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Michele de Sá Dechoum

INVASÃO POR *HOVENIA DULCIS* THUNB. (RHAMNACEAE) NAS FLORESTAS DO RIO URUGUAI: ASPECTOS ECOLÓGICOS E DIRETRIZES PARA O MANEJO

Tese submetida ao Programa de pós graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do Grau de Doutor em Ecologia.
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Coorientador: Prof. Dr. Sergio Martín Zalba

Florianópolis
2015

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Dechoum, Michele de Sá
Invasão por Hovenia dulcis Thunb. (Rhamnaceae) nas florestas do rio Uruguai : aspectos ecológicos e diretrizes para o manejo / Michele de Sá Dechoum ; orientadora, Tânia Tarabini Castellani ; coorientador, Sergio Martín Zalba. - Florianópolis, SC, 2015.
148 p.

Tese (doutorado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas. Programa de Pós-Graduação em Ecologia.

Inclui referências

1. Ecologia. 2. Espécie exótica invasora. 3. Floresta Estacional Decidual. 4. Sucessão ecológica. 5. Unidade de conservação. I. Tarabini Castellani, Tânia. II. Zalba, Sergio Martín. III. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Ecologia. IV. Título.

"Eu tenho uma espécie de dever, de dever de sonhar, de sonhar sempre, pois sendo mais do que uma espectadora de mim mesma, eu tenho que ter o melhor espetáculo que posso. E assim me construo a ouro e sedas, em salas supostas, invento palco, cenário para viver o meu sonho entre luzes brandas e músicas invisíveis."

(Fernando Pessoa, Livro do Desassossego, 1982)

Este trabalho é dedicado ao Sr. Adelar Osowski, por sua incansável luta pela proteção do Parque Estadual Fritz Plaumann.

AGRADECIMENTOS

Agradeço imensamente à minha orientadora Tânia Tarabini Castellani pela oportunidade, parceria, e pelo carinho e dedicação com os quais me acompanhou nesses quatro anos. Agradeço ao meu co-orientador Sergio Zalba por sua amizade, generosidade e por ser tão presente mesmo que à distância. O conhecimento e a postura profissional de vocês são fontes de inspiração para a minha crença sobre o papel do cientista enquanto transformador da sociedade e agente atuante na conservação e restauração de ambientes naturais.

Meus sinceros agradecimentos a meu "segundo" co-orientador Marcel Rejmánek pelo estágio doutoral no exterior, no qual me acolheu com imensas atenção e generosidade. Sinto-me honrada pela oportunidade de conviver e aprender com este grande ecólogo e uma das maiores referências da área de invasões biológicas.

À FATMA, pela autorização da pesquisa na Unidade de Conservação, à FAPESC e à Tractebel Energia pelo financiamento do projeto, à CAPES pela concessão da bolsa de doutorado, ao Programa Ciência sem Fronteiras pela concessão da bolsa de estágio doutoral no exterior (Doutorado Sanduíche), e ao Programa de Pós-Graduação em Ecologia da UFSC pela oportunidade e pelo apoio. Agradeço também ao Instituto Hórus de Desenvolvimento e Conservação Ambiental, pelo apoio institucional e pela parceria para a realização das atividades de campo.

Aos taxonomistas que me auxiliaram com a identificação do material botânico coletado, Prof. Jorge Yoshio Tamashiro, Cassio Daltrini Neto, Tiago Barbosa e Prof. Dr. Daniel Falkenberg. Agradeço imensamente à Sílvia Ziller, Clare Aslan, Elaine Chow, Hugh Safford, Clark Richter e Rafael Zenni, pela atenta leitura dos artigos e pelos úteis e fundamentais sugestões e comentários.

Agradeço à Raquel Elise Müller de Lima, pela companhia e ajuda no campo e pelos divertidos dias no Parque. Agradeço imensamente à toda a equipe da ECOPEF (Equipe co-gestora do Parque Estadual Fritz Plaumann), especialmente ao Rafael, Murilo e Patrícia, pela amizade construída ao longo dos anos, por todo o apoio logístico e nas atividades de campo, e por levarem as questões de invasões biológicas tão a sério no uso público do Parque. Sou também muito grata à bióloga Beloni Marterer, amiga e profissional competente que muito tem feito pela conservação ambiental no estado de Santa Catarina.

Ao apoio inestimável de Adelar Osowski, Maikon Waskiewik e Marcelo Inácio da Silva nas atividades de campo. Sou muito grata à disponibilidade, gentileza e amizade de vocês, que me foram de grande importância nos momentos de maior dificuldade no campo. Agradeço à professora Celi Favassa e aos acadêmicos do curso de Ciências Biológicas da Universidade do Contestado - Concórdia, que me auxiliaram nas atividades de campo. Agradeço também à Sílvia Ziller pelo auxílio no campo e na tradução dos artigos, e à Cristiana Barbosa pelo auxílio no campo.

Aos professores que contribuíram em diferentes etapas do meu doutorado, desde a avaliação de resultados preliminares na SAPECO 2012, Malva Hernández e André Feitas (UNICAMP). Agradeço aos professores e alunos do Programa de pós-graduação em Ecologia da UFSC, pelas disciplinas ministradas e pelas ricas discussões em sala de aula e no curso de campo. Agradeço especialmente ao professor Nivaldo Peroni, por sua importante participação na minha formação profissional, e por compartilhar comigo sua paixão por bicicletas, corridas e florestas. Agradeço também às professoras Natalia Hanazaki, Barbara Segal e Lucrecia Arellano, pelas oportunidades de docência e aprendizado que me proporcionaram ao longo do curso. Agradeço imensamente à Karla Scherer por seu apoio no laboratório.

Agradeço aos membros da banca de qualificação, Prof. Dr. Fernando Rocha, Prof. Dr. Maurício Sedrez dos Reis, Prof. Dr. Nivaldo Peroni e Profa. Dra. Natalia Hanazaki. Também sou muito grata aos membros da pré-banca Prof. Dr. Sidinei Magela, Prof. Dr. Maurício Sedrez dos Reis e Profa. Dra. Natalia Hanazaki, que também compuseram a banca de defesa junto aos professores doutores Vânia Pivello, Adelar Mantovani e Eduardo Giehl.

Aos amigos da Ecologia Guilherme Longo, Manoela Brandão, Luis Macedo-Soares, Cristiana Barbosa e Sofia Zank pelas discussões ecológicas (ou não) e pelos momentos agradabilíssimos que passamos juntos.

À minha família "recebida", meu pai Adib e minha mãe Virgínia, por seu amor, carinho e esforço por minha educação; às minhas doces e queridas irmãs Gisele e Larissa e aos meus amados sobrinhos Rafael e Victor por seu apoio e presença tão importantes na minha vida. Sou extremamente grata à minha família "escolhida", minhas queridas e amadas Sílvia, Sil, Parceira e Carla Ridi, por serem parte de quem sou e por me acompanhar. Agradeço especialmente à Sílvia, por ser minha inspiração profissional, e por sua cumplicidade, companheirismo, delicadeza e paciência no meu caminhar.

