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INVASÃO POR *FURCRAEA FOETIDA* (ASPARAGACEAE) EM AMBIENTES COSTEIROS NO BRASIL: UMA ABORDAGEM SOBRE NICHO ECOLÓGICO, MUDANÇAS CLIMÁTICAS E GENÉTICA DE POPULAÇÕES

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RESUMO

Espécies exóticas invasoras, juntamente com as alterações climáticas, a mudança do uso da terra e as mudanças nos ciclos de nitrogênio e carbono, são identificadas como os quatro principais fatores de perda de biodiversidade global. Neste cenário, estudos sobre modelagem ecológica de nicho (ENM) têm sido cada vez mais utilizados para entender os processos de invasão biológica e como uma importante ferramenta preditiva para orientar ações de gestão e para a compilação de listas negras de espécies com alto risco de invasão. Informações detalhadas sobre o processo de introdução, colonização e propagação das espécies invasoras podem ainda ser levantadas através de estudos da composição e estrutura genética das populações englobando a área nativa e invadida. Em se tratando de plantas clonais, o conhecimento sobre o papel da diversidade genética para o estabelecimento e expansão de área de vida de espécies invasoras ainda é incipiente, o que aumenta a relevância destes estudos. Também é crescente a importância de estudos que avaliem as respostas funcionais de espécies exóticas às mudanças climáticas para antecipar os efeitos das novas condições climáticas sobre a dinâmica da invasão. Neste contexto, a presente tese teve como objetivo principal entender o processo de invasão da espécie exótica *Furcraea foetida* (Asparagaceae) no Brasil, investigar o potencial atual de sua expansão e entender como um aumento da temperatura atmosférica poderá afetar seu potencial de invasão. *Furcraea foetida* é nativa da América Central e norte da América do Sul. A espécie atualmente invade diversas regiões do Brasil, principalmente ao longo da costa Atlântica. No capítulo 1 foi investigada a hipótese de conservantismo de nicho (definido como a tendência de uma espécie manter os requerimentos ambientais ancestrais) durante o processo de invasão biológica. Também foi avaliado o potencial de invasão de *F. foetida* em novos sítios no Brasil com vistas a orientar os esforços de controle e erradicação da espécie exótica. Para a análise de modelagem de nicho, dois modelos recíprocos foram construídos: um usando registros e dados ambientais da área nativa (temperatura, pluviosidade e topografia) para prever a distribuição na área invadida, e um usando registros na área invadida para prever a distribuição nativa. Foi verificado que a espécie exótica expandiu o seu nicho realizado no Brasil, ocupando uma parte do seu nicho fundamental não disponível na área nativa. O primeiro modelo (*forward*-ENM) previu áreas de risco de invasão no Cerrado e região mais interna da Mata Atlântica. Este modelo falhou em prever a ocorrência atual da espécie exótica no sul do país. Já o segundo modelo, calibrado com dados da área invadida (*reverse*-ENM) apoiou a hipótese de que *F. foetida* é originária da bacia do rio Orinoco, bacia amazônica e ilhas do Caribe. O teste de similaridade de nicho sugeriu que as diferenças de nicho são devidas às diferenças na disponibilidade de habitat entre as áreas nativas e invadidas e não devido a mudanças evolutivas. Sugerimos que a pré-adaptação fisiológica (especialmente o metabolismo ácido crassuláceo), a pressão de propágulos pelo histórico de uso e a alta capacidade competitiva são os principais fatores determinantes da distribuição espacial atual de *F. foetida* no Brasil. No capítulo 2 nós utilizamos o marcador molecular ISSR (*inter-simple sequence repeats*) para investigar se populações clonais de *F. foetida* na área nativa (Guiana Francesa) e invadida (Brasil) diferem quanto ao nível de diversidade e estrutura genética. Nós verificamos que as populações na área invadida apresentam níveis similares de diversidade genética com relação às populações da Guiana Francesa na área nativa e também que a variação genética foi mais explicada pelas divergências entre indivíduos dentro das populações. O baixo percentual de variação explicando a divergência genética entre regiões e entre populações, e a ausência de correlação entre a distância genética e geográfica, sugerem que múltiplas introduções ao longo da costa atlântica brasileira têm desempenhado um papel fundamental na manutenção da diversidade. Sugerimos também que a invasividade de *F. foetida* está mais relacionada à fixação de genótipos pré-adaptados através da reprodução clonal do que à alta diversidade genética. Recomendamos que pesquisas futuras incluam populações de outras regiões na escala nativa, além de diferentes tipos de habitats para a melhor compreensão da estrutura genética geral da espécie. No capítulo 3, nós realizamos um experimento com câmaras de topo aberto (*open top chamber* - OTC) para avaliar se o aquecimento da temperatura do ar pode favorecer ou prejudicar o desenvolvimento de bulbilhos de *F. foetida* com base em características funcionais (número de folhas, comprimento foliar, massa seca total, área foliar específica, conteúdo de massa seca foliar e eficiência fotossintética do fotossistema II). Adicionalmente nós avaliamos se o sombreamento decorrente da cobertura vegetal é um fator crítico para o estabelecimento da espécie no ecossistema de costão rochoso. As OTCs aumentaram a temperatura média diária do ar em 0.4°C em relação à temperatura ambiente, resultando em um aumento significativamente maior no crescimento foliar dos bulbilhos. Em locais com cobertura vegetal elevada, houve aumento significativo da eficiência fotossintética (Fv/Fm) e redução do conteúdo de matéria seca foliar (LDMC), indicando um processo de facilitação para o estabelecimento da espécie. Esses resultados evidenciam o potencial de invasão da espécie em novas áreas do país, a ocorrência de mistura genética entre populações e um favorecimento ao estabelecimento inicial diante do aumento da temperatura atmosférica decorrente das mudanças climáticas. Recomendamos incluir *F. foetida* em programas de monitoramento de invasão de plantas, especialmente em áreas prioritárias para conservação. Orientamos ainda que medidas preventivas sejam tomadas para reduzir a introdução e o fluxo entre populações.

Palavras-chave: Espécie invasora clonal. Modelagem de nicho ecológico. Diversidade genética clonal. Aquecimento global.

ABSTRACT

Invasive alien species along with climate change, land-use and changes in nitrogen and carbon cycles, are identified as the four main drivers of global biodiversity loss. In this scenario, ecological niche modeling (ENM) studies have been increasingly used to understand the biological invasion processes as an important predictive tool to guide management actions and to compile black list of species with high risk of invasion. Detailed information on the introduction process, colonization and propagation of invasive species can be accessed through studies of the composition and genetic structure of the populations, encompassing the native and invaded area. In clonal plants, the knowledge about the genetic diversity role for the establishment and expansion of the living area of invasive species is still incipient, increasing the relevance of these studies. Moreover, the importance of studies that evaluate the functional responses of exotic species to climate change is growing. It has the potential to anticipate the effects of new climatic conditions on the dynamics of invasion. In this context, the main goal of this thesis was to understand the process of invasion of the exotic species *Furcraea foetida* (Asparagaceae) in Brazil to investigate the current potential of its expansion and understand how the atmospheric temperature increase could affect its invasion potential. *Furcraea foetida* is native to Central America and north of South America. This specie currently invades several regions of Brazil, mainly along the Atlantic coast. In Chapter 1 we investigated the hypothesis of niche conservatism (defined as the tendency of a species to maintain ancestral environmental requirements) during the process of biological invasion. We also evaluated the potential for invasion of *F. foetida* in new sites in Brazil in order to guide control efforts and eradication of exotic species. For niche modeling analysis, two reciprocal models were constructed. The first one used records and environmental data from the native area (temperature, rainfall and topography) to predict distribution in the invaded area. The second used records in the invaded area to predict the native distribution. It was verified that the exotic species expanded its niche in Brazil, occupying a part of this fundamental niche, not available in their native area. The first model (*forward*-ENM) predicted invasion risk areas in the Cerrado and the innermost region of the Atlantic Forest. This model failed to predict the current occurrence of the exotic species in the south of Brazil. The second model, calibrated with data from the invaded area (*reverse*-ENM), supported the hypothesis that *F. foetida* originated from the Orinoco basin, the

Amazon basin and the Caribbean islands. The niche similarity test suggested that the niche differences are due to variances in habitat availability between native and invaded areas and not due to evolutionary changes. We suggest that the physiological pre-adaptation (especially crassulacean acid metabolism), the pressure of propagules by the use of history and high competitiveness are the main factors determining the current spatial distribution of *F. foetida* in Brazil. In Chapter 2 we used the inter-simple sequence repeats (ISSR) molecular marker to investigate whether clonal populations of *F. foetida* in the native (French Guiana) and invaded (Brazil) area differ in the level of diversity and genetic structure. We also evaluated if there is a relationship between these results and the species invasion success in coastal areas. We found that populations in the invaded area show similar levels of genetic diversity in relation to native populations and also that genetic variation was more explained by divergences among individuals within populations. Adding to this the low percentage of variation explaining genetic divergence between regions and between populations, and the lack of correlation between genetic and geographic distance, we suggest that multiple introductions along the Brazilian Atlantic coast have played a fundamental role in maintaining the diversity. We also suggest that the invasiveness of *F. foetida* is more related to the fixation of pre-adapted genotypes through clonal reproduction than to high genetic diversity. We recommend that future researches include populations of other regions in the native range, as well as different types of habitats for a better understanding of the general genetic structure of the species. In Chapter 3, we performed an experiment with open-top chambers (*open top chamber* - OTC) to assess whether the heating air temperature may favor or hinder the development of *F. foetida* bulbils based on functional traits (number of leaves, leaf length, dry mass, specific leaf area, leaf dry matter content and photosynthetic efficiency of photosystem II). Additionally, we tested if the shading is a critical factor for the species establishment in a rocky shore ecosystem. OTCs increased the mean daily air temperature by 0.4 °C relative to ambient temperature, resulting in a significantly greater increase in leaf growth of bulbils. In areas with high vegetation cover, there was a significant increase of photosynthetic performance (Fv/Fm) and reduction of leaf dry matter content (LDMC), indicating a process of facilitation for the establishment of the species. These results show a broad potential for invasion of the species in new areas of the country, the occurrence of a genetic mix among populations and a favor to the initial establishment related to the atmosphere warming due to climate change. We recommend including *F. foetida* in plant invasion monitoring programs, especially in priority areas for conservation. We also recommend that preventive measures be taken to reduce introduction and flow among populations.

Keywords: Invasive clonal species. Ecological niche modeling. Clonal genetic diversity. Global warming.

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INTRODUÇÃO GERAL

Nas últimas décadas, o aumento das viagens, do comércio e do turismo tem facilitado a translocação de espécies animais e vegetais para além das barreiras físicas e geográficas que dificilmente seriam naturalmente transpostas pelas espécies (Theoharides e Dukes 2007). A maioria das espécies não sobrevive ao trajeto ou, devido às restrições fisiológicas, morre pouco tempo depois de ser introduzida em uma nova região. Aquelas que sobrevivem e geram descendentes, não mais necessitando de introduções repetidas para que possam persistir se tornam naturalizadas (ou estabelecidas) no ambiente, mas não necessariamente são capazes de se propagar (Zenni e Nuñez 2013). Então, uma pequena porcentagem das espécies introduzidas se torna invasora (Rejmanek et al. 2013). Isto ocorre quando a espécie exótica é capaz de produzir descendentes reprodutivos com frequência em grande número e de dispersá-los para longe do local de introdução, gerando novos focos populacionais, com impactos econômicos e ambientais (Richardson et al. 2000; Rejmanek 2011). Espécies exóticas invasoras, juntamente com as alterações climáticas, a mudança do uso da terra e as mudanças nos ciclos de nitrogênio e carbono, são identificadas como os principais fatores de perda de biodiversidade global (Master e Norgrove 2010). As plantas estão entre os organismos mais difundidos globalmente, uma vez que são extensivamente introduzidas para fins agrícolas, agroflorestais, controle de erosão e cultivo como ornamentais (Pysek et al. 2012). Após a introdução, o progresso para a invasão biológica envolverá a interação de múltiplos fatores, tais como fatores abióticos, características da comunidade receptora, atributos biológicos da espécie introduzida (Fridley 2011; Rejmanek 2011), da pressão de propágulos (isto é, número de propágulos e frequência de introdução) (Simberloff 2009) e da composição genética dos propágulos introduzidos (Dlugosch et al. 2015). À medida que as invasões biológicas nas áreas naturais avançam, os esforços de controle e erradicação se tornam mais complexos e ineficientes, enquanto o custo aumenta (Simberloff et al. 2013). Por esta razão, prevenir a introdução e controlar o crescimento populacional ainda na fase de estabelecimento é a estratégia mais segura e eficiente em termos econômicos para reduzir problemas futuros (Pluess et al. 2012). Com o aumento da globalização, é provável que as ocorrências de espécies exóticas invasoras aumentem. A fim de reduzir as pressões diretas sobre a biodiversidade, as medidas para prevenir a introdução e o estabelecimento de espécies invasoras são enfatizadas na Meta de Aichi número 9, componente do Plano

Estratégico para 2020 da Convenção sobre Diversidade Biológica (COP, CBD 2010). Neste contexto, a presente tese teve como objetivo principal explorar o potencial de estabelecimento e invasão da espécie exótica e invasora Furcraea foetida L. Haw. (Asparagaceae).

Furcraea foetida é uma planta originária da América Central e norte da América do Sul (García-Mendoza 2001). Os dados na literatura sugerem que esta espécie tenha surgido na Costa Rica, Panamá, na bacia do Orinoco, na bacia amazônica ou nas ilhas do Caribe, mas não há informações precisas (García-Mendoza, 2001). Por ser usada há muito tempo como fonte de fibra para produção de corda e como planta medicinal, F. foetida foi introduzida em diferentes partes do continente Americano desde a época pré-hispânica, especialmente durante as migrações de índios Arawak, Caribes e Patamonas (García-Mendoza 2001). Folhas jovens maceradas também eram usadas como sabão e xampu por índios Patamonas das Guianas (DeFilipps et al. 2004). Nos séculos XVIII e XIX, esta espécie foi levada para a Europa para uso como planta ornamental (de Zayas 1989; García-Mendoza 2001). Hoje em dia, há registros de invasão na Austrália, Nova Zelândia, Maurício, Estados Unidos (Havaí), África do Sul, Fiji e Chile (Meyer 2000; Macdonald et al. 2003). Na África do Sul, F. foetida foi classificada entre as 18 piores plantas invasoras devido ao seu impacto na estrutura e função do ecossistema, particularmente em áreas secas (Macdonald et al. 2003). No Brasil, os registros mais antigos datam do século XVII, quando foi cultivada para obtenção de fibra (García-Mendoza 2001). Atualmente a espécie é principalmente usada como planta ornamental, fixadora de dunas e para cercas vivas (Sarmento et al. 2013; Pirani e Lopes 2015). É considerada invasora nos estados de Pernambuco, no nordeste, e Rio Grande do Sul, Santa Catarina e Paraná, no sul (I3N Brasil 2016). Os impactos negativos são principalmente atribuídos à reprodução clonal como formação de densos agrupamentos de propágulos ao redor da planta mãe (Crouch e Smith 2011). Como as plantas atingem grande porte, as populações podem alterar a estrutura do habitat e levar à extinção local de espécies nativas (I3N Brasil 2016).

Esta tese é composta por três capítulos. O primeiro capítulo consiste em um estudo de modelagem de nicho ecológico com base em dados climáticos e topográficos da distribuição nativa e invadida por F. foetida, o que permitiu avaliar o risco de invasão em todo o Brasil e identificar possíveis regiões de origem em sua área nativa; o segundo capítulo envolve um estudo da composição e estrutura genética de populações para entender os fatores que determinam a invasividade desta espécie clonal, e o terceiro capítulo trata de um estudo experimental para avaliar a sobrevivência e o estabelecimento de bulbilhos em um cenário de aquecimento global.

USO DA MODELAGEM DE NICHO PARA PREVISÃO DE INVASÃO BIOLÓGICA

A modelagem de nicho ecológico (ENM) tem sido cada vez mais utilizada para prever o risco de invasão por espécies de animais e plantas (Callen e Miller 2015; Kumar et al. 2015). Nestes estudos, o espaço ecológico de ocorrência da espécie é definido por um conjunto de condições ambientais que limitam a sua distribuição no espaço geográfico (Pearson 2007). Enquanto que o nicho fundamental descreve a gama de condições abióticas que uma espécie é capaz de manter uma taxa de crescimento populacional positiva, o nicho realizado descreve as condições que uma espécie persiste submetida a interações bióticas (Wiens and Graham 2005; Pearman et al. 2008).

