarifolia (Desr.) Roem. &Schult.	Native	I	Herb, Liana, scandent/vine
Cyperaceae			
Ptilochaeta sp.		N	Herb
Erythroxylaceae			
Erythroxylum pungens O.E.Schulz	Native	N	Shrub, Tree
Euphorbiaceae			
Cnidoscolus bahianus (Ule) Pax&K.Hoffm.	Native	N	Shrub, Tree
Cnidoscolus quercifolius Pohl	Native	N	Shrub, Tree
Cnidoscolus urens (L.) Arthur	Native	I/N	Shrub, Subshrub
Croton blanchetianus Baill.	Native	I/N	Shrub, Tree
Croton echioides Baill.	Native	N	Shrub, Tree
Ditaxis desertorum (Müll.Arg.) Pax&K.Hoffm.	Native	I	Shrub, Subshrub
Jatropha mollissima (Pohl) Baill.	Native	N	Shrub, Tree
Jatropha ribifolia (Pohl) Baill.	Native	I/N	Shrub, Subshrub

Manihot sp.		I/N	Herb, Liana, scandent/vine, Shrub, Subshrub, Tree
Sapium glandulosum (L.) Morong	Native	N	Shrub, Tree
Sebastiania macrocarpa Müll.Arg.	Native	N	Shrub, Tree
Fabaceae			
Amburana cearensis (Allemão) A.C.Sm.	Native	N	Tree
Anadenanthera colubrina (Vell.) Brenan	Native	I/N	Shrub, Tree
Bauhinia cheilantha (Bong.) Steud.	Native	N	Shrub, Tree
Calliandra sp.		N	Shrub, Subshrub, Tree
Chloroleucon foliolosum (Benth.) G.P.Lewis	Native	N	Shrub, Tree
Chloroleucon sp.		N	Shrub, Tree
Libidibia ferrea (Mart. exTul.) L.P.Queiroz	Native	N	Tree
Mimosa arenosa (Willd.) Poir.	Native	I/N	Shrub, Tree
Mimosa tenuiflora (Willd.) Poir.	Native	I/N	Shrub, Subshrub, Tree
Parapiptadenia sp.		N	Shrub, Tree
Parapiptadenia zehntneri (Harms) M.P.Lima&H.C.Lima	Native	I/N	Shrub, Tree
Piptadenia sp.		N	Liana, scandent/vine, Shrub, Tree
Piptadenia stipulacea (Benth.) Ducke	Native	I/N	Shrub
Poincianella pyramidalis (Tul.) L.P.Queiroz	Native	I/N	Shrub, Tree
Prosopis juliflora (Sw.) DC.	Non-native	I/N	Shrub, Tree
Senna macranthera (DC. ex Collad.) H.S.Irwin&Barneby	Native	N	Shrub, Tree
Tephrosia purpurea (L.) Pers.	Non-native	I	Subshrub
Vachellia farnesiana (L.) Wight &Arn.	Native	I	Shrub
Lamiaceae			
Mesosphaerum suaveolens (L.) Kuntze	Native	I/N	Herb, Shurb, Subshurb
Malvaceae			
Helicteres baruensis Jacq.	Native	N	Shrub
Melochia tomentosa L.	Native	I/N	Shrub, Subshrub
Pseudobombax marginatum(A.St.-Hil., Juss. &Cambess.) A.Robyns	Native	N	Tree
*Sida galheirensis*Ulbr.	Native	I/N	Subshrub

Sida sp1.	Native	I/N	Herb, Shurb, Subshurb
Sida sp2.	Native	I/N	Herb, Shurb, Subshurb
Sida sp3.	Native	I/N	Herb, Shurb, Subshurb
Sida sp4.	Native	I/N	Herb, Shurb, Subshurb
Sida sp5.	Native	I/N	Herb, Shurb, Subshurb
Nyctaginaceae			
Guapira noxia (Netto) Lundell	Native	N	Shrub, Tree
Boerhavia diffusa L.	Non-native	I	Herb
Portulacaceae			
Portulaca elatior Mart.	Native	I/N	Herb
Rhamnaceae			
Ziziphus joazeiro Mart.	Native	N	Tree
Rubiaceae			
Cordiera sp.		N	Shrub, Subshrub, Tree
Sapindaceae			
Serjania sp.		I	Liana, scandent/vine, Shrub
Sapotaceae			
Sideroxylon obtusifolium (Roem. &Schult.) T.D.Penn.	Native	N	Shrub, Tree
Selaginellaceae			
Selaginella sp.	Native	N	Herb
Solanaceae			
Nicotiana glauca Graham	Non-native	I	Shrub
Notidentified 1		I	
Notidentified 2		N	
Notidentified 3		N	
Notidentified 4		N	
Notidentified 5		I	
Notidentified 6		N	
Notidentified 7		N	

Notidentified 8	N
Notidentified 9	N
Notidentified 10	I/N
Notidentified 11	I/N