RESUMO

Espécies exóticas invasoras podem provocar impactos ambientais e econômicos substanciais, sendo atualmente consideradas uma das maiores ameaças à diversidade biológica em escala mundial. Invasões por plantas ocorrem como resultado da combinação de características biológicas e ecológicas das espécies introduzidas, de condições bióticas e abióticas do ambiente nos quais as espécies chegaram, e da pressão de propágulos, tanto com relação ao número do número de eventos de introdução, quanto do número e diversidade genética dos propágulos introduzidos. Ecossistemas com menor diversidade biológica e maiores intensidade e frequência de distúrbios são usualmente mais invadidos do que aqueles com baixos níveis de perturbação e maior diversidade. *Hovenia dulcis*, popularmente conhecida como uva-do-japão, é uma espécie arbórea decídua e zoocórica, nativa do leste asiático, descrita em literatura como espécie pioneira. Foi introduzida e mais intensamente cultivada no oeste de Santa Catarina a partir da década de 1980, quando agroindústrias da região fomentaram seu uso em granjas de suínos e aves. A espécie pode dispersar-se além de suas áreas de cultivo, encontrando-se amplamente distribuída em florestas no estado de Santa Catarina, chegando a ser a espécie mais importante no componente arbóreo-arbustivo. Pode alterar a estrutura e a composição de espécies em comunidades vegetais florestais no sul do Brasil. O objetivo geral desta tese foi investigar fatores-chave da ecologia de invasão pela espécie exótica *Hovenia dulcis* em florestas estacionais deciduais de Santa Catarina, com vistas a fornecer diretrizes para o manejo da espécie. Para tanto, três diferentes estudos foram realizados entre 2011 e 2014, no Parque Estadual Fritz Plaumann, Concórdia (SC), onde a paisagem é composta por fragmentos de Floresta Estacional Decidual em diferentes estágios sucessionais. Para o primeiro estudo, realizado entre julho de 2010 e janeiro de 2011, parcelas foram estabelecidas em vegetação aberta, semiaberta e fechada em diferentes fragmentos, correspondentes a três estágios em um gradiente sucessional, em áreas com e sem *H. dulcis*. Todos os indivíduos com DAP (diâmetro à altura do peito) maior do que 5cm foram identificados e classificados em grupos funcionais, estabelecidos com base na síndrome de dispersão, estratégia de regeneração, estratificação vertical e fenologia foliar. A idade dos indivíduos de *H. dulcis* amostrados foi estimada a partir da contagem de anéis de crescimento de árvores cortadas. Observando-se premissas gerais de invasões biológicas e características ecológicas da espécie, foi construída a hipótese de que o estabelecimento e o sucesso de invasão por *H. dulcis* seriam maiores em estágios sucessionais iniciais, com maior disponibilidade de recursos, e baixas riqueza e diversidade de espécies, assim como diversidade funcional. Uma maior densidade de árvores adultas foi observada em áreas que hoje estão em estágio intermediário de sucessão, mas a espécie é capaz de colonizar áreas em estágio inicial e de persistir em comunidades vegetais em estágio avançado. O processo de colonização pela espécie aconteceu entre 10 a 15 anos atrás em florestas que atualmente estão em estágio sucessional intermediário, e pelo menos há 30 anos em florestas em estágio avançado. Acredita-se que a deciduidade natural da floresta tenha sido um fator que provavelmente facilitou a colonização e a permanência da espécie nos estágios mais avançados de regeneração. Contrariamente ao que se esperava, não foram encontradas diferenças entre comunidades vegetais invadidas e não invadidas nos três estágios sucessionais. Também não foi encontrada relação entre riqueza e diversidade de espécies e diversidade funcional e susceptibilidade à invasão ao longo do gradiente sucessional. Para o segundo estudo, realizado entre os meses de maio a setembro, período de frutificação de *H. dulcis*, em 2012 e em 2013, foi realizada uma caracterização da chegada de propágulos em sítios não invadidos a partir da dispersão a curtas distâncias por aves, e uma avaliação da efetividade de iniciativas de controle de *H. dulcis* na redução na pressão de propágulos nesses sítios. Foram testadas as hipóteses que a dispersão local de sementes a partir de sítios invadidos estaria relacionada à densidade e à distância das fontes de propágulos, e que os padrões de dispersão local seriam alterados quando as fontes de propágulos fossem removidas por meio do corte de árvores. A chegada de sementes levadas por aves foi comparada por meio da instalação de coletores de sementes em sítios não invadidos, que encontravam-se a diferentes distâncias de sítios invadidos por *H. dulcis*, e comparados entre vegetação aberta e fechada. A chegada de sementes também foi comparada entre parcelas controle e parcelas nas quais foi realizado o corte de árvores de *H. dulcis* em um raio de 30 m a contar do centro da parcela. Foi observada uma limitação na dispersão de sementes por aves a curtas distâncias na área de estudo, especialmente em sítios com vegetação aberta. Houve uma relação exponencial negativa entre o número de sementes encontrado nos coletores e a distância de árvores de *H. dulcis* até os sítios não invadidos onde as parcelas foram instaladas; por outro lado, o número de sementes aumentou exponencialmente em relação à área basal das árvores de *H. dulcis* amostradas nas adjacências desses sítios não invadidos. O corte de árvores adultas de *H. dulcis* foi efetivo para reduzir a chegada de propágulos em sítios não invadidos com vegetação fechada, resultando em um menor número de sementes nos coletores em parcelas submetidas ao corte quando comparadas com parcelas controle. Por fim, no terceiro estudo, a germinação de sementes e a sobrevivência e o crescimento de plântulas de *H. dulcis* foram avaliados experimentalmente nos três estágios sucessionais estabelecidos, por 400 dias, entre junho de 2013 e junho de 2014. Testou-se a hipótese de que a germinação de sementes e o crescimento e a sobrevivência de plântulas decresceriam ao longo do gradiente sucessional, e que seriam dependentes da cobertura do sub bosque, da umidade do solo e da espessura da serrapilheira. Foi também testada a hipótese de que a frequência de herbivoria em plântulas de *H. dulcis* variaria entre estágios sucessionais. Os processos de germinação de sementes e estabelecimento de plântulas de *H. dulcis* ocorrem nos três estágios sucessionais estudados, o que evidencia que a espécie apresenta tolerância à sombra na fase de plântula, tornando-a uma invasora em potencial mesmo no interior de florestas com menor abertura de dossel. Maiores porcentagens de germinação foram observadas em vegetação fechada, enquanto a sobrevivência de plântulas foi maior em vegetação semiaberta, e o crescimento de plântulas foi maior em vegetação aberta. A frequência de herbivoria não variou entre estágios sucessionais. Fatores abióticos foram mais importantes do que fatores bióticos na determinação do sucesso de estabelecimento de *H. dulcis*. Foi observada uma relação positiva entre umidade do solo e germinação de sementes, enquanto espessura de serrapilheira influenciou negativamente a germinação de sementes de *H. dulcis*. A porcentagem de solo exposto influenciou negativamente a sobrevivência de plântulas. Considerando-se a capacidade de *H. dulcis* de colonizar e invadir florestas secundárias, especialmente aquelas em estágio intermediário de regeneração, conclui-se que a condição na qual atualmente se encontram as florestas catarinenses seria o cenário ideal para a invasão pela espécie. A suscetibilidade dessas florestas à invasão por *H. dulcis* pode ser ainda maior em virtude do plantio difuso da espécie em propriedades rurais para fins diversos, resultando em uma intensa pressão de propágulos em fragmentos florestais. Sendo assim, recomenda-se que a utilização da espécie seja proibida em projetos de recuperação e restauração ambiental, assim como seu plantio para qualquer fim em unidades de conservação e em suas zonas de amortecimento. Recomenda-se, ainda, que uma distância mínima de plantio de 30 metros de fragmentos florestais deve ser adotada em propriedades rurais, em regiões de domínio de florestas no estado. O uso de espécies nativas em substituição a *H. dulcis*, por meio de políticas públicas e programas de incentivo, são fundamentais para a conservação dos fragmentos remanescentes da Floresta Estacional Decidual de Santa Catarina.