Com base na hipótese do conservantismo de nicho, definida como a tendência de uma espécie de reter os requisitos ambientais ancestrais (Wiens et al. 2010), esses modelos assumem que as espécies só poderão colonizar os habitats semelhantes às suas áreas nativas (Petitpierre et al. 2012). No entanto, estudos recentes demonstraram que espécies exóticas têm uma ampla capacidade de ocupar áreas climáticas diferentes da escala nativa, desde que respeitados seus limites fisiológicos (Gallagher et al. 2010; Beaumont et al. 2014).

Há duas razões principais porque o conservantismo de nicho durante a invasão biológica necessita de investigação. Em primeiro lugar, o conservantismo de nicho é um pressuposto necessário para prever o risco de invasão em regiões específicas, sendo eficiente tanto para detectar áreas de alto risco, ou seja, onde a probabilidade de estabelecimento da espécie é maior (visto que pode não prever a extensão total da invasão; Broennimann et al. 2007), quanto para inferir sobre regiões de origem na área nativa. Neste último caso, um modelo de nicho recíproco deve ser construído com base nos registros de ocorrência e dados ambientais da área invadida e projetado para a área de distribuição natural da espécie exótica, servindo como uma ferramenta auxiliar para reconstruir o histórico de invasão (detectar fontes de introdução na área nativa) (Steiner et al. 2008). Em segundo lugar, a detecção de desvios significativos do conservantismo de nicho pode evidenciar alterações ecológicas ou evolutivas durante o processo de invasão, sugerindo a capacidade da espécie invadir novas regiões (Guisan et al. 2014). Para aumentar a confiabilidade destes modelos construídos no espaço geográfico das ocorrências da espécie estudada, recomenda-se a realização de uma análise complementar de sobreposição de nicho no espaço ambiental de ambas as áreas geográficas (Broennimann et al. 2012).

GENÉTICA DE POPULAÇÕES INVASORAS

A diversidade genética se refere à quantidade total de variação hereditária acumulada ao longo do processo evolutivo de uma espécie, que é gerada através de recombinação e mutação (Hartl e Clark 2010). Chamamos de diversidade intraespecífica, ou polimorfismo, a variação genética, em termos de frequência alélica, que ocorre entre indivíduos de uma mesma espécie. A maneira como esta variação genética está particionada dentro e entre populações determina o nível de estrutura, ou subdivisão populacional da espécie (Hartl e Clark 2010).

O estudo da diversidade e estrutura genética de populações fornece importantes insights para investigar o sucesso de espécies exóticas e invasoras, sendo uma ferramenta importante para aumentar o conhecimento sobre origem geográfica, o processo de colonização, estabelecimento, propagação subsequente e o potencial para adaptação em diferentes ambientes (Sakai et al. 2001). Estas informações podem servir de subsídio para análises de risco de invasão e auxiliar o desenvolvimento de estratégias de manejo e controle de espécies invasoras (Saltonstall 2011).

Em geral, as populações introduzidas são fundadas intencional ou acidentalmente pelo ser humano, a partir de um número reduzido de indivíduos representantes de uma parcela da população original. Assim, espera-se que haja alteração ou redução nos níveis de diversidade genética originais, o que tende a reduzir a viabilidade populacional e o potencial evolutivo (Saltonstall 2011). A perda de diversidade genética em populações recém-estabelecidas pode ocorrer devido ao efeito de deriva genética (mudanças ao acaso na diversidade genética populacional ao longo do tempo), efeito de fundador (um caso especial de deriva genética, no qual a perda da diversidade genética ocorre em populações formadas a partir de uma pequena fração da população original) (Dlugosch e Parker 2008; Uller e Leimu 2011) e gargalo populacional (redução na frequência de um gene devido à redução rápida no tamanho populacional por várias gerações) (Rosenthal et al. 2008; Simberloff e Rejmanek 2011).

No entanto, a diversidade genética pode ser mantida em um nível similar ou até mesmo maior relativo às populações fonte na área nativa se as populações introduzidas forem formadas a partir de múltiplas origens e se houver hibridização e/ou mutações após a colonização (Rosenthal et al. 2008; Gaudeul et al. 2011; Kelager et al. 2013). Embora a alta diversidade genética seja importante sob o ponto de vista evolutivo, pois permite adaptação rápida ao novo ambiente, em uma recente revisão Dlugosch et al. (2015) verificaram que a diversidade genética parece raramente determinar o sucesso de invasão. Isto porque as características que tornam as populações invasoras agressivas são moldadas não pela alta diversidade genética, mas sim por genótipos específicos.

MUDANÇA CLIMÁTICA E O PROCESSO DE INVASÃO BIOLÓGICA

No período anterior à Revolução Industrial, a quantidade de CO_2 na atmosfera permaneceu estável por aproximadamente 10.000 anos (Dukes 2011). À medida que as atividades humanas pós-industriais passaram a emitir quantidades crescentes de gases de efeito-estufa (GEE) para a atmosfera, em especial o dióxido de carbono (CO_2), mais radiação infravermelha passou a ser retida, contribuindo com o aquecimento da atmosfera além dos níveis normais e gerando alterações no padrão de precipitação global (Dukes 2011). Modelos de circulação global preveem que até 2100 a média da temperatura mundial poderá aumentar de 1.0 a 3.7°C devido ao desmatamento, utilização do solo e, especialmente, a queima de combustíveis fósseis (Pachauri et al. 2014). Para a região sudeste da América do Sul, o cenário mais otimista de emissões de GEE prevê um aumento na temperatura média anual entre 0.6 a 2.0°C (Magrin et al. 2014).

As mudanças climáticas já estão apresentando consequências para diversos organismos incluindo as espécies invasoras, um componente importante da mudança ambiental global causada pelo ser humano (Capdevila-Arguelles e Zilletti 2008). Diversos estudos têm indicado que o aquecimento atmosférico irá gerar alterações importantes na distribuição geográfica, no estabelecimento e no impacto de espécies exóticas invasoras (Hellman et al. 2008; Walther et al. 2009; Bellard et al. 2013; Verlinden et al. 2014). Por exemplo, prevê-se que espécies invasoras que são atualmente restritas por temperaturas frias poderão avançar para regiões de altas latitudes e para zonas de maior elevação (Hellman et al. 2008).

Além disso, é previsto também que as populações que atualmente ocorrem apenas ocasionalmente podem se tornar estabelecidas (ou naturalizadas) através da ampliação da estação de crescimento e consequente aumento do sucesso reprodutivo (Walther et al. 2009). Finalmente, as mudanças climáticas podem ainda aumentar o potencial competitivo das espécies invasoras (comumente com tolerâncias ambientais mais amplas) sobre espécies nativas menos adaptadas às novas condições climáticas (Hellman et al. 2008). Neste contexto, espera-se que uma das consequências das mudanças climáticas globais será o agravamento dos impactos das espécies invasoras sobre os ecossistemas atingidos, aumentando as chances de danos irreparáveis à biodiversidade e às funções ecológicas (Dukes e Mooney 1999; Rejmánek et al. 2013).

Porém, estudos com uma abordagem experimental têm mostrado que essas alterações terão consequências contexto-específicas, com efeitos que podem ser prejudiciais (Williams et al. 2007; He et al. 2012; Verlinden et al. 2014) ou benéficos para a espécie invasora (Wang et al. 2011; Chuine et al. 2012), dependendo da espécie em questão e da composição da comunidade invadida. Em um estudo realizado em uma comunidade de pastagem na Austrália, por exemplo, foi observado que um aumento em +2°C na temperatura do ar pode prejudicar as invasoras Hypochaeris radicata e Leontodon taraxacoides (Williams et al. 2007). Os autores verificaram que o aquecimento causou um declínio populacional destas espécies através da redução da germinação de sementes e estabelecimento das plântulas. Em contrapartida, o aquecimento climático pode aumentar a invasividade da liana Ipomoea cairica no sul da China, promovendo o incremento em biomassa e crescimento do caule destas plantas (Wang et al. 2011). Outro estudo realizado no oeste da Europa observou que a elevação da temperatura pode alterar relações de dominância entre espécies nativas e invasoras que co-ocorrem produzindo efeitos distintos em casos específicos, como o aumento da dominância da invasora Senecio inaequidens e de Epilobium hirsutum, sobre a nativa Plantago lanceolata e invasora Solidago gigantea, respectivamente (Verlinden et al. 2014).

Uma variedade de manipulações experimentais tem utilizado sistemas ativos de aquecimento, ou seja, com controle do fluxo de energia (como por exemplo, estufas climatizadas ou lâmpadas de infravermelho) para simular as previsões de mudanças climáticas e seus efeitos sobre espécies de plantas invasoras (Williams et al. 2007; Wang et al. 2011; Verlinden et al. 2014). Geralmente, esses experimentos necessitam de mecanismos adicionais de correção de efeitos indesejados como sistemas de arrefecimento e umidificação (Kimball et al. 2005; Verlinden et al. 2014). Tais efeitos têm sido minimizados, ou mesmo superados, com o uso de câmaras de topo aberto (OTCs), um dispositivo simples e de baixo custo que foi desenvolvido pela The International

Tundra Experiment (ITEX) para passivamente (ou seja, através do aprisionamento da energia solar) gerar um ambiente aquecido artificialmente (Marion et al. 1997; Hollister e Webber 2000). A utilização destas OTCs foi validada por Hollister e Webber (2000) e têm sido amplamente utilizadas em estudos com espécies nativas de regiões de alta latitude e elevação (Klanderud 2005; Yin et al. 2008; De Frenne et al. 2010; Cavieres and Sierra-Almeida 2012). Porém, não há relatos de experimentos usando OTCs em regiões subtropicais (onde a previsão mais otimista prevê um aumento de até +2°C na temperatura média anual; Magrin et al. 2014), muito menos para avaliar o efeito do aquecimento sobre as plantas invasoras.

OBJETIVO GERAL

O objetivo deste trabalho foi entender o processo e o risco atual de expansão da espécie exótica *Furcraea foetida* no Brasil, assim como avaliar se os efeitos das mudanças climáticas afetarão seu potencial de invasão.

OBJETIVOS ESPECÍFICOS

1. Modelar o nicho ecológico de *F. foetida* na área nativa e áreas invadidas no Brasil para investigar a hipótese do conservantismo de nicho durante o processo de invasão e os fatores ambientais que limitam a distribuição dessa espécie, com vistas a determinar o potencial de invasão de novos sítios no país e orientar os esforços de controle e erradicação;

2. Investigar a diversidade genética e a estrutura das populações na área nativa e invadida para compreender os fatores envolvidos na invasividade, no processo de colonização e na distribuição geográfica de *F. foetida* invasora em zonas costeiras;

3. Avaliar a resposta dos propágulos (bulbilhos) ao aquecimento da temperatura do ar sob diferentes níveis de sombreamento de forma a prever os efeitos das possíveis novas condições climáticas sobre o estabelecimento e disseminação desta espécie invasora.

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CAPÍTULO 1 - CHANGES IN THE REALISED NICHE OF THE INVASIVE SUCCULENT CAM PLANT *FURCRAEA FOETIDA*[1]

Abstract

Furcraea foetida (Asparagaceae) is a native plant of the Tropical Americas but there is no information about its country of origin. The species was introduced into Brazil and is now considered invasive, particularly in coastal ecosystems. To date, nothing is known about the environmental factors that constrain its distribution and there is only inconclusive information about its location of origin. We used reciprocal distribution models (RDM) to assess invasion risk of *F. foetida* across Brazil and to identify possible source regions in its native range. We also tested the niche conservatism hypothesis for this species using Principal Components Analyses and statistical tests of niche equivalency and similarity between its native and invaded ranges. For RDM analysis, we built two models using maximum entropy, one using records in the native range to predict the invaded distribution (forward-Ecological Niche Model or forward-ENM) and one using records in the invaded range to predict the native distribution (reverse-ENM). Forward-ENM indicated invasion risk in the Cerrado region and the innermost region of the Atlantic Forest, however failed to predict the current occurrence in southern Brazil. Reverse-ENM supported an existing hypothesis that *F. foetida* originated in the Orinoco river basin, Amazon basin and Caribbean islands. Prediction errors in the RDM and multivariate analysis indicated that the species expanded its realised niche in Brazil. The niche similarity test further suggested that the niche differences are because of differences in habitat availability between the two ranges, not because of evolutionary changes. We hypothesize that physiological pre-adaptation (especially, the crassulacean acid metabolism), human-driven propagule pressure and high competitive ability are the main factors determining the current spatial distribution of the species in Brazil. Our study highlights the need to include *F. foetida* in plant invasion monitoring programs, especially in priority conservation areas where the species has still not been introduced.

Keywords: ecological niche models; reciprocal distribution models; niche conservatism; invasion risk; clonal plant

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Introduction

Some non-native species do not survive the journey to new habitats or die shortly after being introduced (Zenni & Nuñez 2013). Those species that reproduce (usually releasing propagules close to the parent plant) and are able to persist in the environment without direct human intervention, become naturalized, but are not necessarily invasive (Richardson et al. 2000). The biological invasion stage is reached when naturalized plants increase population size and colonise new areas in the exotic range, potentially causing damage to biodiversity and ecological functions in the invaded areas (Richardson et al. 2000; Rejmánek *et al.* 2013). As biological invasions advance across natural areas, eradication, containment and control efforts become more complex and inefficient and their cost increases (Simberloff *et al.* 2013).

Measures to prevent the introduction and establishment of invasive species are emphasised in Aichi Biodiversity Target 9 of the Strategic Plan 2020 of the Convention on Biological Diversity (CBD/COP-10), and thus research to subsidise efficient strategies, especially focusing on early invasion stages, is required. In this context, ecological niche modelling (ENM) has been increasingly used to predict invasion risk of animals (Palaoro *et al.* 2013; Riul *et al.* 2013; Kumar *et al.* 2015) and plants (Bradley 2013; Beaumont *et al.* 2014; Callen and Miller 2015) in target regions. ENM can be used as a predictive tool for the compilation of “black lists” of species with high invasion risk (Di Febbraro *et al*. 2013) or it can be used to guide management actions while taking into account potential niche shifts or geographical redistribution following climate change, e.g. as has been done in the Australian weed risk assessment system (Beaumont *et al*. 2014).

An ENM is calibrated with native occurrence records and environmental data to characterise a species’ realised niche, which is a subset of its fundamental niche (Peterson 2011). A species’ fundamental niche includes the entire set of conditions in which the species is physiologically able to survive and reproduce, whereas the realised niche is the subset of those conditions in which the species actually occurs as the result of constraints such as biotic interactions and dispersal limitation (Hutchinson 1957). Based on the niche conservatism hypothesis, defined as a species’ tendency to retain ancestral environmental requirements (Wiens *et al.* 2010), an ENM would predict highest invasion risk of a species in those regions most similar to its native range in terms of climate and/or other environmental factors (Peterson 2003). Nevertheless, because some species are able to occupy different environments than those present in their native ranges, simple climate matching may give inaccurate results, as has been reported for species of plants (Broennimann *et al.* 2007; Gallagher *et al.* 2010; Beaumont *et al.* 2014), insects (Fitzpatrick *et al.* 2007; Medley 2010), amphibians and reptiles (Tingley *et al.* 2014; Rodrigues *et al.* 2016). When shifts in a species' niche are observed during the invasion process, these shifts may be the result of adaptive evolution of environmental tolerances (genetic alterations), or differences in biotic constraints (e.g. absence of natural enemies), dispersal barriers or available habitats (Guisan *et al.* 2014). ENMs calibrated with occurrences from invaded ranges have been considered as a complementary approach for investigating invasive species, both to test the niche conservatism hypothesis and to identify the likeliest source of invasive populations in their native range (Fitzpatrick *et al.* 2007; Zhu *et al.* 2012). In this study we used Principal Components Analyses (PCA) and a reciprocal geographic distribution model (which uses an ENM calibrated with occurrence data from the native range as well as an ENM calibrated with data from the invaded range) to predict the distribution of *Furcraea foetida* (L.) Haw (Asparagaceae) in its native and invaded ranges and to test the hypothesis of niche conservatism in this species.