Palavras-chave: Espécie exótica invasora. Floresta Estacional Decidual. Sucessão ecológica. Unidade de conservação.

ABSTRACT

Invasive alien species can cause substantial economic and environmental impacts, and are currently considered one of the greatest threats to biodiversity at the global scale. Plant invasions occur as results of the combination of introduced species biological and ecological traits, biotic and abiotic conditions of the receiving habitat, and propagule pressure, considering the number of introduction events as well as the number and genetic diversity of introduced propagules. Ecosystems of lower biodiversity and higher intensity and frequency of disturbance are generally more invaded than those where disturbance is rare and diversity is high. *Hovenia dulcis*, known as japanese cherry, is a deciduous, zoochorous tree native to East Asia, described in scientific literature as a pioneer species. It was introduced and more intensely cultivated in the western region of Santa Catarina state after 1980, when the regional agroindustry fostered its use for shading in poultry and pork farms. The species disperses beyond cultivation areas, being widely found in forest areas in Santa Catarina state, and having been found as the most important species in the shrub-tree layers of forests. It can change the structure and species composition in forest communities in southern Brazil. The general goal of our research was to investigate key factors of the invasion ecology of the alien species *Hovenia dulcis* in seasonal deciduous forests in Santa Catarina in order to generate guidance for practical management. Three different studies were carried out at the Fritz Plaumann State Park in the municipality of Concordia between 2011 and 2014, in a landscape composed of fragments of Seasonal Deciduous Forest in different successional stages. In the first study, sample plots were set up in open, semi-open, and closed vegetation in different fragments between July, 2010, and January, 2011. These fragments correspond to three stages in a successional gradient, in areas invaded and not invaded by *H. dulcis*. All trees with DBH (diameter at breast height) larger than 5cm were identified and classified in functional groups, defined according to dispersal syndrome, regeneration strategy, vertical stratification, and leaf phenology. The age of sampled *H. dulcis* trees was estimated from the growth rings of felled trees. The hypothesis that species establishment and invasion success by *H. dulcis* would be greater in initial successional stages, where resource availability is higher while species diversity and functional diversity are lower, was elaborated based on general premises of biological invasion and known ecological traits of the species. Higher adult tree density was verified in areas in intermediate successional stages, but the species is capable of colonizing areas in initial stages and of persisting in advanced stages. The colonization by the species took place 10 to 15 years ago in forests currently in an intermediate successional stage, and at least 30 years ago in forests in the advanced stage. The natural deciduous characteristic of the forest may have been a factor that facilitated the colonization by the species, as well as its persistence in advanced successional stages. On the contrary to what was expected, no differences were found between invaded and non-invaded plant communities in the three successional stages, and no relationship was found between species richness and diversity, or between functional diversity and susceptibility to invasion along the successional gradient. In the second study, the arrival of propagules due to short-distance dispersal by birds in invaded and non-invaded areas was registered and characterized during *H. dulcis* fructification periods in 2012 and in 2013. An assessment of the effectiveness of control measures of *H. dulcis* in reducing propagule pressure on these sites was also carried out. The hypotheses that local seed dispersal from invaded sites could be related to density and distance of propagule sources, and that local dispersal patterns could be altered when the propagule sources were removed by tree felling, were tested. Seed arrival by birds was assessed by installing seed collectors in non-invaded sites at different distances from sites invaded by *H. dulcis*, then compared between open and closed vegetation. Seed arrival was also compared between control plots and plots were all *H. dulcis* trees were felled within a 30m radius from the center of plots. A limitation in short distance seed dispersal by birds was observed in the study area, especially in open vegetation. A negative exponential relationship was found between the number of seeds in seed collectors and the distance of *H. dulcis* trees to non-invaded sites where the plots were set up; on the other hand, the number of seeds increased exponentially in relation to *H. dulcis* trees basal areas surrounding the non-invaded plots. Felling *H. dulcis* trees was effective to reduce propagule arrival in non-invaded sites in closed vegetation, as it resulted in smaller numbers of seeds in collectors in felled plots compared to control plots. In the third study, *H. dulcis* seed germination, seedling survival and growth were assessed experimentally in the three successional stages during 400 days between June 2013 and June 2014. The hypothesis that seed germination and seedling survival and growth would decrease along the successional gradient, and that they would be dependent upon undergrowth cover, soil moisture, and litter thickness, was tested, as well as the hypothesis that herbivory frequency in *H. dulcis* seedlings would vary between successional stages. The seed germination and seedling establishment processes were observed in the three successional stages studied, which provides evidence that the species tolerates shade in the seedling phase, characterizing the species as a potential invasive even in forests with scarce canopy openness. Higher germination percentages were observed in closed vegetation, while seedling survival was higher in semi-open vegetation, and seedling growth was higher in open vegetation. Herbivory frequency did not vary between successional stages. Abiotic factors were more important than biotic factors in determining establishment success of *H. dulcis*. A positive relationship was found between soil moisture and seed germination, while litter thickness influenced seed germination negatively. Percentage of bare soil also influenced seedling survival negatively. Considering that *H. dulcis* is capable of colonizing and invading secondary forests, especially those in intermediate regeneration stages, we concluded that the current condition of Santa Catarina forests are an ideal setting for the species invasion. The susceptibility of invasion of these forests to *H. dulcis* tends to be even greater due to diffuse plantings of the species in rural properties for diverse uses, resulting in intense propagule pressure to forest fragments. It is therefore recommended that this species is banned from use in environmental restoration projects, as well as from planting for any purpose in protected areas and their buffer zones. We also recommend that a minimum distance of 30m from forest fragments be adopted for plantings in rural properties in all forest areas in the state. Fostering the use of indigenous species to replace *H. dulcis* through public policies and incentive programs is essential for the conservation of remaining fragments of seasonal deciduous forests in Santa Catarina.

Keywords: Invasive alien species. Seasonal deciduous forest. Succession. Protected area.

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SUMÁRIO

INTRODUÇÃO GERAL

O PROCESSO DE INVASÃO BIOLÓGICA

Um maior esforço de introduções intencionais e assistidas por meio do comércio internacional e uso de espécies exóticas invasoras para fins econômicos diversos tem facilitado a chegada e o estabelecimento dessas espécies em hábitats anteriormente não colonizados (Rejmánek et al., 2013). No arquipélago de Galápagos, por exemplo, a taxa de chegada de plantas vasculares era em média de uma espécie a cada 10.000 anos, por meio de correntes marinhas ou transportadas por aves. Ao longo dos últimos 470 anos, a taxa de introduções assistidas por intervenção humana tem sido de 1,2 novas espécies estabelecidas por ano, o que representa um aumento de 13.000 vezes quando comparadas às migrações naturais (Tye, 2006). Muitas das espécies introduzidas permanecem em áreas degradadas ou são incorporadas à comunidade vegetal local sem necessariamente provocar impactos, ao menos que sejam perceptíveis ou mensuráveis (Richardson et al., 2000; Rejmánek et al., 2013). Uma pequena porcentagem, entretanto, pode provocar impactos ambientais e econômicos substanciais (Rejmánek et al., 2013).