Furcraea foetida is a native plant of the Tropical Americas, but there is no information about its country of origin (García-Mendoza 2001). It is thought that this species first evolved in Costa Rica, Panama, the Orinoco basin, the Amazon basin or the Caribbean islands (García-Mendoza 2001). Because it has long been used as a source of fibre to produce rope, *F. foetida* was introduced by humans throughout America in ancient times, especially during the migrations of Arawak and Carib Indians (García-Mendoza 2001). In the eighteenth and nineteenth centuries, this species was taken to Europe for use as an ornamental plant (García-Mendoza 2001; de Zayas 1989). Today, there are invasion records of *F. foetida* in Australia, New Zealand, Mauritius, the United States (Hawaii), South Africa, Fiji and Chile (Meyer 2000; Macdonald *et al.* 2003; Crouch and Smith 2011). In South Africa, *F. foetida* was ranked among the 18 worst invasive plants because of its impact on ecosystem structure and function, particularly on dry areas (Macdonald *et al.* 2003). In Brazil, the oldest records date from the seventeenth century, when it was cultivated for fibre (Garcia-Mendoza 2001). Since then, this economic activity has declined and *F. foetida* is now cultivated mainly as an ornamental plant, for sand dune fixation and for living fences (Sarmento *et al.* 2013; Pirani and Lopes 2015).

The large continental extent of Brazil – an area of 8.5 million km² – its Atlantic coast ranging over 7,367 km and its many distinct climate zones, including humid tropics in the north, a semi-arid zone in the northeast and temperate areas in the south, making it particularly appealing for studies addressing the environmental conditions that may prevent or facilitate the stablishment of an invasive species. Currently, *F. foetida* is considered invasive in the state of Pernambuco in the northeast and in the states of Rio Grande do Sul, Santa Catarina and Parana in the south (I3N Brasil 2016). Within these regions, the species occupies different types of habitat, such as steppes and forests. In the Atlantic Forest, it is found in seasonal semi-deciduous forest, sub-montane rain forest and coastal environments (rocky shorelines, coastal dunes, sand flats and coastal islands). *Furcraea foetida* has strong negative impacts on native ecosystems as a result of its clonal reproduction. Each plant grows thousands of plantlets on its inflorescences, which fall to the ground, easily rooting and forming dense clusters around the mother plant (Crouch & Smith 2011). Because the individual plants grow very large, the high density populations that result greatly change habitat structure and lead to species replacement (I3N Brasil 2016).

Even though *F. foetida* occurs in protected areas and government policies already include the species in official Brazilian invasion lists (Leão *et al*. 2011; CONSEMA 2012; IAP 2015), there are no published studies about the environmental factors that constrain this species' distribution to guide control and eradication efforts. To fill this gap, five key questions were investigated in this study: i) Is the niche of *F. foetida* the same in its native and exotic ranges? ii) If there were changes in the species' niche during invasion, along which environmental axes did it? iii) What are the environmental conditions that explain the current distribution of *F. foetida* in the native and invaded ranges? iv) Which areas are at greatest risk of invasions in Brazil? v) Where did *F. foetida* originate in its native range?

Methods

Study species

Furcraea foetida's common names include piteira, Mauritius hemp, green aloe, Cuban hemp, giant false agave, false agave, giant cabuya and cocuiza. It is a monocarpic plant, thus dying after flowering, and has a life span of 5-20 years. It has a basal rosette of leaves that can grow up to 4 m in diameter and over 2 m in height. It produces a woody floral stem up to 10 m tall (Pirani & Cordeiro 2002) (Fig. 1A). It reproduces essentially clonally by a rare mechanism called pseudovivipary, in which vegetative propagules called bulbils are produced in reproductive structures (Crouch & Smith 2011) (Fig. 1B). Long-distance dispersal may be facilitated by water, especially sea water in coastal regions, and by humans (Hueck 1953; Sarmento *et al.* 2013).

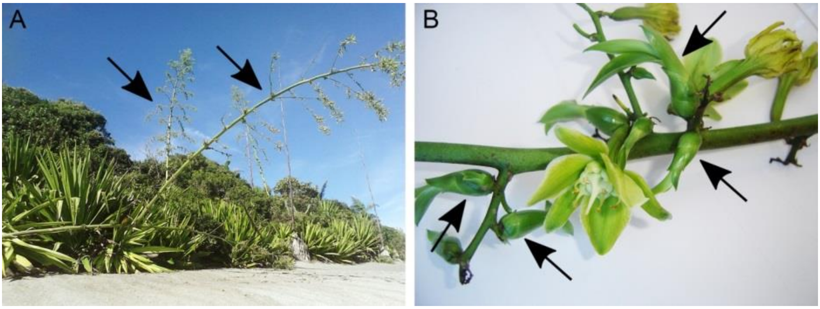

Fig. 1 Invasive populations of *Furcraea foetida* in a coastal island at the extreme south of Brazil. Arrows indicate the inflorescence (A) and bulbils in the inflorescence (B).

Occurrence data

Furcraea foetida occurrence data were obtained from expert observations and from the following databases: the *Global Biodiversity Information Facility* (available at http://www.gbif.org), *SpeciesLink* (available at http://www.splink.org.br), The Horus Institute for Environmental Conservation and Development (I3N Brasil 2016), the Reflora Virtual Herbarium (available at http://www.reflora.jbrj.gov.br/), the Venezuela National Herbarium and French Guiana's Herbier IRD. We cleaned the set of records by removing i) coordinates located in urban areas (to prevent inclusion of plants cultivated in gardens), ii) all records taken before 1950 (to avoid incongruence between occurrence records and environmental data); and iii) all records without geographic information. We obtained only a small number of occurrence data from the literature and databases, likely because of the difficulty of making herbarium specimens of the large individuals of this species. Thus, to increase the size of our data set, we additionally collected data for 26 invasive populations in the field (Fig. 2). In total, we compiled data for 58 occurrences in Brazil and 39 in the native range (Costa Rica, Colombia, Venezuela, Guyana, Suriname and French Guiana).

Environmental variables

Our starting environmental data set included altitude and 19 climatic variables including temperature, precipitation and derived bioclimatic variables. Altitude was included because it is an important descriptor of the topographical features which may indicate microclimatic and land use variation on landscapes that constrain plant invasion (see Pauchard and Alaback 2003). All environmental variables were obtained from WorldClim version 1.4 (Hijmans *et al.* 2005) at the 0.08° × 0.08° grid resolution (~10 km^2). We obtained values for all the predictor variables over the entire extent of the invaded and native ranges. We then excluded a subset of correlated variables in order to reduce dimensionality and multicollinearity, to avoid overfitting and reduced predictive power (Peterson 2011). We did this by selecting variables depending on the variation inflation factor (VIF) and then reducing the list of variables until none had $\sqrt{\mathrm{VIF}} > 2$ (Tab. S1). The final set of variables we selected to build ENMs (hereafter referred to as the environmental variables) included: mean diurnal range (mdr/BIO2), isothermality (iso/BIO3), precipitation of the wettest month (pwm/BIO13), precipitation seasonality (ps/BIO15), precipitation of the warmest quarter (pwq/BIO18) and altitude (alt).

Reciprocal distribution model

Because modelling species distribution based only on native ranges likely underestimates areas suitable for invasion, we used a reciprocal distribution model (RDM, Fitzpatrick & Weltzin (2005). RDMs combine a traditional environmental niche model, based on environmental layers and occurrences sampled in the native range and used to predict the invaded range (forward-ENM), with a “reverse” model built in the invaded range to estimate the potential native range (reverse-ENM; Fitzpatrick *et al.* 2007). In addition, when reciprocal models incorrectly predict invaded and native distributions, this may indicate a niche shift, and this information can be used to improve management decisionmaking (Broennimann *et al.* 2007; Fitzpatrick *et al.* 2007; Beaumont *et al.* 2009). We did not model the species’ distribution based on native and invasive records pooled together because of its occurrence in distinct climatic zones in Brazil when compared to Central America and northern South America, therefore raising potential differences in *F. foetida*’s realised niche between its native and invaded ranges. When such differences exist, modelling based on pooled occurrences is inappropriate, as it results in very broad niche estimation and a poor representation of the species’ actual distribution (Peterson 2011).

We built the RDM in MaxEnt 3.3.3 (Phillips *et al.* 2006). MaxEnt is one of the most robust methods for generating species distribution models with presence-only data (Elith *et al.* 2006) and small sample sizes (Hernandez *et al.* 2006; Pearson *et al.* 2007; Wisz *et al.* 2008). MaxEnt implements a maximum entropy algorithm that contrasts presences with pseudo-absences drawn from background locations, i.e. areas accessible by dispersal, but where presence/absence is unknown (Barve *et al*. 2011; Merow *et al*. 2013). Because *F. foetida* was probably recorded mostly near larger cities, we corrected for this potential sampling bias by selecting a buffer area to use as the background area for each analysis. We selected separate buffer areas for the native range and for the invaded range. We also used geographic filtering to remove duplicate records (Aiello-Lammens *et al*. 2015).

Each buffer area was delimited as follows: 1) calculating a spatial distance matrix between all pairs of occurrences; 2) finding the longest distance in the minimum spanning tree of the distance matrix; 3) truncating the distance matrix by removing values larger than the distance found in step 2; 4) calculating the mean distance in the truncated distance matrix; 5) using the mean distance from step 4 (~300 km) as a radius to draw circles around each occurrence and 6) merging all circles into a single polygon (the buffer area). Next, using the buffer as a mask on the rasters of environmental variables, we selected ten thousand raster cells at random from each buffer/background area to be used as pseudo-absences (Phillips *et al.* 2006). The use of a buffer prevents the selection of pseudo-absences from areas too far away from known records, which would artificially inflate the model's predictive ability (Vanderwal *et al.* 2009). We then assumed that the area within the buffer is available for the species in terms of dispersal but is not entirely occupied by it because of abiotic and biotic constraints.

To perform geographical filtering (Aiello-Lammens *et al.* 2015), we ran two preliminary Maxent models, one in the native and another in the invaded range, to remove duplicated records, i.e. those falling in the same raster cell. We removed 19 samples in the invaded and 6 samples in the native range. During these first runs, we also split the records into 70% for model calibration (training) and 30% for model validation using a p-ROC test (details in the *Model valitadion* section). This meant that we ran model calibration (steps below) using 20 occurrences in the native range and 27 in the invaded range.

For the forward-ENM, the model calibrated in the native range (native model) was projected over the invaded range generating a prediction of the potential distribution of the species in Brazil. This potential distribution was then contrasted with the current distribution in Brazil that was predicted by the model calibrated only with records in the invaded range (invasive model). For the reverse-ENM, the invasive model was projected over the native range, generating a prediction of the potential native range. This was then contrasted with the current distribution in the native range that was predicted by the native model. The best set of environmental variables for predicting *F. foetida* presences in Forward-ENM and Reverse-ENM was estimated using two tests generated by MaxEnt (Phillips 2010): the relative contribution of each variable during the model training process and the gain in predictive power by the inclusion of each variable alone using the Jackknife test.

Model validation

We evaluated the accuracy of the models by the true skill statistic (TSS), and the area under the receiver operating characteristic curve (AUC) and partial-area ROC curves. TSS is a measure that takes into account both omission and commission errors and is calculated as: TSS = Sensitivity + Specificity – 1, where sensitivity measures the ability to correctly predict presences and specificity measures the ability to correctly predict ausences (Allouche et al. 2006). TSS ranges from -1 to +1, where +1 indicates perfect predictions and values of zero or less indicate a performance no better than random (Allouche et al. 2006). AUC is a measure of a model’s ability to correctly distinguish presences from pseudo-absences (Merow *et al.* 2013). AUC < 0.5 indicate that the model is not better than a random selection AUC values range from 0.5 when model performance is random, to 1, when a model has perfect predictive ability. Models with AUC > 0.9, 0.7 < AUC < 0.9, and 0.5 < AUC < 0.7 indicate, respectively, great, moderate and poor performance (Swets 1988). A model performs no better than a random classifier when AUC < 0.5.

Evaluating the ROC has some disadvantages in ecological niche modelling applications, mainly because this method gives equal weight to errors of commission (false presence predictions) and of omission (false absence predictions) (Lobo *et al.* 2008). To address this problem, we checked partial-area ROC curves with test datasets as an additional validation strategy (Peterson *et al.* 2008). In these curves, instead of the X axis representing the number of commission errors, which can only be known with true absence data, the X axis represents the proportion of the total area in which the species is predicted to occur. In this case, an AUC-ratio can be estimated as the proportion between the observed AUC-value and its null expectation as calculated by combinatory probability or resampling (Peterson *et al.* 2008). When the AUC-ratio is larger than 1, it indicates that the model performs better than a random classifier. We calculated partial ROC using the Partial ROC software (Barve 2008), setting the omission error rate at 5%, and assessed the statistical significance of the AUC-ratio with a Z-test.

Niche overlap analysis in environmental space

Because species distribution models can be biased by a differing extent and distribution of environmental gradients between ranges (Guisan *et al.* 2014), we used a method proposed by Broennimann *et al.* (2012) to directly measure niche overlap between the native and invaded ranges in a gridded environmental space. In this method, the total environmental space of both geographic areas, obtained from a principal components analysis (PCA), is divided into cells, each representing a unique vector of environmental conditions v_{ij} occurring at one or more locations in geographical space. The method then uses kernel density functions to calculate the smoothed density of number of occurrences (o_{ij}) and of available environments (e_{ij}) along the environmental axes of the PCA. Based on the values of o_{ij} and e_{ij}, an occupancy index, z_{ij}, is estimated. The values of z_{ij} range between 0 and 1, enabling the unbiased comparison of occurrence densities between areas that do not have the same distribution of environmental conditions. For this analysis, we used all records: 39 in the native and 58 in the invaded ranges. We built two PCAs from the z_{ij} values plotted on the environmental space, representing the species niches occupied by *F. foetida* in its native and invaded ranges.

We then calculated Schoener’s D index to quantify niche overlap between *F. foetida*’s native and invaded ranges. This index is calculated based on occupation (occurrence density corrected by environmental availability) of the environmental space, which is represented by the first two axes of the PCA (Warren *et al.* 2008; Broennimann *et al.* 2012). The D index varies between 0 (no overlap) and 1 (total overlap). This metric is independent of grid resolution because it is based on kernel functions.

Finally, we carried out two randomisation tests to assess niche equivalency and niche similarity between the native and invaded ranges (Warren *et al.* 2008). The niche equivalency test evaluated whether the native and invaded niches are indistinguishable. For this test, we created pseudo-replicates by pooling occurrences from the two geographical areas and then randomly dividing them into two groups while keeping the original sample sizes. For each pseudo-replicate, we calculated the D index value. We then contrasted our original observed D-value with a null distribution of 100 pseudo-replicated D-values. We rejected the hypothesis of niche equivalency if the probability of the observed D-value falling in the null distribution was lower than 0.05 ($P < 0.05$). The niche similarity test asked the more relaxed question of whether the environmental space occupied in one range is more similar or more different to the environmental space occupied in the other range than would be expected at random. That is, whether similarities/dissimilarities between the native and invaded niches are more likely to be explained by ecological factors or by chance (Warren *et al.* 2008). For this test, the species' distribution in one range was overlapped with the distribution in the other range, by randomly assigning each occurrence a new location in the other range. For each such pseudo-replicate, we calculated the D-value. This procedure was carried out 100 times in each direction (from the native to the invaded and from the invaded to the native range) to generate two new null distributions of D-values. We rejected the hypothesis of niche similarity if the probability of the observed D falling in the null distribution was lower than 0.05 in a two-tailed test ($P < 0.05$). This set of analyses was carried out using the algorithm proposed by Broennimann *et al*. (2012) in R version 3.0.2 (R Core Team 2014).

Results

Reciprocal distribution model

Native and invaded model were accurate as indicated by the TSS statistics (0.51 ± 0.1 and 0.61 ± 0.2, respectively). The native model had an AUC < 0.7 and the invasive model an AUC < 0.9, indicating poor and moderate predictive ability, respectively. However, predictive performance as measured by partial-AUC was for both models significantly better than random (Z-test; $P < 0.0001$), with values of partial AUC ± SD of 1.42 ± 0.2 for the native range and 1.55 ± 0.3 for the invaded range.

The forward-ENM (Fig. 2A and 2B) accurately predicted the occurrence of *F. foetida* in the northeast, southeast and southern coast of Brazil, but it failed to predict the species' occurrence in the extreme south of the country. Another discrepancy was that the native model also identified most of the Brazilian Central Highlands as highly suitable for the species, but there are few invasion records in this region. Isothermality and precipitation of wettest month contributed most to the native model following the Jackknife test (Fig. S1) and also demonstrating high contribution during model training, reaching contributions of 34.5% and 32.8%, respectively.

The reverse-ENM (Fig. 2C and 2D) greatly underestimated the native range of *F. foetida* in Costa Rica, Colombia, Venezuela, the innermost region of the Guianas and Amapá State (northern Brazil). The invasive model accurately predicted the native distribution only in the coastal regions of the Guianas (French Guiana, Guyana, Suriname and southeast Venezuela) and Amapá (northern Brazil), and in the coastal islands of Venezuela. Furthermore, it predicted maximum suitability in a larger region than predicted by the native model, in areas including the northern and southern coasts of the Yucatan Peninsula, the Caribbean islands (some Greater and Lesser Antilles, and the Bahamas), the coasts of Honduras and Nicaragua, Panama, the coastal regions of Ecuador, the Orinoco River mouth and the Amazon basin. Altitude and mean diurnal range contributed most in the model of the invaded range as indicated by the Jackknife test (Fig. S1) and showing a high contribution to model training, their contributions being 40.2% and 33.9%.

Niche overlap analysis in environmental space

The principal component analysis (PCA) showed a displacement of the invaded range niche centroid (the area with highest occurrence probability density in environmental space) toward higher mean diurnal temperature range (mdr), lower precipitation of the wettest month (pwm), lower precipitation seasonality (ps) and a greater volume of precipitation in the warmest quarter (pwq) as compared to the native range niche centroid (Fig. 3A-C). The native and invaded ranges showed low niche overlap (Schoener’s D = 0.217; Fig. 3) and the niche equivalency hypothesis was rejected (P = 0.02; Fig. 3D). The niche similarity tests did not reject the null expectation (P > 0.05 in both directions), indicating that differences in the realised niche can be explained by differential availability of environmental conditions in the native and invaded ranges (Fig. 3E-F).

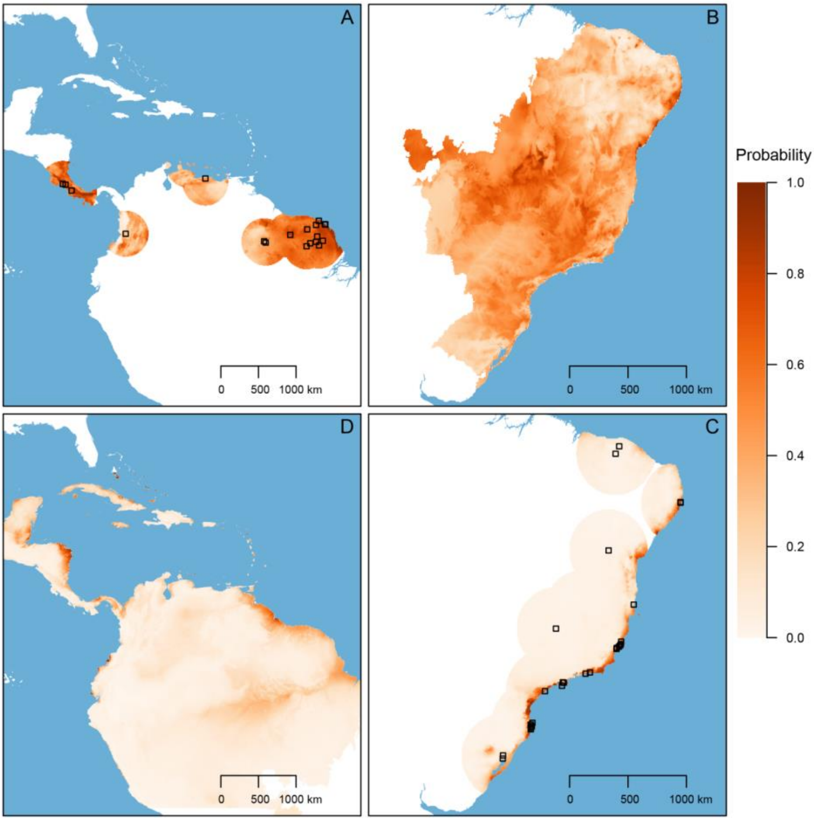

Fig. 2 Logistic output of maximum entropy niche models of *Furcraea foetida*'s geographic distribution using environmental data and current occurrences (black open squares). Habitat suitability increases from light to dark. (A) Native model based on occurrences in the native range (Central America and northern South America). (B) Native model projected onto invaded range (Brazil, except for the Amazon, which is within its native range). (C) Invasive model based on occurrences in the invaded range. (D) Invasive model projected onto the native range.

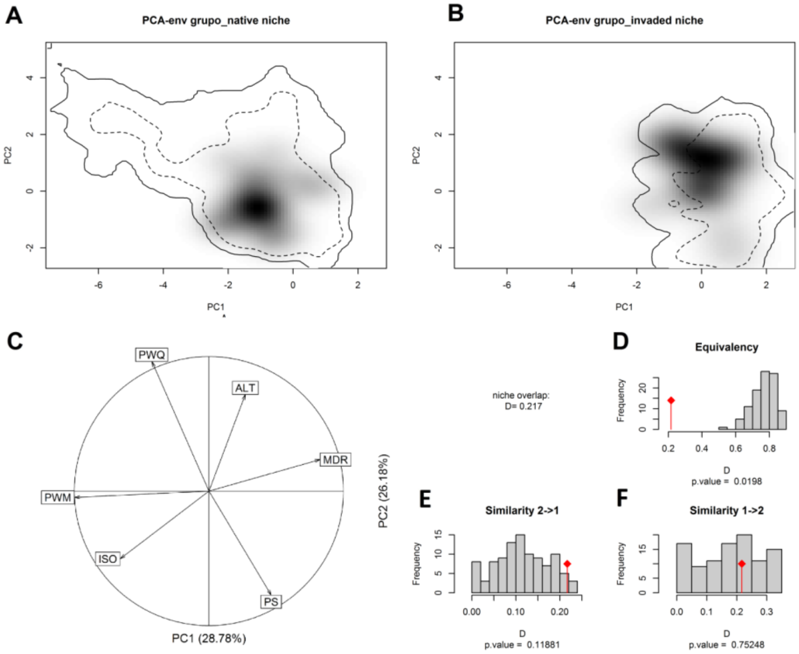

Fig. 3 *Furcraea foetida*’s niche in its native and invaded ranges, with tests of niche overlap and similarity. (A, B) *Furcraea foetida*’s niche in environmental space, as defined by the first two axes of a principal component analysis (PCA). The X axis represent the 100 pseudo-replicated D-values. The shaded area represents species occurrence density by cell. The solid and dashed contour lines delimit 100% and 50%, respectively, of the background area in the environmental space. (A) The species’ niche in its native range in Central America and northern South America. (B) The species’ niche in its invaded range in Brazil (excluding the Amazon region). (C) Contribution of the climatic variables to the first two PCA axes and contribution percentage of the first two axes for data variation. (D-F) Observed niche overlap *D* between the two ranges (red bars with a diamond) and simulated niche overlaps (grey bars) on which tests of niche equivalency (D), niche similarity between invaded and native ranges (E) and niche similarity between native and invaded ranges (F) were calculated. The significance of each test is given under each histogram.

Discussion

Even though *Furcraea foetida* retained only 20% of its native ecological niche in the invaded region, we showed that differences in the realised niche result from differences in habitat availability (i.e. environmental conditions) between the native and invaded ranges rather than changes in habitat preference, which would be expected in the case of niche evolution during invasion. This latter phenomenon requires an actual change in species' preferences, placing populations away from the environmental conditions encountered in its native range. Our findings do not support directly such a change and instead show that *F. foetida* preferred environmental conditions are similar in both native and invaded ranges, but that conditions identical as those from the native range are lacking in the invaded range. Niche overlap analysis indicated that *F. foetida* expanded its realised niche in Brazil toward regions with higher temperature range (mdr) and precipitation of warmest quarter (pwq). The prediction error in the reciprocal distribution model (RDM) supported this hypothesis, indicating that in Brazil, *F. foetida* occupies a part of its fundamental niche that is not available in its native range. The output of the invasive model associates *F. foetida* with lower average temperature range and low altitude regions, given the presence of invasive populations covering up subtropical regions of Brazil, especially in coastal environments.

The forward-ENM partially failed to predict the current distribution of *F. foetida* in the invaded range, especially in the extreme south of Brazil. This can be explained because in the native range the distribution of *F. foetida* correlates with high isotermality and high precipitation of the wettest month, with seasonality being a result of differences in rainfall levels. Southern Brazil, in turn, has little rainfall seasonality, but substantial annual differences in temperature. The forward-ENM model predicted that *F. foetida* should occur in areas from which we have the oldest known records of cultivation in Brazil - in the tropical region of northeast, where there is a record from the seventeenth century, when it was cultivated by the Dutch in the states of Ceará and Pernambuco (García-Mendoza 2001), and in the southeast, where there is a record from the nineteenth century (Neuwied 1820). Other studies of introduced species using climate-based models calibrated on the native range have also accurately predicted areas of first introduction but not the total extent of invasion, e.g. studies of the invasive herbaceous plants *Centaurea maculosa* in North America (Broennimann *et al*. 2007) and *Eragrostis plana* in South America (Barbosa *et al*. 2013) and of the dengue mosquito *Aedes albopictus* in the US, Europe and South America (Medley 2010). The failures in these climate-based reciprocal models indicate a niche shift occurring at the genetic and/or ecological level, i.e. in the fundamental and/or realised niche of the invasive species. As in these previous studies, the failures of our reciprocal distribution model might indicate changes in the realised niche of *F. foetida* in its invaded range.

The ability of alien species to colonise and survive in environmental conditions within the introduced range that are not found in the native range has been demonstrated in several studies with plants (Beaumont *et al*. 2009; Gallagher *et al*. 2010; Beaumont *et al*. 2014). Many key factors have been mentioned as driving non-native species to expand their realised niche when introduced to a novel region (reviews in Alexander & Edwards 2010; Lloret et a. 2005; Guisan *et al*. 2014; Gallagher *et al*. 2015). In the case of *F. foetida*, we believe that the key factors driving its successful establishment across a wide environmental gradient in Brazil are physiological pre-adaptation (particularly succulence and CAM metabolism), high competitive ability (associated with functional traits, such as clonal reproduction and large leaf size) and human-driven propagule pressure.

The high water use efficiency associated with succulent leaves and CAM metabolism (which allows stomata to be opened for fixing CO_2 only at night) are physiological traits which allows *F. foetida* to thrive in a broad range of environmental conditions, from low stress conditions to high stress conditions, such as short periods of drought and salt spray (García-Mendoza 2001; Francis 2009). Recent studies about bioenergy production have shown that succulent CAM species of the genera *Agave* and *Opuntia* have a strong ability to withstand climate change, with high CO_2 uptake over a wide range of temperatures and higher biomass production in warmer climates (Holtum & Winter 2014; Owen *et al*. 2015).

Other studies have found high competitive ability of CAM plants with clonal reproduction introduced to environmental conditions distinct from those in their native ranges (e.g. *Opuntia* in north-eastern Spain, Gimeno & Vilá 2002; *Agave* in south-east Spain, Badano & Pugnaire 2004). Badano & Pugnaire (2004) found high rates of clonal reproduction and establishment in *Agave* in sandy soils in its invaded area, even though such soils are rare in its native range. Likewise, clonal propagation can explain the invasiveness of *F. foetida*, as it generates huge numbers of clonal propagules, making it very competitive against native plants (Crouch & Smith 2011). Indeed, clonal reproduction is commonly mentioned as triggering invasion success, largely via increasing populations by lateral expansion and reducing or preventing the growth of surrounding native plant communities (Badano & Pugnaire 2004; Lloret *et al*. 2005). Vegetative propagation and large leaf size were positively associated with average alien species abundances and succulence was important during invasion of ruderal habitats across five Mediterranean islands (Lloret et al. 2005).

The colonization of new areas by *F. foetida* is commonly assisted by humans because its bulbils lack adaptations for any natural dispersal strategy (Hueck 1953). The distribution of invasive *F. foetida* populations across a wide latitudinal range, skewed towards the eastern part of Brazil, seems to be strongly related to its historical use and the number and timing of introduction events (Simberloff 2009). Up until the 1940's and '50's, *F. foetida* fibres were used for a wide variety of products, including handicrafts and fishing equipment such as ropes, fishing nets, buoys and rafts (Sarmento *et al*. 2013). From this time on, because synthetic fibres became extensively available, these uses of the species were abandoned. This historical use and its current use in fixing mobile dunes (Pirani & Lopes 2015), explain why *F. foetida* has invaded mostly the Atlantic Forest coastal ecosystems, such as salt marshes, rocky coasts and coastal islands.

Although our results point to changes only in the realised niche of *F. foetida*, in dealing with an introduced species used for cultivation, potentially under artificial selection, and supposedly originated from other species (in this case, *F. tuberosa*; see García-Mendoza 2001), we cannot rule out the possibility of genetic changes. Furthermore, recent studies have shown mutations in somatic cells of *Agave* propagules, a genus morphologically and physiologically similar to *Furcraea* (González *et al*. 2003; Infante *et al*. 2006). Such changes taking place in the invaded range, whether because of selection or mutation, could change the species' fundamental niche (Broennimann & Guisan 2008; Mukherjee *et al*. 2011). Nevertheless, there is no enough evidence for changes in the fundamental niche of this species and this possibility should be tested with molecular experimental approaches and ecophysiological trials (Alexander & Edwards 2010). For example, through an approach involving field data, molecular analysis and growing in common garden experiments, a study showed high genetic diversity, local adaptation and phenotypic plasticity in introduced *Wedelia trilobata* populations, a clonal invasive weed in southern China (Si et al. 2014).

Suitable areas predicted by the reverse-ENM in the native distribution - around the Orinoco river basin, in the Amazon basin and on Caribbean islands - support the existing hypotheses about the region in which *F. foetida* evolved as a species (García-Mendoza 2001; see also Drummond & Prain, 1907). This indicates that these regions are possible sources for the introduction of *F. foetida* into Brazil. In addition to these areas, reverse-ENM also predicted suitable areas in eastern Mexico, the coastal region of Honduras, Nicaragua, Ecuador and Panama. These results from the reverse-ENM, combined with the current broad distribution and the historical use of *F. foetida* in Brazil, provide strong evidence that there were multiple independent human-assisted introduction events. Multiple introductions can result in high genetic variability in the introduced populations, increasing the chance that there will be individuals already adapted to survive/reproduce in the new place, on which natural and artificial selection can act (Maron *et al*. 2004). To conclusively evaluate our results about the origin of *F. foetida*, population genetic studies must be carried out, both in its native and invaded ranges (Maron *et al*. 2004; Mukherjee *et al*. 2011).

The forward-ENM model results indicate at risk of *F. foetida* invasion in the Brazilian Central Highlands, where currently there are no records of established populations. This region is covered mainly by the Cerrado, an ecoregion considered a ‘biodiversity hotspot’ (Myers et al. 2000). The forward-ENM model also predicted high invasion risk in the innermost region of the Atlantic Forest, a hotspot whose coastal areas have already been invaded. To achieve the Aichi Biodiversity Target 9 of the Strategic Plan 2020 of the CBD, and to help reduce direct pressures on native biodiversity, we highlight the need to include *F. foetida* in plant invasion monitoring programs, especially for these areas under high conservation priority where the species has not yet been introduced.

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Suplementary

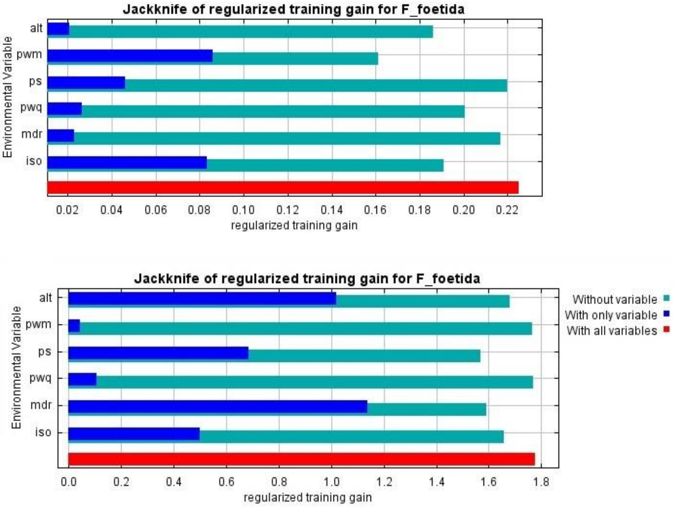


Fig. S1 Results of jackknife evaluation of relative importance of predictors for training gain in (A) Forward-ENM and (B) Reverse-ENM such that: alt: altitude, pwm: precipitation of wettest month, ps: precipitation seasonality, pwq: precipitation of warmest quarter, mdr: mean diurnal range, and iso: isothermality.