O conjunto de espécies exóticas introduzidas em uma determinada região é decorrente de fatores históricos ligados ao tipo, à intensidade e à frequência de atividades humanas (Kueffer, 2013). Atividades florestais e agroflorestais, controle de erosão e horticultura são reconhecidas por levar à translocação de plantas além das suas áreas de distribuição natural (Dickie et al, 2014; Rejmánek, 2014). Uma vez que uma espécie é introduzida, algumas barreiras devem ser transpostas ao longo do processo de invasão biológica para que a espécie seja chamada de invasora, conforme descrito por Richardson e colaboradores (2000). A primeira barreira, denominada geográfica, é ultrapassada quando a espécie consegue transpor um limite geográfico que naturalmente limita sua distribuição e que só é ultrapassado em decorrência de assistência humana. A espécie passa então a ser chamada de introduzida ou exótica uma vez que a transpõe. A segunda barreira, denominada barreira de estabelecimento ou naturalização, é transposta quando fatores bióticos e abióticos limitantes à sobrevivência e à reprodução são superados. Espécies que ultrapassam esta segunda barreira são ditas naturalizadas ou estabelecidas. A barreira de invasão propriamente dita requer que a espécie introduzida produza descendentes reprodutivos em áreas distantes de onde ocorreu a introdução, em ambientes naturais.

Richardson et al. (2000) sugeriram a taxa de disseminação a partir do(s) ponto(s) de introdução como critério para se definir se uma espécie é introduzida pode ser chamada de invasora. Assim, uma taxa de disseminação de mais 100 metros ao longo de 50 anos para espécies que se reproduzem por sementes seria o mínimo para que essas espécies sejam denominadas invasoras. Já para espécies que se reproduzem por raízes, rizomas ou estolões, esse valor deve ser de mais de seis metros ao longo de três anos. É importante destacar que, embora existam outras definições para o termo espécie exótica invasora (Mack, 1997; Cronk & Fuller, 2005), a abordagem de Richardson e colaboradores (2000) foi a adotada neste trabalho por descrever a invasão como um processo biológico, sem necessidade de inferência a impactos ambientais ou econômicos (Valéry et al. 2008).

Um número crescente de estudos têm documentado como a invasão por plantas exóticas pode alterar a biodiversidade (Powell et al., 2011), a hidrologia (Le Maitre, 2004), a ciclagem de nutrientes (Ehrenfeld, 2003), propriedades do solo (Ehrenfeld, 2010), regimes de distúrbios (Mack & D'Antonio, 1998) e a frequência de incêndios (Brooks et al., 2004), assim como interações tróficas acima e abaixo do nível do solo (Levine et al., 2003). Os frequentes efeitos observados nesses processos evidenciam que certas plantas exóticas podem modificar o funcionamento de ecossistemas (Wardle et al., 2011; Vilà et al., 2011). Em uma recente revisão sobre o impacto de plantas em um contexto global, Pysek e colaboradores (2012) concluíram que espécies exóticas invasoras provocam impactos significativos na sobrevivência da biota nativa, na atividade de animais residentes, na produtividade da comunidade residente, na composição de tecidos vegetais e na frequência e intensidade de incêndios.

FATORES DETERMINANTES PARA O SUCESSO DE PLANTAS INVASORAS

Invasões por plantas ocorrem como resultado da combinação de características biológicas das espécies introduzidas, de características das comunidades que as recebem, de fatores abióticos locais e da pressão de propágulos da espécie introduzida (Fridley, 2011). A pressão de propágulos é um mecanismo determinante para o sucesso de invasões em diferentes escalas (Lockwood et al., 2005; Simberloff, 2009), e pode ser definida por seus dois componentes principais: o número de propágulos introduzidos e o número de eventos de introdução (Simberloff, 2009). Há ainda um componente genético, intitulado diversidade de propágulos, que se refere ao número de populações-fonte que são geneticamente distintas (Lockwood et al., 2005). Quanto mais intensa a pressão de propágulos e quanto maior a diversidade genética das populações-fonte, maior a chance de estabelecimento de uma espécie exótica (Crawford & Whitney, 2010; Zenni & Simberloff, 2013).

Já o conceito de suscetibilidade do ambiente à invasão por espécies exóticas (*invasibility*, em inglês) pode ser compreendido como o resultado de diversos fatores, incluindo fatores abióticos do ambiente, a habilidade competitiva das espécies residentes e o regime de distúrbios (Rejmánek, 1989; Lonsdale, 1999; Huston, 2004; Whitfield et al., 2014). Aumentos na disponibilidade de recursos como luz, água e nutrientes, assim como a redução na competição por recursos em decorrência de distúrbios, podem facilitar o estabelecimento de plantas exóticas (Davis et al., 2000; Goldstein & Suding, 2014). Moles et al. (2012), em uma análise recente feita sobre a relação entre distúrbios e o sucesso de invasão por plantas exóticas, destaca que não é estritamente a ocorrência de um distúrbio que facilita processos de invasão, mas sim a alteração no regime natural de distúrbios em um ambiente. Efeitos de distúrbios na suscetibilidade à invasão podem também ocorrer devido a alterações na composição de espécies na comunidade, resultando em comunidades compostas por espécies com diferentes níveis de resistência a distúrbios e taxas de recuperação após sua ocorrência (Symstad, 2000).

A hipótese de que existe uma relação causal entre a suscetibilidade à invasão e a biodiversidade de um ecossistema, intitulada resistência biótica, é atribuída a Charles Elton (Fridley, 2011). De acordo com Elton (1958), ecossistemas com mais alta biodiversidade seriam mais resistentes a espécies invasoras do que ecossistemas com baixa biodiversidade. Na maior parte dos estudos realizados para testar esta hipótese, compararam-se a riqueza de espécies nativas com a riqueza de espécies exóticas, sendo uma alta riqueza de espécies introduzidas considerada uma medida inversa de resistência biótica (Jeschke, 2014). Alguns estudos mostram que esta relação existe e é positiva em grandes escalas, como em escala de paisagem (Stohlgren et al., 1999; Davies et al., 2011), e negativa em escalas de unidades amostrais menores (por exemplo, parcelas com área inferior a 1m²). Esses resultados aparentemente conflitantes constituem o que tem sido chamado de “paradoxo em invasão” (*invasion paradox*, em inglês). Tanto o número de espécies nativas e o número de espécies exóticas são reguladas de modo similar pelo mesmo conjunto de fatores, tais como interações bióticas, microclima, heterogeneidade espacial, regimes de longo prazo de disponibilidade de recursos (Tilman, 2004; Davies et al., 2005; Stohlgren et al., 2006; Fridley et al., 2007). Entretanto, diferentes fatores parecem atuar mais fortemente em diferentes escalas espaciais (Fridley et al., 2007). Em escalas espaciais menores, de maneira geral predominam condições ambientais homogêneas, sendo interações bióticas mais importantes na abundância de espécies nativas e exóticas. À medida que aumenta a escala espacial, a heterogeneidade espacial também aumenta, o que tem um efeito direto sobre as espécies presentes (Fridley et al., 2007). Em síntese, interações bióticas que dominam em pequena escala são substituídas pelo ambiente físico em grandes escalas (Fridley et al. 2007).