Tab.S1 Variation inflation factor (VIF) for entire set of values for de predictor variables within the entire extent of both calibration areas. Bio1 - Annual Mean Temp, Bio2 - Mean Diurnal Range (Mean of monthly (max temp - min temp)), Bio3 - Isothermality (Layer2/Layer7) (* 100), Bio4 - Temp Seasonality (stand dev *100), Bio5 - Max Temp of Warmest Month, Bio6 - Min Temp of Coldest Month, Bio7 - Temp Annual Range (Layer5-Layer6), Bio8 - Mean Temp of Wettest Quarter, Bio9 - Mean Temp of Driest Quarter, Bio10 - Mean Temp of Warmest Quarter, Bio11 - Mean Temp of Coldest Quarter, Bio12 - Annual Precip, Bio13 - Precip of Wettest Month, Bio14 - Precip of Driest Month, Bio15 - Precipitation Seasonality (Coefficient of Variation), Bio16 - Precip of Wettest Quarter, Bio17 - Precip of Driest Quarter, Bio18 - Precip of Warmest Quarter, Bio19 - Precip of Coldest Quarter, Alt – Altitud. * Predictor variabels selected for the model, with √VIF value < 2.

Bio1	**Bio2***	**Bio3***	**Bio4**	**Bio5**	**Bio6**	**Bio8**	**Bio9**	**Bio10**	**Bio11**	**Bio12**	**Bio13***	**Bio14**	**Bio15***	**Bio16**	**Bio17**	**Bio18***	**Bio19**	**Alt***
793.71	74.85	37.19	895.45	158.09	467.91	12.95	18.08	945.06	3398.26	54.91	49.89	72.10	7.58	81.83	101.89	4.96	5.68	15.01
537.59	73.80	36.28	94.51	149.82	467.30	12.90	18.08	476.48		53.52	49.78	71.68	7.55	81.36	101.81	4.96	5.67	14.90
	57.02	31.58	54.19	115.45	399.20	12.36	17.27	139.92		53.14	49.69	71.37	7.54	81.30	100.76	4.80	5.65	14.69
	9.49	13.81	24.04	75.87		12.13	16.43	116.19		52.67	49.25	70.55	7.52	80.61	99.71	4.77	5.37	14.50
	5.42	11.91	21.61	23.20		8.27	15.53			52.47	49.21	68.79	7.28	80.59	97.93	4.41	5.37	12.82
	5.41	11.78	21.17	23.18		8.19	15.40			43.71	48.94	7.43	7.07	75.04		4.40	5.30	12.69
	5.35	11.76	21.05	22.98		8.19	15.40			32.44	17.54	6.67	6.58			4.40	5.16	12.34
	5.35	10.93	19.50	22.09		8.17	15.39				4.55	5.12	4.84			3.66	4.51	11.96
	2.20	9.73	19.49			5.52	10.80				4.46	5.06	4.84			2.98	4.45	9.79
	1.65	4.94				5.06	7.49				4.20	5.04	4.76			2.98	4.23	6.80
	1.61	3.13				5.06					4.01	5.04	4.64			2.60	4.23	4.46
	1.58	2.04									3.98	4.87	4.52			2.53	4.17	1.36
	1.58	1.89									3.97		2.51			1.96	4.02	1.30
	1.56	1.76									1.97		1.60			1.69		1.27

CAPÍTULO 2 - MULTIPLE INTRODUCTIONS CAN ACT IN THE MAINTENANCE OF GENETIC VARIABILITY OF AN INVASIVE CLONAL SPECIES IN COASTAL ENVIRONMENTS

Abstract

Furcraea foetida (L.) Haw. (Asparagaceae) is an invasive plant in various tropical and subtropical regions of the world. In Brazil, the species invade mainly along the Atlantic coast. The reproduction is essentially clonal, with efficient production of thousands vegetative propagules per individual. The occupation of the southern regions of the country resulted from the expansion of the ecological niche, suggesting its high invasiveness. The actual distribution seems to be related to its historical use and human-driven propagule pressure. In this study we hypothesize that the maintenance of genetic diversity of clonal populations is mainly given by multiple introductions events. We also hope that the introduction of new genotypes from different sources should increase the genetic differentiation among individuals within the same population and decrease among populations. The objective of this study was to evaluate the genetic diversity and structure of populations in the native and invaded range to understand the factors involved in the geographic distribution in coastal environments. For this purpose we used ISSR molecular markers (inter-simple sequence repeats) to investigate: i) the level of genetic diversity of clonal populations; ii) the distribution of genetic diversity between native and invaded areas; iii) the variability and genetic structure of populations in the native and invaded area. Three populations in the native area (French Guiana) and nine in the invaded area (southeast and south of Brazil) were sampled. Invaded populations showed similar levels of genetic diversity in relation to the native populations. Genetic variation in both areas was explained due to divergences among individuals within populations than between populations and between regions. Based on the history of human use, we believe that multiple sources of introduction are the main factor in maintaining clonal diversity. We recommend that human-mediated dispersal should be prevented in order to halt the continued expansion.

Keywords: ISSR, clonal invasive, clonal diversity, genetic structure, multiple introductions

Introduction

The science of biological invasions, an important component of global change, is a growing field of studies concerned with the detection, understanding and mitigation of the health, economic and environmental impacts generated by the anthropogenic introduction of animal and plant species into ecosystems where they originally did not occur (Simberloff et al. 2013). Information on the composition and genetic structure of populations encompassing the native and invaded area can provide valuable insights into the invasion histories (since introduction, colonization, and subsequent propagation) and the reproductive system of the species concerned (Barret et al 2008; Dlugosch & Parker 2008; Simberloff & Rejmánek 2011; Kelager et al. 2013; Bock et al. 2015). With the accidental or intentional translocation of species globally, changes in the genetic diversity, structure and degree of differentiation may occur in newly introduced populations as a function of a genetic drift, founder effect and demographic bottlenecks (Dlugosch & Parker 2008).

In general, naturalized populations of species that have been intentionally introduced multiple times over an extended period of time tend to accumulate more genetic diversity (especially if the extent of native area is large) than naturalized populations from single or occasional introduction (Dlugosch & Parker, 2008; Keller & Taylor 2010; Verhoeven et al. 2010; Bock et al. 2015). However, several researches indicate that the role of genetic diversity can vary in plants with different reproductive modes and for this reason, it will not necessarily be a determining factor for invasion success (Wang et al. 2005; Li et al. 2006; Dlugosch et al. 2015; Geng et al. 2016). In plants with clonal reproduction for example, it is expected that a proliferation of identical genotypes will increase the importance of genetic drift by decreasing the effective size of the population (Reusch et al. 2000).

Molecular markers have been widely used to investigate whether the genetic diversity of clonal populations can determine the invasiveness of these plants, as well as if there is a relationship with the invasion history (eg geographical origin, dispersion mechanisms, and number of introductions), local adaptation and/or phenotypic plasticity (Wang et al. 2005; Li et al. 2006; Kelager et al. 2013; Si et al. 2014; Geng et al. 2016). Some of these studies have observed that invasive clonal plants are able to thrive even at an extremely low or nonexistent level of genetic diversity as indicated for populations of aquatic plants *Alternanthera philoxeroides* (Wang et al. 2005; Geng et al. 2016) and *Eichhornia crassipes* (Li et al. 2006), both invasive in south of China.

The authors suggested that the invasiveness of these species was mainly determined by the fixation of genotypes well adapted to the new environment, by the phenotypic plasticity and by the fast vegetative propagation ability, characteristics that compensate for a low genetic diversity. But, in some cases, similar levels of genetic diversity among native and introduced populations also have been verify in clonal plants, such as *Rosa rugosa* (native to East Asia) in northern Europe (Kelager et al. 2013) and *A. philoxeroides* (native to Argentina) in the USA (Geng et al. 2016), both probably reflecting different introductions histories.

Native to Central America and North of South America, *Furcraea foetida* (Asparagaceae) is a clonal plant that is invading Brazilian coastal ecosystems such as rocky shorelines, coastal dunes, sand flats and coastal islands, but also occur in secondary forests at 2000 meters above sea level. The oldest records of *F. foetida* in Brazil date back to the seventeenth century, when it was cultivated in the northeast of the country by the Dutch for the production of fibers (Garcia-Mendoza 2001). With the substitution of this resource for synthetic fibers, the species is currently cultivated mainly as an ornamental plant and as a living fence (Pirani & Lopes 2015). Actually, there are records of invasion in several countries such as Australia, New Zealand, Mauritius, the United States (Hawaii), Fiji and Chile (Meyer 2000), being classified among the 18 worst invasive plants in South Africa (Macdonald et al. 2003). In Brazil, *F. foetida* is included in the official lists of exotic and invasive species (Leão et al. 2011; CONSEMA 2012; IAP 2015), and some management strategies have already been applied, such as mechanical eradication and spraying of herbicides (I3N-Brasil 2016).

The impact on the structure and function of ecosystems is mainly attributed to the high competitive ability associated to production of thousands of vegetative propagules (bulbils) and to the large size that adults reach (Crouch & Smith 2011). Beside this, the gravitational dispersal (with most bulbils falling around the parent plant) form dense population groups that exclude native vegetation (Crouch & Smith 2011). The production of fruits and seeds is unknown in the natural environment both in native and invaded regions (Hueck 1953; Garcia-Mendoza 2001; Pirani & Cordeiro 2002), and cited as rare in South Africa, where the plant is invasive (Crouch & Smith 2011). Colonization of new areas is commonly man-assisted, with no further adaptations to natural dispersion for long distances (Hueck 1953). However, water can also act as a secondary vector, since the bulbils fall directly into the sea (personal observation). The invasiveness of *F. foetida* should also to be relating to its wide physiological capacity (attributed mainly to succulence and CAM metabolism), and human-driven propagule pressure (Barbosa et al. 2017).

A recent study showed that *F. foetida* expanded their realized niche to novel environments in Brazil, occupying a part of its fundamental niche that does not is available in the native range and suggesting the high invasive potential of the species (Barbosa et al. 2017). Althought somatic mutations have been observed in *Agave* propagules, a genus morphologically and physiologically similar to *Furcraea* (González *et al.* 2003; Infante *et al.* 2006), Barbosa et al (2017) concluded that the wide latitudinal range of distribution of the species seems to be strongly related to its historical use and to the number and timing of introduction events. Then, in this study we hypothesize that the maintenance of genetic diversity of clonal populations is given by multiple introductions events. We also hope that the introduction of new genotypes from different sources should increase the genetic differentiation among individuals within the same population and decrease among populations. We use ISSR (inter-simple sequence repeats) molecular markers to evaluate the genetic diversity and structure of *F. foetida* populations in the native and invaded range to understand the factors involved in the geographic distribution in coastal environments. From this, three questions were investigated: i) the level of genetic diversity of clonal populations; ii) the distribution of genetic diversity between native and invaded areas; iii) the variability and genetic structure of populations in the native and invaded area.

Methods

Population sampling

Samplings were conducted in two regions distributed along the East Coast of South America (Fig. 1). In the southern coast of Brazil, 76 individuals were sampled from five populations and in the southeastern, 80 individuals were sampled from four populations (Tabela 1; Fig. 1). In French Guiana we collected 66 individuals from three populations (Table 1; Fig. 1). All populations were collected in coastal ecosystems (except Roche des Abeiles in French Guiana, located approximately 100 km from the coast). Rocky soil is similar in all populations. To ensure better quality of DNA, the collection of plant tissue was always made from the youngest leaf of the rosette. Adjacent individuals were avoided in order to prevent collection of the same genet. Samples were dehydrated over silica gel and stored at -80°C.

DNA extraction and ISSR protocol

DNA was extracted from approximately 50 mg of leaf sample according to Doyle and Doyle (1987) protocol. PCR amplifications were performed in a total volume of 20 µL, containing 2.0 µL 10x PCR buffer, 50 mM $MgCl_2$, 2 mM dNTPs, 20 µM primer, 5 units Taq polymerase (Kit Invitrogen Recombinant), H_2O and DNA template. The amplification program consisted of an initial denaturation at 94 °C for 1.5 min, followed by 37 cycles of 40 s at 94 °C, 45 s at 50 °C, 1.5 min at 72 °C and a final extension of 5 min at 72 °C. Amplification products were electrophoretically separated at a constant voltage of 100 V for 3 h in 1.5 % agarose gels with 0.5x TAE buffer, stained with ethidium bromide and photographed under UV light. A 100 bp DNA ladder was used to indicate the molecular size of the fragments.

To evaluate the diversity and genetic structure of *F. foetida* populations, we used inter-simple sequence repeat (ISSR), a dominant PCR-related nuclear markers associated to microsatellites that have been proved effective in discriminating different clones (Wang et al. 2005; Li et al. 2006; Geng et al. 2016). The ISSR marker has been used in similar studies of *Agave* (Vargas-Ponce et al. 2009; Torres-Morán et al. 2010; Aguirre-Dugua and Eguiarte 2013; Trejo et al. 2016). A total of 16 ISSR primers successfully applied in others similar studies with Furcraea and Agave species were tested for amplification reactions, from which seven were selected due to reproducibility (Table 2).

Data analyses

From the molecular ISSR data analysis, the fragments amplified were visually evaluated through images of agarose gels. Smeared and weak bands were excluded. The loci identified of all individual for each primer generated a matrix of presence (1) or absence (0) of bands. From this data, the estimates of genetic diversity parameters, as total number of loci in each population (N), mean Shannon's index of phenotypic diversity (I), percentage of polymorphic loci (P), and mean expected heterozygosity (H_e), were computed with GenAlEx 6.5 software (Peakall and Smouse 2012).

Considering the multiloci phenotype as a haplotype, the binary data were converted to a matrix of Nei's genetic distance (Nei 1978) and a Principal Coordinate Analysis (PCoA) was performed to examine

Table 1. Status of invasion, location and number of individuals collected (N) of *F. foetida* (Asparagaceae) distributed along the coast of South America.

Region	Locality	Population	Coordinates	*N*
Invaded range				
South-Brazil	Naufragados	NAU	27°50'90.14"S, 08°34'11.45"W	18
South-Brazil	Campeche	CAMP	27°41'30.37"S, 08°27'54.98"W	17
South-Brazil	Anhatomirim	ANH	27°25'42.01"S, 08°33'49.58"W	18
South-Brazil	Arvoredo	ARV	27°17'36.57"S, 08°21'59.82"W	06
South-Brazil	Galé	GAL	27°10'21.18"S, 08°24'16.87"W	17
Southeast-Brazil	Camburi	CAMB	23°46'41.95"S, 05°38'30.94"W	20
Southeast-Brazil	Alcatrazes	ALC	24° 06'00.59"S, 45°41'45.54"W	24
Southeast-Brazil	Calhetas	CAL	23°49'56.55"S, 45°31'19.22"W	24
Southeast-Brazil	Ilha Bela	IB	23°49'10.10"S, 45°22'38.64"W	12
Native range				
North-French Guiana	Roche des Abeiles	RAB	4°3'33.90"N, 52°45'28.53"W	09
North-French Guiana	Montravel	MON	4°54'32.97"N, 52°15'31.11"W	30
North-French Guiana	Roche Verte	RVE	4°55'6.05"N, 52°21'6.28"W	27

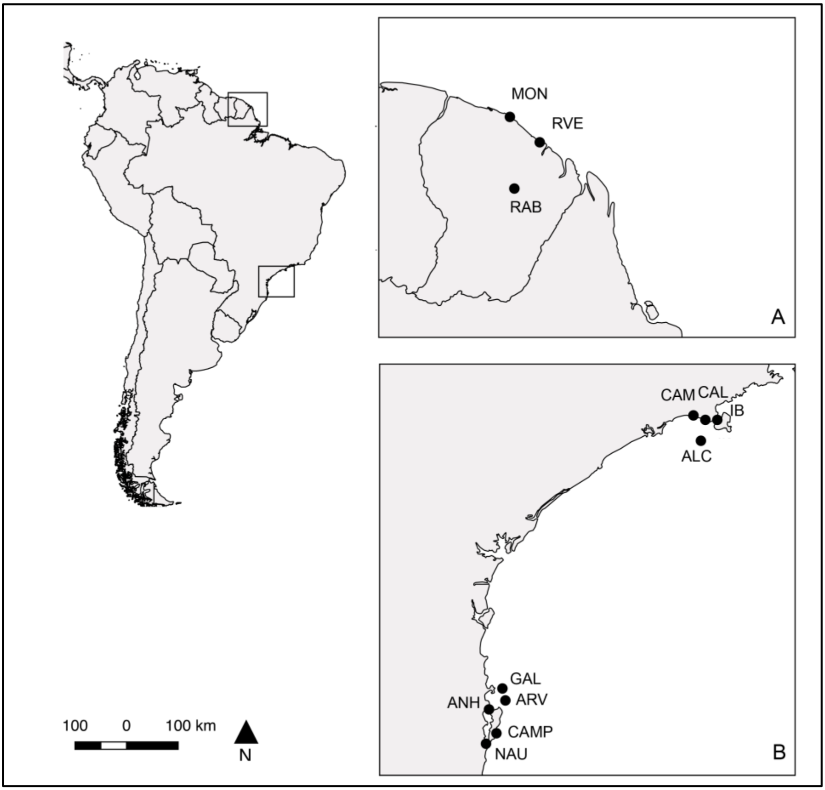


Fig. 1 *Furcraea foetida* populations sampled along the East Coast of South America in A) native range (French Guiana) and B) invaded range (Brazil). For population names, see Table 1.

overall patterns of genetic similarity among genotypes and among 12 populations using GenAlEx 6.5. The analysis of molecular variance (AMOVA) was performed (also based on matrix of Nei's genetic distance) in Genealex 6.5 for four different hierarchical levels: (1) overall dataset (invasive + native); (2) regional subsets (invasive X native), (3) invasive populations and (4) native populations. A fifth AMOVA was performed for the groups (K = 3) indicated by Bayesian analysis. The null hypothesis (H_0) for AMOVA is that subpopulations can be considered part of a single large random mating genetic population (Peakal and Mouse 2012).

A Bayesian structure analysis for overall dataset (invasive + native) was performed using the software STRUCTURE 2.3 (Falush et al. 2007; Pritchard et al. 2010). The Bayesian analysis infers the clustering number of structured populations genetically homogeneous (K) and the probability for each individual to belong to respective population (or to come from an external source). Bayesian method is more appropriate for dominant markers because accounts more appropriately for the inherent ambiguity of recessive (absent) alleles, do not assume previous knowledge of the inbreeding and Hardy-Weinberg equilibrium (HWE) and performs well even with relatively small numbers of loci and populations (Holsinger et al. 2002). The number of presumed populations (K) was set of K=1 to K=13. For each K, ten independent runs were performed with 100,000,000 Markov Chain Monte Carlo (MCMC) runs for each one, with a burn-in of 100,000 iterations. We used 'admixture model' and 'alleles correlated among populations', with the other parameters set as default (Pritchard et al. 2010). To identify optimal population clustering number, we calculated the average of each K log probability value (LnP(D)), through all runs as suggested by Pritchard et al. (2000) and the statistic **Δ**K, a good predictor of the real number of clusters for dominant markers according to Evanno et al. (2005).

To check isolation by distance, i.e. how much of the genetic differentiation between pairs of populations can be explained by geographical distance, a Mantel test (Mantel 1967) was applied using Genealex 6.5 to assess whether there is a significant relationship between the matrix of pairwise genetic differentiation (ϕ_{ST}) and geographical distances (log-transformed) between overall populations with 999 random permutations.

Table 2. Primers used for ISSR amplification of *Furcraea foetida* (Asparagaceae).

Primer name	Primer sequence	N loci	N (%)
MANNY	$(CAC)_4RC$	10	12.3
811	$(GA)_8C$	08	9.9
827	$(AC)_8G$	14	17.3
AG09	$(GACA)_3RG$	19	23.5
AG10	$YR(GACA)_3$	11	13.6
UBC814	$(CT)_8TG$	04	4.9
OMAR	$(GAG)_4RC$	15	18.5

N loci: number of loci analyzed for each primer
Y = pyrimidine (C or T); R = purine (A or G)

Results

Genetic diversity

The primers generated a total of 81 polymorphic fragments, ranging from 4 to 19 per primer (Table 2). In the invaded range, ARV population had the lowest number of fragments (69) and the ANH the highest (79) (Table 3). In the native range, the number of fragments ranged from 73 (RAB) to 78 (RVE). The percentage of polymorphic loci varied from 18.52% (ARV) to 62.96% (ANH) among populations in the invaded range and from 25.93% (RAB) to 50.62% (RBV) in the native range. The expected heterozygosity (H_e) ranged from 0.077 (ARV) to 0.221 (ANH) in the invaded range, and from 0.136 (RAB) to 0.162 (RVE) in the native range. The same populations in the invaded range (ARV and ANH) also showed, respectively, the lowest (0.111) and highest (0.330) values for Shannon Index. In the native range again, RAB and RVE showed the lowest (0.136) and highest (0.162) Shannon Index values, respectively (Table 3). One exclusive allele was observed on ANH.

Genetic differentiation among populations

The genetic differentiation was moderate among all populations ($\phi_{ST} = 0.112$; Table 4) and was lower within the native range (0.027) than invaded range (0.120). Values were always statistically significant ($P < 0.05$). In both cases, the genetic variability among individuals within the same population explained most of the total variation, ranging from 88% to 97%. The Principal Coordinate Analyses (PCoA; Fig. 2) showed that 51.41% of the population's variation was explained by the first two axes of the multivariate space. The first principal coordinate captured 31.22% of the total variance and separated the islands ARV e GAL (both from the same archipelago of the Arvoredo Marine Biological Reserve) from the others Brazilian populations (Fig. 2). The second principal coordinate explained 20.19% of the total variance. There was no ordering of discrete groups and there is some overlap in both axes, suggesting admixture of genetically distinct lineages among populations and regions.

The Bayesian Structure analysis confirmed PCoA results, indicating an optimal value of K = 2 distinct genetic groups ($\Delta K = 12.32$) but no population presented an exclusive genetic pool (Fig. 3). The clustering in three distinct genetic pools was also indicated with similar probability ($\Delta K = 11.4$), and agreed better with the multivariate analyses (Fig. 2), bringing together the Brazilian populations, except ARV and GAL. These latter populations share the same genetic pool of native populations (RAB, MON and RVE). The third clustering is composed mainly by individuals from ANH population, but many individuals in all other populations have ancestry coefficients highly related to this cluster (Fig. 3). The genetic differentiation of these three groups (ϕ_{ST}) was 0.130 (Table 4). No correlation between genetic differentiation (measured with ϕ_{ST}) and geographic distances among populations was shown by the Mantel test for all populations ($R^2 = 0.011$; $P = 0.0047$).

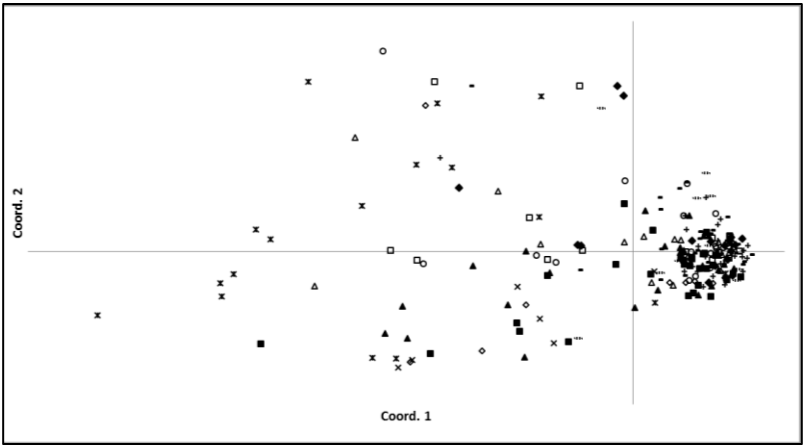
Table 3. Estimates of genetic diversity parameters of twelve populations of *Furcraea foetida* (Asparagaceae) in invasive and native range based on 81 ISSR loci. *N* total number of loci in each population, *I* mean Shannon's index of diversity, *P* (%) percentage of polymorphic loci, H_e mean expected heterozygosity and standard deviation in parentheses. Population codes are defined in Table1

Population	*N*	*I*	*P (%)*	H_e
Invaded range				
NAU	73	0.195 (0.031)	39.51	0.131 (0.022)
CAMP	72	0.163 (0.029)	34.57	0.108 (0.020)
ANH	79	0.330 (0.032)	62.96	0.221 (0.022)
ARV	69	0.111 (0.026)	18.52	0.077 (0.018)
GAL	77	0.251 (0.032)	46.91	0.169 (0.023)
CAMB	75	0.262 (0.033)	50.62	0.177 (0.023)
ALC	73	0.241 (0.031)	49.38	0.160 (0.022)
CAL	71	0.172 (0.03)	34.57	0.116 (0.021)
IB	74	0.188 (0.030)	37.04	0.126 (0.021)
Total mean	74	0.213(0.010)	41.56	0.143(0.007)
Native range				
RAB	73	0.137 (0.027)	25.93	0.092 (0.019)
MON	77	0.211 (0.029)	44.44	0.136 (0.019)
RVE	78	0.247 (0.030)	50.62	0.162 (0.021)
Total mean	76	0.198 (0.017)	40.33	0.130 (0.011)
Total (*I*+*N*)	81	0.209 (0.009)	41.26	0.140 (0.006)

Table 4. Results of molecular variance analysis (AMOVA) for the three hierarchical levels of *Furcraea foetida* populations and among two different genetic pools obtained by Bayesian structure clustering (see Figure 3).

Hierarchical levels	Subdivisions	Total (%)	Statistics
Total (invasive + native)	Among populations	11	
	Within populations	89	ϕ_{ST}= 0.112*
Invasive X native	Among regions	2	
	Among populations	10	
	Within populations	88	ϕ_{ST}= 0.122*
Invasive	Among populations	12	
	Within populations	88	ϕ_{ST}= 0.120*
Native	Among populations	3	
	Within populations	97	ϕ_{ST}= 0.027*
Groups of the Bayesian analysis (STRUCTURE 2.3)	Among regions	5	
	Among populations	8	
	Within populations	87	ϕ_{ST}= 0.130*

Significance of p values (< 0.05) given by *



NAU ◇ CAMP □ ANH △ ARV ✕ GAL ⧗ CAMB ○ ALC + CAL ▬ IB ┅
RAB◆ MON■ RVE▲

Figure 2 Principal coordinate analysis (PCoA) from the matrix of Nei's genetic distances based on ISSR loci of individuals from twelve populations of *Furcraea foetida*, nine in the invaded (Brazil) and three in the native (French Guiana) range (axis 1 = 31.22 % and axis 2 = 20.19% of variance). For population names see Table 1.

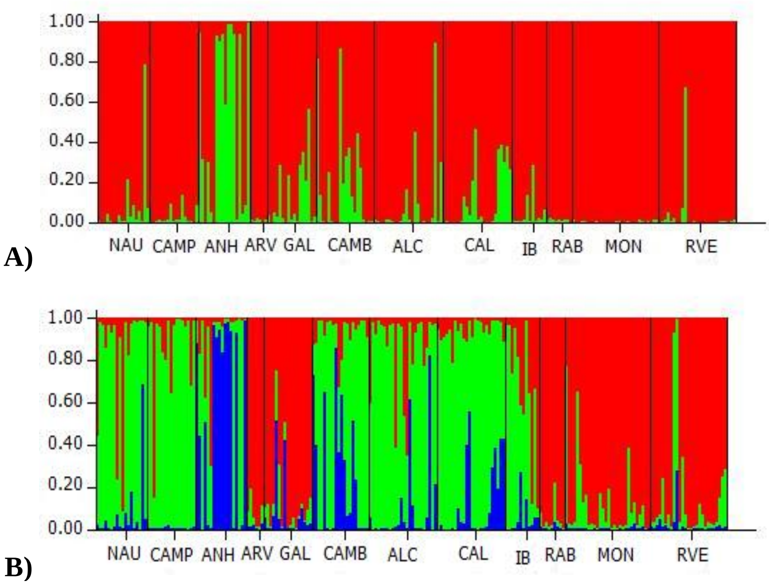


Figure 3. Summary plot of the (A) two different genetic pools (K = 2; ΔK = 12.32) and (B) three different genetic pools (K = 3; ΔK = 11.39) based on ISSR loci obtained by Bayesian structure clustering of 222 individuals from a twelve populations of *Furcraea foetida*. Columns correspond to the multiloci genotype of each individual broken into K colored segments representing the posterior probability of each inferred cluster. Abbreviations indicate nine populations in the invaded range (NAU, CAMP, ANH, ARV, GAL, CAMB, ALC, CAL and IB) and three in the native range (RAB, MON and RVE) according to Table 1.

Discussion

This study showed that the clonal diversity in coastal invasive populations of *F. foetida* in most cases was similar to the native populations in French Guiana. Then, there was no negative effect in quantity of diversity associated with bottleneck events. Among the possible source of genetic variation in clonal plant populations (as gene flow recombination, mutation, and polyphyletic origins of founding individuals) (Ellstrand & Roose 1987), since have no known reproductive alternative to vegetative reproduction (at least in populations sampled), the maintenance of genetic diversity in *F. foetida* must come from somatic mutations, but mainly from multiple origins of the founding clones.

Considered an important source of heritable variation for clonal plants, somatic mutations have been suggested to maintain the level of genetic diversity in several clonal plants populations (Li et al. 2004; Meloni et al. 2013; Si et al. 2014). These mutations in somatic cells should affect only one allele at each locus, leading to a gradual accumulation of heterozygous loci which in turn will be fixed in a clonal population as cannot be eliminated by sexual reproduction (Burrell et al. 2015). With a long life cycle of up to 20 years, somatic mutations in the lines of origin and throughout many mitotic generations in *F. foetida* may lead to some accumulation of variation in the long term. The strengthening of the hypothesis of somatic mutations in *F. foetida* also arises from previous studies with related species. Using amplification fragment length polymorphism (AFLP) and inverse sequence-tagged repeat (ISTR), mutations in somatic cells were verified in *Agave* species through the presence of genetic variation in vegetative propagules, such as in *A. fourcroydes* Lem. (González et al. 2003; Infante *et al*. 2003), *A. americana* L., *A. angustifolia* Haw, *A. deserti* Engelm. and *A. sisalana* Perrine ex Engelm. (Infante et al. 2006), and *A. tequilana* (Torres-Morán et al. 2010).

However, because the mutation rates are very slow and considering the dynamics of colonization, the history of multiple introductions at different times and by human action should be the main responsible for the maintenance of genetic variability in invasive populations (Ellstrand & Roose 1987; Pappert et al. 2000; Gaudeul et al. 2011; Kelager et al. 2013). Formed by genetic variation of lineages not necessarily related, *F. foetida* populations are moderately structured (ϕ_{ST} = 0.112), mainly explained by the divergence among individuals within populations (89%), expected if founding individuals had diverse genetic origins (Pappert et al. 2000). This hypothesis is also suggested since the native populations were more similar to each other (ϕ_{ST} = 0.027) than Brazilian coastal populations to each other (ϕ_{ST} = 0.120) suggesting the entry of propagules from other regions not covered in the present study.

The low percentage of variation explaining the divergence among regions (2%) and among populations (10%) also indicated high genetic interchange among coastal populations after initial introduction. The structure analysis that identified two genetic groups (K = 2) agree with this, showing that there is overlap between populations and at the same time, that there is genetic difference among individual within populations. In addition, in agreement with the AMOVA results, the structure analysis indicated that native populations belong almost exclusively to a single gene pool, with only one individual in RVE showing high probability of belonging to outside group. An alternative explanation for it could be that the frequency of some rare alleles in the native area increased during species expansion in the invaded range, or may also be originating from another non-sampled region in the native area.

Considering K = 3, a more subtle genetic structuring is indicated, with the three genetic groups significantly divergent from each other. This result indicated that French Guiana populations share the same clonal lineage between themselves (in red) and among ARV and GAL, which in turn separated from the other invasive populations (Fig. 2). This result supports a recent study that suggest, through reciprocal ecological niche modeling, the northern South America (mainly along the coastal regions) as the proximal origin of some introductions of *F. foetida* into Brazil (Barbosa et al. 2017). In addition, a third cluster (in blue) frequent in the invaded populations indicates that French Guiana populations do not encompass all of the native range of the species.