Estudos experimentais confirmaram a relação negativa entre riqueza de espécies vegetais residentes e suscetibilidade à invasão em pequenas escalas (Fargione & Tilman, 2005 ; Maron & Marler, 2008) e mesmo em unidades amostrais maiores (4 m²; Petermann et al., 2010). A explicação mais plausível para a baixa suscetibilidade à invasão em comunidades com maior diversidade de espécies nativas parece não ser o número de espécies por si, mas sim a complementaridade de espécies no uso de recursos, usualmente menos disponíveis em comunidades com maior número de espécies (Tilman, 2004). Ou ainda, ecossistemas com alta biodiversidade seriam mais estáveis e ofereceriam poucas oportunidades de nicho para espécies exóticas invasoras, tornando-os assim mais resistentes à invasão (Ives & Carpenter, 2007; Jeschke, 2014).

Destaca-se, ainda, que a resistência biótica pode ocorrer nas diferentes etapas do processo de invasão, não só em decorrência de competição com espécies nativas, mas também em consequência de outras interações negativas com espécies residentes, tais como predação, herbivoria e doenças (Levine et al. 2004). Em uma metanálise sobre resistência biótica em invasões por plantas exóticas, os autores concluíram que interações bióticas não são suficientes para repelir invasões, mas que restringem a abundância de espécies exóticas uma vez que as mesmas estejam estabelecidas (Levine et al., 2004). Além disso, quando introduzidas fora da sua área de distribuição natural, espécies vegetais ficam usualmente livres de seus inimigos naturais, incluindo predadores, patógenos e parasitos (Blossey, 2011). A hipótese de que a ausência do controle *top-down* facilita o estabelecimento e a consequente invasão por espécies introduzidas (*enemy release hypothesis*, em inglês), entretanto, não é cientificamente amparada. Na recente metanálise publicada por Chun e colaboradores (2010) mostrou-se que espécies exóticas dificilmente ficam livres de inimigos naturais quando levadas para fora de sua área de distribuição natural e que, quando esta liberação acontece, nem sempre resulta em melhor performance dos indivíduos introduzidos.

A capacidade de uma espécie exótica de se reproduzir e se disseminar a partir do ponto onde foi introduzida e se estabelecer em novas áreas é denominada potencial de invasão (*invasiveness*, em inglês) (Rejmánek, 2011). O potencial de invasão de plantas introduzidas pode variar entre populações de uma mesma espécie (Sakai et al., 2001) e é determinado por diferentes atributos biológicos que variam em importância de acordo com o local onde a espécie é introduzida (Rejmánek et al., 2013). Características relacionadas aos eventos de introdução podem mascarar o potencial de invasão associados aos atributos biológicos (Rejmánek, 2011). Neste sentido, a pressão de propágulos, o conjunto genético, o tempo de residência e a assistência humana podem ser determinantes para o sucesso de uma espécie introduzida (Bufford & Daehler, 2011; Rejmanek et al., 2013). Em uma análise feita com 117 plantas exóticas invasoras, Zenni (2013) concluiu que a composição da flora invasora no Brasil é decorrente da combinação de padrões recentes de ondas de migrações humanas e de introduções voluntárias assistidas por motivos comerciais, especialmente para horticultura e uso como forrageiras.

Entre espécies lenhosas, atributos biológicos correlacionados com o potencial de invasão podem também variar de acordo com o grupo taxonômico (Grotkopp et al., 2002; Richardson et al., 2011; Moodley et al., 2013). Enquanto o tamanho da semente, o intervalo de tempo entre eventos de frutificação e o tempo necessário para atingir a maturidade reprodutiva são características correlacionadas com potencial de invasão no gênero *Pinus* (Grotkopp et al., 2002), o tamanho de semente foi um importante preditor do potencial de invasão de espécies de Proteaceae (Moodley et al., 2013). Diferentes atributos podem ser associados aos diferentes estágios do processo de invasão, sendo que alguns deles apresentam respostas distintas em diferentes estágios (Dawson et al., 2009; Bufford & Daehler, 2011; Moodley et al., 2013). Por exemplo, durante a fase de estabelecimento, sementes maiores são importantes pois apresentam uma maior quantidade de reservas; já na fase de disseminação para novas áreas, sementes menores apresentam uma vantagem, pois permitem a dispersão a longas distâncias (Bufford & Daehler, 2011; Moodley et al., 2013).

FRAGMENTAÇÃO FLORESTAL E INVASÃO POR PLANTAS EXÓTICAS

A dinâmica de regeneração em florestas neotropicais é amplamente determinada por distúrbios naturais (Hubbel et al., 1999). Quando distúrbios de origem humana geram fragmentação e perda de hábitat, mudanças significativas no regime natural de distúrbios acontecem, favorecendo espécies exóticas invasoras (Hyatt, 2008; Moles et al., 2012), especialmente em clareiras e em bordas (Fine, 2002; Denslow & DeWalt, 2008; Hobbs, 2011). Intensos processos de fragmentação e perda de hábitat têm alterado drasticamente a disponibilidade de recursos, e a estrutura, dinâmica e composição de espécies em florestas neotropicais (Laurance et al., 2000; Michalski et al., 2007; Denslow & DeWalt, 2008), o que também tende a facilitar processos de invasão biológica.

Quando espécies introduzidas são afins aos novos hábitats, mesmo ecossistemas vistos como resistentes à invasão podem se tornar suscetíveis a espécies exóticas (Lugo, 2013; Rejmánek et al., 2013). Evidências indicam que poucas espécies são capazes de invadir comunidades vegetais em estágios sucessionais avançados, especialmente em florestas tropicais (Rejmánek, 1989; Fine, 2002; Meiners et al., 2002). Entretanto, uma boa parte da explicação para esta relação são as características do conjunto de espécies que são mais comumente introduzidas em função dos objetivos de uso: espécies de rápido crescimento e que são r-estrategistas. Muitas dessas espécies não são tolerantes à sombra, o que faz com que estas desapareçam do ambiente durante os primeiros anos de sucessão secundária (Rejmánek et al., 2013). Por outro lado, espécies que apresentam tolerância à sombra podem invadir comunidades vegetais em estágios sucessionais mais avançados, e portanto representam um desafio para o manejo de áreas protegidas (Martin et al., 2009).