Although in general no bottleneck event could be detected, lower level of genetic diversity, possibly associated to the recent colonization, number of introduction events and propagule sources (Dlugosch & Parker 2008; Kelager et al. 2013) were observed in specific cases. For example, the lowest value of genetic diversity of the Arvoredo Island (ARV) can be explained due to a single recently introduction, and them, there was no time to accumulate genetic diversity through mutation (see Ellstrand & Rosse 1987; Geng et al. 2016). In this island, the introduction of exotic plants possibly occurred during recent human occupation, between 1849 and 1877 (Paes 2016). In 1877, a lighthouse was built, as well as other auxiliary techniques of the Brazilian Navy, due to the increasing demand for navigation. In

1990, the Arvoredo Marine Biological Reserve (icmbio.gov.br/rebioarvoredo) was created, which encompassed ARV and other three islands, including the Galé island–GAL (where there are no historical occupation records). From then on, the access to the archipelago is limited and the possibility of entry of new propagules through both by human and marine dispersal seems unlikely, since this island is 15 km away from the coast.

In contrast, the Anhatomirim (ANH) island showed the highest value of genetic diversity, even higher than those in the native populations. This island is the closest to the coast (approximately 300m) which indicates the possibility of natural dispersal by the sea since there are several populations of *F. foetida* that can be sources of vegetative propagules along the coastline. In addition, because in ANH island there is a historical fortress built in the 18th century, currently there is an expressive influx of tourists. In the locality, there is a naturalized population on the east coast (where genetic material was sampled) and also other individuals planted as ornamental in the landing area on the west coast, highlighting the importance of human intervention as a source of continuous introduction for ANH island.

Human-mediated dispersion has been reported as the main driver for maintenance of clonal diversity in invasive populations (Li et al. 2004; Kelager et al. 2013; Burrel et al. 2015). Knowing this, the pattern of variation (high variation among individuals within populations) and genetic structure (low differentiation among populations) verified for invasive populations of *F. foetida*, together with the lack of correlation of genetic and geographic distances, as would be expected in the case of greater influence of the natural dispersion, suggest that the human-mediated dispersion has played a key role in maintaining of the clonal diversity along the Atlantic coast of Brazil. We also suggest that the success of *F. foetida* invasions could be explained more parsimoniously by the nature of genetic variation (with pre-adapted genotypes) than the total amount of genetic diversity per se (see Dlugosch et al. 2015). The succulent leaves and CAM metabolism (which allows stomata to be opened for fixing CO_2 only at night) are important morphophysiological traits that allow *F. foetida* to thrive in a wide range of climatic conditions, resistance to salinity and its high propagative ability (Barbosa et al. 2017), can overcame the stochastic loss of genetic diversity during invasion process (Wang et al. 2005). Then, the non-need for a lag time for adaptation should facilitate a rapid colonization and expansion of *F. foetida* even for regions of subtropical climate as in southern Brazil. Although moderate genetic diversity and divergence among native and introduced regions is revealed to populations along the Atlantic coast, future research should encompass other sources in the native range, also including different habitats such as in high-elevation, in order to understand the overall genetic structure of this clonal invasive plant.

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CAPÍTULO 3 - WARMING EFFECTS ON THE COLONIZATION OF THE CLONAL INVASIVE PLANT *FURCRAEA FOETIDA* (ASPARAGACEAE) IN A COASTAL ECOSSYSTEM

Abstract

Global warming is expected to cause significant changes in the distribution of species globally, altering ecosystem function and services. These impacts can exacerbate by synergism with other global change drivers, such as biological invasions. *Furcraea foetida* (Asparagaceae) is a CAM species native to Central America and northern South America. In Brazil it is currently invading coastal ecosystems in the Atlantic Forest biome, forming dense population clusters that exclude native species. We addressed whether warming may favor or impair development of *F. foetida* bulbils based on functional traits, and assessed whether plant cover of native species influenced *F. foetida* establishment in a rocky shore ecosystem. We used open-top chambers which increased air temperature during daylight hours by 0.4°C relative to ambient. Short-term warming effects enhanced leaf length without increasing number of leaves, dry mass, specific leaf area, leaf dry matter content (LDMC) or photosynthetic efficiency of photosystem II (Fv/Fm). However, plant cover decreased LDMC and helped maintain high Fv/Fm values, having thus an indirect positive effect on *F. foetida* establishment. Even though manipulated temperature did not reached IPCC forecasts for 2100, small, short-term changes in temperature had effects on plant performance. Thus, we suggest that *F. foetida* may be favored in an optimistic scenario of climate change, increasing its negative effects on biodiversity of coastal ecosystems.

Keywords: CAM species, climate change, facilitation, invasions, open-top chambers, warming.

Introduction

Climate change, and particularly warming, has been the focus of many studies concerned with its environmental and economic impacts (Rustad 2008; Hou et al. 2014; Knutti et al. 2015). Changes of species distribution and ecosystem function and services are often consequence of global warming, which is expected to intensify by synergism with other global change drivers such as the rise in atmospheric CO_2 levels, changes in global trade routes, habitat fragmentation, alterations of disturbance regimes and biological invasions (Dukes & Mooney 1999; Walther et al. 2009; Bradley et al. 2010). Global circulation models predict for southeast South America - in an optimistic scenario - an increase in mean annual temperature of 0.6°C–2.0°C, and of 2.2°C–7°C in the most pessimistic scenario (Magrin et al. 2014).

Recent research has shown that an important consequence of global change is the worsening of biological invasion impacts on ecosystems, eroding biodiversity and ecological functions (Dukes and Mooney 1999; Rejmánek et al. 2013). The distribution of invasive species can be widely modified as climate becomes suitable, allowing them to successfully colonize habitats where they currently fail (Smith et al. 2012). Thus, climate change will also increase the competitive ability of some invasive species with physiological tolerances wider than native species, less adapted to new environmental conditions (Walther et al. 2009; Verlinden et al. 2014). Nevertheless, experimental manipulations have shown that warming can have site-specific consequences, with effects that can either be positive (Wang et al. 2011; Chuine et al. 2012; He et al. 2012) or negative (Williams et al. 2007) for invasive species, depending on specific traits and the native competitors (Verlinden et al. 2014). Williams et al. (2007) for example, observed warming causing population decline of two invasive weeds in Australian temperate grasslands, with negative effects on seed production, seedling emergence and establishment of *Hypochaeris radicata* and *Leontodon taraxacoides.*

We carried out a field experiment to assess the effect of warming on the colonization success of an invasive clonal plant species, *Furcraea foetida* L. (Haw.) (Asparagaceae). Native to Central and northern South America (García-Mendoza 2001), *F. foetida* was introduced into Brazil as source of fiber but at present is mostly used as ornamental and in live fences (Barbosa 2011). The species is currently distributed along a wide latitudinal range in the eastern part of the country, invading mainly coastal systems of the Atlantic Forest biome, such as coastal dunes and rocky shores, including coastal islands

(Barbosa et al. 2017a-b). Its invasiveness is highly associated with reproduction by thousands of bulbils per plant, which form dense cluster around the mother plant that competes with native vegetation (Barbosa et al. 2017a). Adult *F. foetida* plants reach large sizes (about 4 m in diameter) and high densities. These characteristics may significantly alter the structure of local plant communities (Barbosa et al. 2017a). In addition, its ability to occupy a wide climatic zone (as in tropical and subtropical regions of the Americas) can be attributed to the succulence of its leaves and CAM metabolism (Barbosa et al. 2017b). Currently, it is invading countries such as Australia, Chile, New Zealand, South Africa, the United States and overseas departments of France, including the Reunión Island (Baret *et al*., 2006; Crouch and Smith 2011; Gargominy *et al.* 1996; Macdonald *et al.* 2003; Meyer 2000).

Previous studies with species morphologically similar to *F. foetida* showed that high temperatures can be a limiting factor for survival during early development stages. In desert environments, where temperatures in exposed areas at soil surface can exceed 70°C in summer, survival of *Agave deserti* and *A. macroacantha* seedlings was associated with sheltered microhabitats (Franco and Nobel 1988; Arizaga and Ezcurra 2002). In stressful habitats marginal to the Brazilian Atlantic rainforest, such as coastal dune and rocky shore, exposed soils temperatures may also exceed 70°C in summer, and then, vegetation cover of native community may provide appropriate environmental conditions for germination and growth of other species (Scarano 2002). Thus, a better understanding of the response of propagules (bulbils) to warming and the effects of different levels of native vegetation cover is critical to anticipate the effects of new climate conditions on the colonization and spread of invasive species. In this framework, we tested 1) if warming may impair physiological parameters of *F. foetida* bulbils in the short-term; and 2) whether the native vegetation cover of the rocky shore ecosystems can facilitate establishment of *F. foetida.*

Methods

Field site

The field site was located in the northwest coast of the Campeche Island (27°69'S, 48°46'W) in a place invaded by *F. foetida*. The Campeche Island is 1.5 km apart from Santa Catarina Island and 17.5 km to the continental coast, in southern Brazil. The island has a total area of 531,200 m^2 and approximately 4,480 m of coastline (Mazzer and Panitz 2006). The local climate is subtropical humid (Cfa) in Köppen classification. Mean annual temperature for the last ten years was 20.9°C with a mean maximum of 28.8°C in February and minimum of 10.3°C in July (Tonetta et al. 2016). Rainfall is more frequent in summer than in winter, averaging 1876 mm per year (Fuentes and Petrucio 2015).

Open-top chambers

We use open-top chambers (OTCs) as a simple, low-cost approach to passively (i.e., through the trapping of solar radiation) generate an artificially heated environment (Marion et al. 1997; Hollister and Webber 2000). The use of OTCs was popularized by the International Tundra Experiment (ITEX) and it efficacy has been validated in studies involving native species of high latitude regions, particularly tundra ecosystems (Marion et al. 1997; Hollister and Webber 2000), as well as in alpine systems in Norway (Klanderud 2005), quartz fields in South Africa (Musil et al. 2005), and the Chilean Andes (Cavieres and Sierra-Almeida 2012). OTCs have been also used in temperate forest in China (Yin et al. 2008), and Belgium (De Frenne et al. 2010). OTCs were made with 1 mm-thick acrylic material with high transmittance ratio of solar radiation (approximately 90%) and low transmittance of infrared radiation (Marion et al. 1997). OTCs were cone-shaped, 40 cm high, 60 cm in basal diameter (i.e., 0.28 m^2) and an open top of 25 cm in diameter.

Experimental setup

In early January 2015, 17 OTCs and 17 control sites were randomly distributed in an area of 1000 m^2 on a rocky shore community. In this locality, plant community is composed by herbaceous and sub-shrubs species adapted to strong winds and salty spray, and is dominated by the sub-shrub *Varronia curassavica*, and the rainforest liana *Stigmaphyllon ciliatum*. A shallow sand soil is developed on granitic rocks (Mazzer and Panitz 2006). All sites sampled were composed by the same soil type and wind exposure with variation only on the percentage of plant cover. Each control site was delimited by the basal area of OTCs (0.28 m^2).

Air temperature was recorded simultaneously inside and outside (20 cm apart) OTCs with iButton sensors (Maxim Integrated, San Jose, CA, USA) placed 10 cm aboveground. Hourly measurements were taken during the summer season in seven samples between 20 Jan-16 Feb 2015 and in the remaining 10 samples in 19 Feb–8 Mar 2015. Temperature was again recorded in the mid-autumn season (04 Nov–24

Apr 2015). During this period we measured all 17 sampling units at once. We collected 50 *F. foetida* bulbils directly from the inflorescence of 5 reproductive plants (3 in the Campeche island and 2 in Santa Catarina island) on 15 Jan 2015. Bulbils were thoroughly mixed and 136 bulbils were selected at random for the experiment. Four bulbils were planted in each of the 34 sample units, one in the center and three with a triangular distribution 15 cm from the central bulbil and 15 cm from the edge, totaling 68 bulbils planted within OTCs and 68 in control plots. All bulbils were harvested at the end of autumn (16 Jun 2015) after five months of growth.

Vegetation cover

At the end of the experiment, we estimated the percent plant cover for each sampling unit. We used a digital camera (Canon PowerShot SX160; focal length: 5-80 mm; maximum resolution 16 megapixel) positioned at ground level and with the lens facing upward in the center of each plot (inside and outside OTCs). Percent plant cover was estimated using the CPCE software (Kohler and Gill 2006) which, on each image, selected at random fifty points and each was assigned to categories ‘cover’ or ‘no cover’.

Physiological parameters

To evaluate the effects of warming and shading on *F. foetida*, the 128 bulbils surviving by the end of experiment were harvested, placed in plastic bags and taken to the laboratory, where we determined number of leaves, leaf length, total dry mass (DM), specific leaf area (SLA), leaf dry matter content (LDMC), and efficiency of photosystem II (Fv/Fm). The last measurement was taken within 3 h after collection (14:00-15:00 hours).

To evaluate Fv/Fm, we used the youngest mature leaf of each bulbil using a portable PEA fluorometer (Plant Efficiency Analyser, Hansatech Instruments, King's Lynn, UK) after 20 min dark adaptation (Baker and Rosenqvist 2004). Parameters involving leaf mass content (SLA and LDMC) were measured on a leaf disc obtained from the same leaves used for Fv/Fm measurements with a 1.5 cm hole puncher. Leaf discs were individually weighed to obtain fresh mass and then placed in distilled water for 24 h. Then, they were carefully blotted dry and weighed again to obtain saturated mass (at full turgor). Later, leaf discs were dried at 70°C for 96 h to obtain dry mass. Specific leaf area (SLA) was calculated as the ratio between leaf area and dry mass (Dwyer et al. 2014). Leaf dry matter content (LDMC) was calculated as the ratio between dry and saturated mass (Pérez-Harguindeguy et al. 2013). Total dry mass was measured on the whole bulbil, except roots as they could not be fully extracted.

Statistical analyses

The value of each physiological/functional parameter was averaged among the four bulbils in each sample. The effect of temperature (inside and outside OTCs) and the effect of plant cover on these variables, and the interaction between them, were evaluated by Generalized Linear Models (GLM). Gamma distribution and the log link function were used for number of leaves, DM, LDMC and Fv/Fm; a Gaussian distribution was assumed for leaf length and SLA, totaling seven models. All GLM analyses and figures were produced with R software (version 3.2.2) (R Core Team 2015) using the "car" and the "MASS" packages.

Results

OTCs increased average air temperature during the whole experiment period (20 Jan to 16 Jun 2015) by 0.4°C in our rocky shore ecosystem (Table S1). Heating was more effective during daytime (7–18 h), rising temperature 0.6°C with respect to ambient particularly in the hottest hours of the day (between 11 h and 16 h) (Table S1; Figure S1). Notably, the largest warming contribution did occur with maximum temperatures, which achieved 1.3°C above ambient inside OTCs (Table S1). OTCs heating were slightly more effective in summer than in autumn. In summer, OTCs increased mean daily temperature by 0.5°C, especially on daylight hours (0.8 °C) but particularly at peak temperature (1.8°C).

Mean vegetation cover was 68.3 ± 4.1% in sites with OTCs and 65.2 ± 6.2% in control sites. The range of variation was 30–90% in OTC sites and 18–98% in control sites. Warming increased bulbils leaf length (Table S2 and S3; Figure 1) but had no effect on other measured parameters (Table S2 and S3). Combined all sample units (within OTCs and control areas), we recorded a decrease in LDMC and an increase in Fv/Fm as plant cover increased (Table S3; Figure 2A–B).

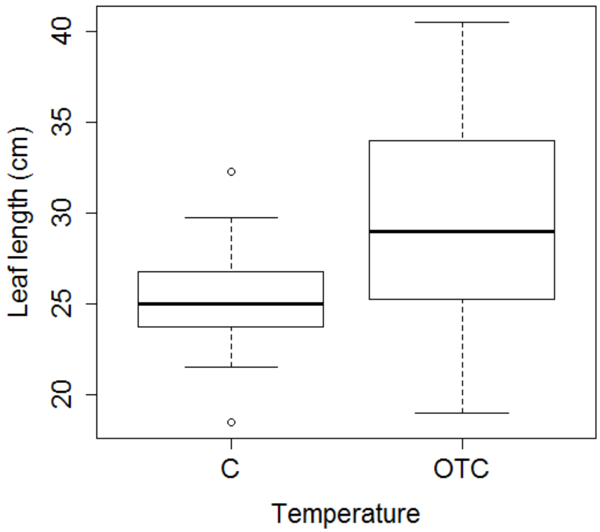

Fig. 1 Boxplot of leaf length of *Furcraea foetida* bulbils inside the open-top chambers (OTC) and in control sites.