A FLORESTA ESTACIONAL DECIDUAL DE SANTA CATARINA E A INVASÃO POR *Hovenia dulcis*

As florestas estacionais neotropicais são caracterizadas como formações florestais com diferentes níveis de deciduidade que ocorrem nas regiões tropicais e subtropicais dos continentes centro e sul americano (Beard, 1955). Distribuem-se de forma disjunta e fragmentada em uma área que recobre parte da América do Sul, da América Central e do Caribe (Murphy & Lugo, 1986). No Brasil, essas florestas são os remanescentes de um "arco pleistocênico" constituído por uma extensa área de florestas sazonais que ocorrem desde a caatinga, no nordeste, até a região sul (Prado & Gibbs, 1993). A Floresta Estacional Decidual de Santa Catarina está inserida neste arco, originalmente cobrindo 8% da área do estado ao longo do eixo principal do rio Uruguai e de seus afluentes, em altitudes que variam de 200 a 600 metros e com precipitação anual média de cerca de 1.800 mm (Klein, 1972; IBGE, 2012). Como as chuvas são bem distribuídas ao longo do ano, acredita-se que a deciduidade da floresta não seja determinada por escassez hídrica, mas por diferenças marcantes entre as temperaturas médias de inverno e verão, influenciadas pela diminuição do fotoperíodo no outono e inverno (Alberti et al., 2011), sendo que mais de 50% das espécies emergentes e do dossel perdem as folhas (Klein, 1972). A Floresta Estacional Decidual apresenta famílias e gêneros amplamente característicos de florestas secas, mas também recebe acentuada influência florística das florestas ombrófilas situadas a leste (Gasper et al., 2013). Sendo assim, alguns autores afirmam que a Floresta Estacional Decidual de Santa Catarina representa algo como uma transição entre aquelas típicas de ambientes ombrófilos da margem Atlântica e as estacionais que tendem a predominar para oeste (Oliveira-Filho & Fontes, 2000; Gasper et al., 2013).

A ocupação sistemática do oeste catarinense pelo colonizador europeu ocorreu entre as décadas de 1920 e 1960, com a chegada de imigrantes italianos e alemães descendentes das etnias estabelecidas no Rio Grande do Sul (Ruschel et al., 2003). A atividade extrativista de madeira na Floresta Estacional Decidual foi intensamente praticada pelos imigrantes visando à implantação da agricultura e da pecuária e ao uso e comércio da madeira (Ruschel et al., 2003). Em decorrência do histórico de ocupação e uso de seus recursos, florestas estacionais encontram-se mais acentuadamente fragmentadas e descaracterizadas do que florestas ombrófilas em Santa Catarina, indicando a necessidade de ações e políticas relacionadas à sua conservação (Gasper et al., 2013). Em Santa Catarina, restam cerca de 16% da área de cobertura original da Floresta Estacional Decidual, sendo que cerca de 90% dos fragmentos são menores do que 50 ha (Vibrans et al., 2012).

Hovenia dulcis Thunb. (Rhamnaceae) é uma espécie arbórea decídua, nativa no leste asiático (Kopachon et al., 1996) e invasora em florestas na América do Sul e na Tanzânia (Kopachon et al., 1996; Hyun et al., 2010; Zenni & Ziller, 2011; Rejmánek & Richardson, 2013). É descrita como espécie pioneira, de crescimento rápido, com 10 a 25 metros de altura, que se reproduz sexuadamente por sementes (Carvalho, 1994). Frutifica entre março e outubro no Brasil (Carvalho, 1994), com pico de frutificação no inverno, entre junho e julho (Dechoum, observação pessoal). Apresenta infrutescências compostas por cápsulas globosas escuras e secas, com seis a sete mm de diâmetro, que contêm de duas a quatro sementes e que estão presos a um pedúnculo marrom, rico em carboidratos, que se torna espessado e carnoso ao amadurecer (Carvalho, 1994; Zhou et al., 2013). Tanto em sua área de distribuição natural quanto em florestas na América do Sul, sementes intactas são consumidas (Hendges et al., 2014) e dispersas por aves e mamíferos (Takatsuki, 1988; Mottajunior et al., 1994; Cáceres & Monteiro-Filho, 2001; Hirsch, 2009; Tsuji et al., 2011; Lima, 2014).

No Estado de Santa Catarina, já em 1972, a espécie era largamente difundida para cultivo, tanto na zona litorânea quanto no planalto (Jonhston & Soares, 1972). Na região oeste do estado, *H. dulcis* foi mais intensamente cultivada a partir da década de 1980, quando agroindústrias da região fomentaram seu uso em granjas de suínos e aves (Selle, 2009). Desde sua introdução na região, *H. dulcis* tem sido extensivamente plantada em propriedades rurais para uso madeireiro (Selle, 2009) e para arborização de culturas, pastagens, cerca viva, uso em serraria e produção de energia (Carvalho, 1994). Nas recentes amostragens feitas para o Inventário Florístico Florestal de Santa Catarina, observou-se que a espécie pode se dispersar além de suas áreas de cultivo, estabelecendo-se em bordas e clareiras de fragmentos florestais secundários na Floresta Ombrófila Densa e na Floresta Estacional Decidual, podendo chegar a ser a espécie mais importante no componente arbóreo-arbustivo (Vibrans et al., 2012b). *Hovenia dulcis* atualmente consta na lista oficial de espécies exóticas invasoras dos estados do Paraná, Santa Catarina e Rio Grande do Sul (Paraná, 2009; Santa Catarina, 2012; Rio Grande do Sul, 2013). No Rio Grande do Sul, a espécie foi enquadrada na categoria 1, o que significa que estão proibidos seu transporte, criação, soltura ou translocação, cultivo, propagação (por qualquer forma de reprodução), comércio, doação ou aquisição intencional sob qualquer forma. Já no Paraná e em Santa Catarina, foi enquadrada na categoria 2, o que significa que sua criação ou cultivo são permitidos sob condições controladas, estando sujeitas a normas e condições específicas a serem definidas pelos órgãos ambientais competentes.

Esta tese trata de aspectos da ecologia de invasão da espécie exótica *H. dulcis*, sendo a área de estudo o Parque Estadual Fritz Plaumann. O Parque está localizado no município de Concórdia, meio oeste catarinense, às margens do rio Uruguai, em uma região de transição entre Floresta Ombrófila Mista e Floresta Estacional Decidual. A tese está dividida em três capítulos, escritos em inglês e na forma de artigos. No primeiro capítulo, compararam-se áreas em três estágios sucessionais, com e sem indivíduos adultos de *H. dulcis*, do ponto de vista de estrutura, diversidade e diversidade funcional das comunidades vegetais. O segundo capítulo trata da caracterização da chegada de propágulos em sítios não invadidos, a partir da dispersão a curtas distâncias, e da avaliação de iniciativas de controle na redução na pressão de propágulos nesses sítios. Já no terceiro capítulo, a germinação de sementes e a sobrevivência e o crescimento de plântulas foram avaliados experimentalmente em três estágios sucessionais da floresta. Ao final, há uma conclusão geral, também escrita em português.

OBJETIVO GERAL

O objetivo geral deste estudo foi investigar fatores-chave da ecologia de invasão pela espécie exótica *Hovenia dulcis* em florestas estacionais deciduais de Santa Catarina, com vistas a fornecer diretrizes para o manejo da espécie.

OBJETIVOS ESPECÍFICOS

Os objetivos específicos deste estudo foram:

1. caracterizar a estrutura, a diversidade e a diversidade funcional das comunidades vegetais em diferentes estágios de sucessão, com e sem a presença de *H. dulcis*;

2. avaliar a pressão de propágulos em sítios não invadidos por *H. dulcis* em diferentes estágios sucessionais, e relacionar a chegada de propágulos à distância e à abundância de fontes de sementes;

3. avaliar o efeito do corte de árvores adultas de *H. dulcis* na redução da pressão de propágulos em sítios não invadidos em diferentes estágios sucessionais; e

4. avaliar a germinação de sementes e o crescimento e sobrevivência de plântulas de *H. dulcis* em condições experimentais, em diferentes estágios successionais.