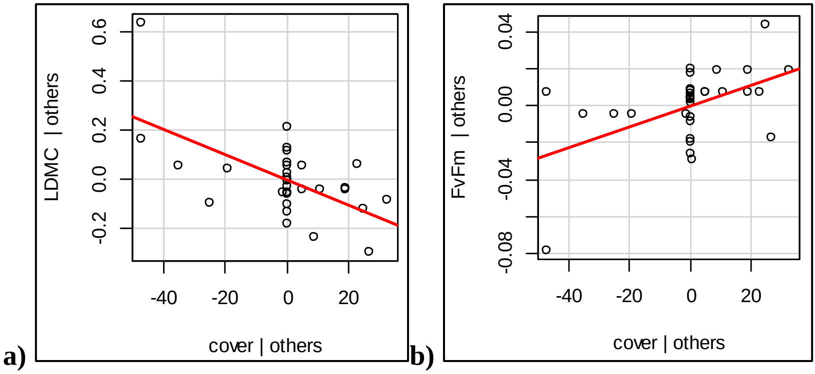

Fig. 2 Relationship between physiological parameters of *Furcraea foetida* bulbils and percent plant cover on all sample sites combined (inside and outside OTCs) after examining the effect of other variables. (a) Added variable-plots (partial-regression plots) of leaf dry matter content (LDMC) and (b) photosynthetic efficiency of photosystem II (Fv/Fm).

Discussion

Although our warming did not reach the optimistic IPCC scenario of 0.6-2°C increases projected for 2100 (Magrin et al. 2014), a small temperature increase was able to generate short-term responses in *F. foetida* bulbils. This increase did stimulate bulbils growth in terms of leaf length. This responses, however, suggests that temperature is still within the optimal range for the species, as suggested also by Fv/Fm values of 0.82 both inside and outside OTCs (Table 3) typical for healthy leaves (Björkman and Demmig 1987). Recent reports show that increased CO_2 and higher temperatures, especially at night (when CO_2 fixation takes place) increased the productivity of CAM species (Garcia-Moya et al. 2010; Holtum and Winter 2014; Owen et al. 2015). Our OTCs did not heat at night, when temperature is critical for enzyme activity (Luttge 2004), and consequently did not lead to biomass gain.

High plant cover influenced positively Fv/Fm values in our plants suggesting that, counterintuitively, high irradiance may be detrimental for this species. Plant cover may also help to maintain high soil water, indirectly enhancing photosynthetic performance (Song et al. 2010). The significant reduction in LDMC with increasing plant cover recorded in *F. foetida* can be related to greater water availability in shaded sites. In succulent species low LDMC may be directly related to SLA (Pérez-Harguindeguy et al. 2013) but in our site there was no relationship between LDMC and SLA; i.e., LDMC decreased while SLA did not, suggesting that plants may be nutrient-limited in this sandy soil since SLA responds to both shade and nutrient availability and should increase in shady places.

Surprisingly, there was no effect of plant cover on leaf length, number of leaves, or bulbil dry mass, suggesting that shade favored water balance and photosynthesis, while other factors, for example, reduction of photosynthetically active radiation (PAR), may limit CO_2 assimilation as shown elsewhere in succulent species, mostly cacti and agaves in desert environments (Franco and Nobel 1988; 1989). It has been reported that the grass species, *Hilaria rigida*, facilitated establishment of *Agave deserti* seedlings by reducing maximum soil temperature and by increasing nitrogen levels (Franco and Nobel 1988). However, low radiation in shaded areas reduced CO_2 uptake and growth, of *Agave deserti* seedlings within thickets of the grass *Hilaria rigida* (Franco and Nobel 1988) the same as reported for seedlings of the cactus species, *Carnegiea gigantea*, growing under *Ambrosia deltoidea* and *Cercidium microphyllum* shrubs (Franco and Nobel 1989).

The physiological parameters evaluated in this study are important for determining *F. foetida* seedling ability to tolerate variations in temperature, light, water and CO_2 in natural environments, which in turn are useful to assess colonization and establishment ability of potentially invasive species under a perspective of global climate change (Song et al. 2010). We conclude that, under demanding abiotic conditions, a small, short-term increase in temperature has a positive effect on leaf growth of *F. foetida* bulbils. We also evidenced that plant cover in the rocky shore facilitated the colonization of invasive species. Our data also emphasize that, since *F. foetida* is native to tropical regions where temperature is higher than in invaded subtropical regions of Brazil, this species is physiologically pre-adapted to tolerate high temperatures. Thus, we suggest that *F. foetida* may be favored in an optimistic scenario of climate change, increasing its negative effects on biodiversity of coastal ecosystems.

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Table S1. Mean daily temperature (24h), daytime (7–18h), nighttime (19–6h), maximum and minimum air temperature in the period 20 Jan–18 Mar 2015 (summer), and 11–24 Apr 2015 (autumn) and for the whole period of the experiment, inside and outside OTCs.

	Daily ± SD		Daytime ± SD		Nighttime ± SD		Maximum–Minimum	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
Summer	25.2±1.2	24.7±1.2	26.9±1.7	26.1±1.5	23.4±1.3	23.2±1.3	32.1±22.1	30.3±21.9
Autumn	23.3±0.5	23.0±0.3	24.8±0.9	24.3±0.5	21.8±0.3	21.8±0.7	28.5±20.8	27.7±20.7
Jan–Apr	23.8±0.7	23.4±0.6	25.3±1.2	24.7±0.6	22.5±0.7	22.4±0.8	29.5±21.1	28.2±21.0

Table S2. Summary statistic (mean value, standard error, minimum and maximum) for number of leaves, leaf length, specific leaf area (SLA), dry mass (DM), leaf dry matter content (LDMC) and photosynthetic efficiency of photosystem II (Fv/Fm) of bulbils planted inside (OTC) and in control sites (C) (n=17).

	Number of Leaves		Leaf length (cm)		SLA (cm^2/mg)		DM (g)		LDMC (mg/g)		Fv/Fm ($\mu mol\ m^{-2}\ s^{-1}$)	
	OTC	C	OTC	C	OTC	C	OTC	C	OTC	C	OTC	C
Aver.	3.2	3.6	29.4	25.3	16.2	15.4	2.5	2.2	50.6	54	0.82	0.82
SE	0.1	0.1	1.5	0.8	0.7	0.6	0.5	0.2	1.4	3.4	0.01	0.01
Min.	2	3	19	18.5	12.6	12.1	1.1	1.2	38.9	36.6	0.64	0.76
Max.	4	5	40.5	32.3	20.8	21.5	5.3	4.2	61.3	91.4	0.85	0.86

Table S3. Generalized linear models explaining the effects of temperature (°C) and vegetation cover (%) for number of leaves, leaf length, specific leaf area (SLA), dry mass (DM), leaf dry matter content (LDMC) and photosynthetic efficiency of photosystem II (Fv/Fm) of bulbils planted inside OTCs and in control sites (n = 17).

Response variables	Fixed effects	Estimate	SE	t value	Pr(>|t|)	AIC
Number of Leaves	T(°C)	-0.2142	0.211	-1.015	0.319	
	Vegetation Cover	-0.0003	0.002	-0.159	0.875	
	T(°C) x Vegetation Cover	0.0016	0.003	0.529	0.601	56.6
Leaf Length	T(°C)	+3.960	1.532	2.585	**0.015** *	
	Cover	+1.395	0.917	1.522	0.139	
	T(°C) x Vegetation Cover	+2.482	1.720	1.444	0.160	197.07
SLA (cm^2/mg)	T(°C)	0.7727	0.913	0.8460	0.4040	
	Vegetation Cover	-0.385	0.544	-0.7080	0.4850	
	T(°C) x Vegetation Cover	0.2066	10.02	0.206	0.838	162.6
DM (g)	T(°C)	-0.057	0.154	-0.3710	0.7130	
	Vegetation Cover	-0.060	0.093	-0.6470	0.5230	
	T(°C) x Vegetation Cover	0.1867	0	1.096	0.282	89.6
LDMC (mg/g)	T(°C)	+0.001	0.045	0.026	0.979	
	Vegetation Cover	-0.104	0.026	-3.901	**0.001*****	
	T(°C) x Vegetation Cover	+0.037	0.049	0.753	0.458	214.34
Fv/Fm (µmol m^{-2} s^{-1})	T(°C)	+0.011	0.007	1.641	0.112	
	Vegetation Cover	+0.012	0.004	3.096	**0.004****	
	T(°C) x Vegetation Cover	-0.008	0.008	-1.118	0.273	-169.5

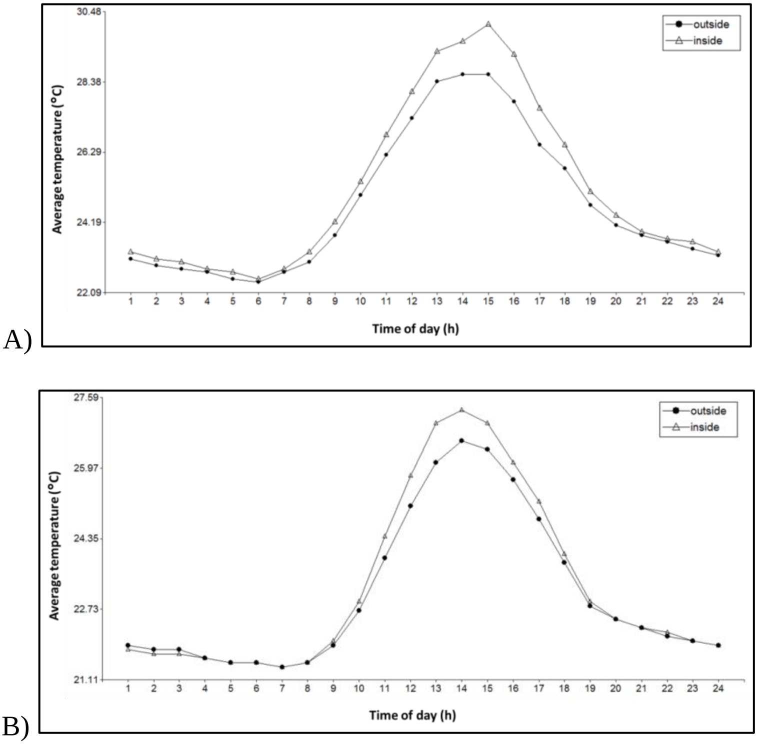

Fig. S1 Mean air temperature recorded hourly inside and outside OTCs (A) in summer (20 Jan–18 Mar 2015) and (B) in autumn (11–24 Apr 2015)

CONCLUSÃO GERAL

Furcraea foetida é consideradauma espécie exótica invasora e não deve ser apenas considerada uma espécie naturalizada ou casual. Isto porque, após a introdução, suas populações tem a capacidade de persistir sem intervenção do homem, por períodos superiores a 10 anos, e também por seus propágulos vegetativos (bulbilhos) serem capazes de dispersar para distâncias maiores do que 100 m em menos do que 50 anos. Sua invasividade é devida à produção de milhares de bulbilhos que caem, em grande maioria, ao redor da planta mãe, resultando em adensamentos populacionais de indivíduos que chegam a atingir 4 m de diâmetro de roseta. *Furcraea foetida* apresenta ampla capacidade fisiológica decorrente principalmente do armazenamento de água em suas folhas suculentas e do metabolismo CAM fotossintético. Essas características morfofisiológicas e a sua estratégia de propagação clonal permitem que à espécie possa prosperar em muitas zonas climáticas. Além disso, a dispersão contínua pelo homem, atualmente para uso como ornamental ou cercas-vivas, aumenta o risco de invasão pela espécie.

No primeiro capítulo deste trabalho, onde realizamos um estudo de modelagem de nicho ecológico, observamos que o modelo construído com dados ambientais e ocorrências de *F. foetida* no Brasil quando projetado para a área nativa reforçou a hipótese existente de que a espécie é originária da bacia do rio Orinoco, bacia amazônica e ilhas do Caribe. Concluímos que no Brasil a espécie exótica estabeleceu-se principalmente no leste do país, invadindo, sobretudo ecossistemas costeiros. Durante o processo de invasão, *F. foetida* ocupou no Brasil uma parte do seu nicho fundamental que não está disponível na área nativa (América Central e norte da América do Sul), expandindo o seu nicho realizado para regiões com maior amplitude de temperatura e precipitação no trimestre mais quente, que é característico de clima subtropical. O teste de similaridade de nicho indicou que as diferenças de nicho realizado são devido a diferenças na disponibilidade de habitat entre as duas áreas (nativa e invadida) e não devido a mudanças evolutivas. O modelo construído com dados ambientais da área nativa quando foi projetado para o Brasil (exceto região Amazônica) indicou que as regiões de alto risco de invasão por *F. foetida* são no Cerrado e regiões mais interiores da Mata Atlântica, onde ainda há baixa evidência de ocorrência da espécie. Importante ressaltar que apesar de os modelos de nicho ecológico ter limitações metodológicas, estes estudos são um importante instrumento de auxílio para a prevenção de invasões biológicas.

Já no segundo capítulo, as análises genéticas evidenciaram que as populações costeiras de *F. foetida* no Brasil possuem níveis similares de diversidade genética com relação às populações nativas da Guiana Francesa, não apresentando, em geral, efeito negativo de gargalo populacional. Observamos também que há alta variação genética entre indivíduos dentro das populações, sugerindo que as populações ao longo da costa atlântica brasileira são provenientes de múltiplas fontes de introdução. Ao mesmo tempo, a baixa divergência entre as populações e a ausência de correlação com a distância geográfica entre elas indicou que a dispersão pelo homem tem desempenhado um papel fundamental na manutenção da diversidade genética de *F. foetida*. Sugerimos ainda que algum acúmulo de variação ao longo do ciclo de vida da planta, que pode atingir até 20 anos, pode ser decorrente de mutações nas células somáticas. Orientamos que pesquisas futuras devem abranger uma gama maior de populações na escala nativa, incluindo diferentes tipos de habitats, o que permitirá uma melhor compreensão da estrutura genética e consequentemente, do histórico de invasão desta planta clonal invasora.

No terceiro e último capítulo, com base no experimento com câmaras de topo aberto, constatamos que um aumento na temperatura média diária do ar de apenas 0.4°C em relação à temperatura ambiente, em curto prazo (cinco meses) aumentou o crescimento foliar dos bulbilhos de *F. foetida*. Este resultado sugere que a espécie pode se tornar mais agressiva em um cenário mais otimista de aquecimento global (um aumento na média da temperatura anual 0.6°C–2.0°C) previsto pelo IPCC para o final de 2100, visto que as fases iniciais de colonização e estabelecimento poderão ser favorecidas. Este resultado também reforça o atual risco de a espécie se estabelecer com sucesso e se tornar invasora em regiões que apresentam médias de temperaturas mais quentes do que o sul do Brasil, como a região do Cerrado, previsto no primeiro capítulo. Observamos ainda que houve maior quantidade de armazenamento de água nas folhas e a eficiência fotossintética foi aumentada em sítios com alto sombreamento, evidenciando a importância da facilitação nos estágios iniciais do ciclo de vida de *F. foetida*.

Assim, esta tese evidenciou o alto potencial de *F. foetida* se estabelecer com sucesso não somente ao longo de toda a costa Atlântica brasileira, mas também nas regiões mais interiores do país como no planalto central. Considerando que a identificação e controle dos principais riscos de espécies exóticas em unidades de conservação e suas zonas de amortecimento são previstas pelo Sistema Nacional de

Unidades de Conservação (SNUC – LEI 9.985/2000), recomendamos que a utilização de *F. foetida* como planta ornamental, assim como o seu plantio para qualquer fim, seja proibida dentro das unidades de conservação no Brasil. Recomendamos ainda que os planos de controle das populações já estabelecidas priorizem o monitoramento das plantas reprodutivas, para que se cortem os pendões de inflorescências antes da formação dos bulbilhos. Recomendamos ainda que os esforços de controle devem especialmente considerar os locais com maior cobertura da vegetação nativa visto que os bulbilhos tem maior chance de sobrevivência e estabelecimento na presença de espécies facilitadoras.