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CAPÍTULO 1 - COMMUNITY STRUCTURE, SUCCESSION AND INVASIBILITY IN A SEASONAL DECIDUOUS FOREST IN SOUTHERN BRAZIL[1]

ABSTRACT

Majority of invasive trees colonize grasslands, shrublands, and temperate forests. *Hovenia dulcis* is an exception, because it is one of the most pervasive invaders in Brazilian subtropical forests where it has changed their structure and composition. This study has aimed to identify the clues for its success by defining the structural and functional characteristics of plant communities in different stages of succession with and without *H. dulcis*. Following the general assumptions of invasion ecology, we expected that *H. dulcis* establishment and invasion success would be significantly higher in early successional communities, with high resource availability and low species richness and diversity, as well as low functional diversity. Contrary to this hypothesis, no differences were found between plant communities invaded and non-invaded by *H. dulcis* at three different succession stages. No relationship was found between species richness and diversity and functional diversity, with respect to invasibility along the successional gradient. *Hovenia dulcis* is strongly associated with semi-open vegetation, where the species was found in higher density. The invasion of open vegetation is more recent, providing evidence of the species's ability to invade plant communities in early successional stages. We concluded that the colonization by *H. dulcis* was associated with forest openness, but the species is also able to colonize semi-open vegetation, and persist in the successionally more advanced communities.

KEYWORDS: invasive trees; *Hovenia dulcis*; subtropical forests; functional diversity; biotic resistance; disturbance.

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[1] Artigo publicado na revista Biological Invasions em dezembro de 2014 - DOI 10.1007/s10530-014-0827-6. Autores: Michele Dechoum, Tânia Castellani, Sergio Zalba, Marcel Rejmánek, Nivaldo Peroni, Jorge Yoshio Tamashiro

INTRODUCTION

Ecosystem invasibility is the result of several factors, including physical environmental characteristics, the competitive ability of resident species, and the disturbance regime of the habitat (Rejmánek 1989; Lonsdale 1999; Huston 2004; Whitfield et al. 2014). The availability of resources such as water, light and nutrients, and the reduction in competitive interactions following disturbance facilitate the establishment of alien plants (Davis et al. 2000; Goldstein and Suding 2013). Indirect effects of disturbance on invasibility may also occur due to changes in community composition that may end with species differing in their resistance to disturbance and post-disturbance rates of recovery (Symstad 2000).

Elton (1958) proposed that susceptibility to invasion is also directly affected by community species richness. According to this hypothesis, rich communities are more resistant to invasions because the competition for resources is also higher than in species poor communities. In the case of plant communities, this mechanism may function through competition with native species (Levine 2000) or through other negative interactions triggered by resident species including predation, herbivory and diseases, upon the arrival of an introduced species (Levine et al. 2004). From a functional perspective, higher species richness results in higher functional diversity as long as the species in the community present different functional traits and therefore different strategies to acquire resources (Byun et al. 2013). Higher functional diversity would reduce susceptibility to invasion through the preemption of available resources (Tilman et al. 1997; Pokorny et al. 2005; Brown and Rice 2010; Ammondt and Litton 2011). Additionally, functional trait similarities between resident species and introduced species result in superimposed resource requirements and, as a consequence, in competition among species and biotic resistance (Funk et al. 2008; Byun et al. 2013).

Intact or undisturbed communities are expected to present low susceptibility to invasion by alien species (Elton 1958). Undisturbed forests in particular are considered highly resistant to invasion, in large part because of low light availability (Rejmánek 1989, 1996; Fine 2002; Von Holle et al. 2003; Whitfield et al. 2014). Forests, however, have been intensely threatened by human activities, which result in habitat loss and fragmentation (Laurance and Peres 2006). Fragmentation promotes rapid and predictable shifts in patterns of biological organization across population to ecosystem levels due to a myriad of processes including habitat loss, sample effect, creation of forest edges, rupture of biological connectivity, subdivision/isolation of populations, and post-isolation proliferation of invasive species (Laurance et al. 2002, 2006; Fahrig 2003). Forest fragmentation may facilitate invasion in forests because resource availability is increased, especially on the edges created between original and transformed areas (Fine 2002; Denslow and DeWalt 2008; Hobbs 2011). Land use changes sometimes involve an increased use of introduced species (Hobbs 2011), which can expose natural habitats to propagule pressure of alien species present in surrounding degraded or managed areas (Denslow and DeWalt 2008). Furthermore, many opportunistic animal dispersers can occupy fragment borders and altered matrices, promoting the spread of plant invaders (Buckey et al. 2006).

Given that many invasive alien species usually present traits associated with early successional stages (high seed production, fast growth, short juvenile period - Rejmánek and Richardson 1996; Pysek and Richardson 2007; Catford et al. 2012), early successional communities often host higher numbers and proportions of invasive alien species than those in advanced stages (Rejmánek 1989). However, some studies have shown evidence that an important group of forest invasive species are neither dependent on disturbance nor restricted to early successional stages of plant communities (Webb et al. 2000; Martin et al. 2009), showing shade tolerance and ability to invade closed-canopy forests (Gilbert and Lechowicz 2005; Martin and Marks 2006; Major et al. 2013).

Neotropical seasonal forests are defined as forest types with different degrees of deciduousness occurring in tropical and subtropical regions of Central and South America (Beard 1955). The seasonal deciduous forest has a disjoint distribution in all Brazilian biomes of the tropical and subtropical regions (IBGE 2012). Originally, this type of forest covered 8% of the state of Santa Catarina, southern Brazil (Klein 1978), occurring in the Uruguay River basin at elevations ranging from 200 to 600 meters, with annual precipitation of ca. 1,800 mm/year (Klein 1972). This forest is characterized by a closed canopy dominated by Lauraceae and emergent deciduous species, mostly Fabaceae, and a subcanopy dominated by *Sorocea bonplandii*, *Gynnanthes concolor* and *Trichilia* spp. (Klein 1972). It is nowadays highly fragmented and restricted to 16% of its original area in Santa Catarina state (7,670.57 km²), with 90% of the remnants smaller than 50 ha (Vibrans et al. 2012). Apart from fragmentation, other causes of environmental degradation of these forests include current or historical selective logging and invasion by alien species, such as *Hedychium coronarium* and *Impatiens walleriana* (Dechoum and Ziller 2013). Additionally, the natural deciduousness, alone, may make these forests more susceptible to invasion than tropical ombrophilous forests because it opens a window of opportunity for disturbance-dependent alien species to invade.

The overall objective of this study was to define the composition, structure and functional characteristics of woody plant communities in fragments with and without the presence of *H. dulcis*. Our specific objectives were: (1) to compare density, basal area, height and age of *H. dulcis* trees among successional stages; (2) to assess the influence of soil characteristics and canopy openness on abundance and basal area of the native plant species sampled; (3) to compare density, basal area, richness, diversity, evenness and functional diversity among successional stages and among plots with and without *H. dulcis*; (4) to identify functional groups that contributed more significantly to the separation of plots with and without *H. dulcis* for each successional stage; and (5) to identify possible positive or negative associations among native species and *H. dulcis* in the plots. We hypothesized that *H. dulcis* is best able to establish in and invade plant communities in early successional stages with high resource availability and low species richness and diversity, as well as low functional diversity, and that its presence in successionally advanced forests could be explained by colonization following disturbance events in the past. Because *H. dulcis* is widespread in this part of Santa Catarina state, we assumed that propagule pressure of this species was equivalent across the studied area.

MATERIAL AND METHODS

STUDY SPECIES

Hovenia dulcis Thunb. (Rhamnaceae) is native to east Asia. The species' natural distribution ranges from Japan, Korea and east China to the Himalayas, up to altitudes of 2000 m. It grows preferably in sunny locations on moist sandy or loamy soils (Yun and Lee 2002; Hyun et al. 2009). It is cultivated in plantations in China (Hyun et al. 2009), invasive in South American forests (Zenni and Ziller 2011) and Tanzania (Rejmánek and Richardson 2013), and has been introduced as a rare ornamental plant in different regions including the USA, Australia, New Zealand, and Central Africa (Hyun et al. 2009). Adult trees reach an average 10 to 15 m in height and 20 to 40 cm in diameter, although in southern Brazil they grow up to 25 m in height and 50 cm or more in diameter (Carvalho 1994a). The fruits are small, dry globose capsules carrying 2-4 seeds bound to a cinnamon-colored fleshy peduncule which is sweet and tasty. Seeds are more or less circular, measuring 4 to 8 mm in diameter, and dispersed by animals. The main dispersers in Brazil are mammals of medium size, such as *Dasypus* and *Euphractus* armadillos (Carvalho 1994a) and *Didelphis aurita* (Mammalia, Marsupialia) (Cáceres and Monteiro-Filho 2001). Infructescence consumption by the monkey species *Sapajus nigritus* was observed in the study area (Hendges et al. 2012), and consumption by the bat species *Platyrrhinus* (*Vampyrops*) *lineatus* was observed in Espirito Santo state (Brazil) (Zortéa 1993).

In the second half of the 20th century, human occupation of the western part of Santa Catarina state led to the introduction of *H. dulcis* (Vibrans et al. 2012). The species has been extensively planted in rural properties for wood since its introduction (Selle 2009), as well as for shade over cultivation areas and pasture, wind-breaks, sawmills, and energy production (Carvalho 1994a). *Hovenia dulcis* can change the structure and composition of plant communities in seasonal, dense, and mixed ombrophilous forests (Bardall et al. 2004; Schaff et al. 2006; Boeni 2011).

DESCRIPTION OF STUDY AREA

This study took place at the Fritz Plaumann State Park, a 740 hectare protected area established in 1998 in Concordia (Santa Catarina state, Brazil) (27º 16’18” and 27º 18’ 57” S; 52º 04’ 15” and 52º 10’ 20” W) along the Uruguay River, a region of Cfa (subtropical) climate in the Köppen-Geiger classification. The park is located in the Atlantic forest domain, in a transition area between seasonal and mixed ombrophilous forest (IBGE 2012) containing the threatened species *Ocotea odorifera* (Vell.) Rohwer (Lauraceae) (Brasil 2008). All the data for this study were collected in seasonal deciduous forest fragments.

As all data were collected in the field between July 2010 and January 2011, it was assumed that the vegetation in the area has been under regeneration for at least 13 years. Three vegetation types were defined in the sampling areas: open, semi-open and closed forest, according to current physiognomy, time of abandonment, and history of use (aerial photographs from 1978, 2005, 2008 and 2011, and Siminski et al. 2011). Open and semi-open areas were formerly used for agriculture and/or grazing. Open areas had a herbaceous or herb-shrub cover and few isolated small-size trees of pioneer species, while semi-open areas were characterized by open forest with a low layer of trees (average height around seven meters) dominated by native pioneer tree species. Closed areas were under selective logging, which enabled the tree layer not to be totally suppressed and the physiognomy of a closed forest with a higher tree layer to be preserved (average height about 10 meters), with a greater vertical stratification compared to the other vegetation types. These vegetation types were considered successional stages, following a sequence from open to semi-open and closed vegetation types.

DATA COLLECTION

Twenty 10 m x 20 m plots per vegetation type were set up, 10 with and 10 without *H. dulcis*, making a total of 60 plots. A minimum distance of 100 meters was kept between plots. All trees with diameters above 5 cm at breast height (DBH), living or dead, were identified, and had their height visually estimated. For the trees whose identification was not possible in the field, herbarium specimens were collected and sent to experts.

The native species sampled were classified into functional groups (FG) according to dispersal syndrome, regeneration strategy, vertical stratification, and foliar phenology. Species dispersal syndromes were *animal*, *wind* or *self-dispersed* (Van der Pijl 1982). Regeneration strategies refer to *non-pioneer* species as those that regenerate in the undergrowth of mature forests, and *pioneer* species as those that require light to regenerate (Hartshorn 1978; Whitmore 1989). Vertical stratification was divided into *undergrowth* species, represented by small trees and shrubs which flower and bear fruit in the lower forest stratum (<10m); *canopy* species, which occur in the canopy or sub-canopy); and *emergent* species, which stand out above the forest canopy. Foliar phenology refers to *deciduous* species as those that totally or partially lose their leaves during the cold season, or *evergreen* species as those that do not drop their leaves every year.

The species were classified according to field observations and/or literature (Klein 1972; Reitz 1974; Reitz et al. 1978; Reitz et al. 1988; Carvalho 1994b; Ivanauskas and Rodrigues 2000; Mikich and Silva 2001; Budke et al. 2005; Sobral et al. 2006; Giehl et al. 2007; Ruschel et al. 2007; Yamamoto et al. 2007; Franco 2008; Costa et al. 2011; Kilka and Longhi 2011; Loregian et al. 2012). Although the combination of four parameters and ten classes within these parameters results in 36 possible functional groups, the existing species fell into only 19 groups, as some of the combinations did not match the characteristics of the species sampled (Appendix I).

An assessment of the percentage of canopy openness was carried out based on photographs taken with a digital camera (Nikon Coolpix L20) set on a tripod, positioned one meter above the ground at the center of each plot. These photographs were evaluated through the CPCe software (Kohler and Gill 2006), providing canopy openness percentage results based on a matrix of points distributed at random over each of the images. Two categories, "covered" and "uncovered", were visually identified under each of the random points. Two photographs were taken in each plot, the first one in July 2012, the second one in January 2013, in order to make measurements at the minimum and maximum foliar presence, respectively.

Five sub-samples of approximately 100g of surface soil (to 10 cm depth) were collected, one in each vertex and one in the center of each plot, then pooled to be used as a single sample per plot. The samples were analyzed in the Physical, Chemical and Biological Laboratory of the Integrated Company for Agricultural Development of Santa Catarina State for texture, pH, phosphorous, available potassium, organic matter, exchangeable aluminum, exchangeable calcium, exchangeable magnesium, sodium, H + Al, cation exchange capacity (CEC) and base saturation (V). Soil samples were analyzed from 51 of the 60 plots.

DATA ANALYSIS

Differences in values of canopy openness among vegetation types and among areas with and without *H. dulcis* were tested by permutation tests for two-way analysis of variance (ANOVA) with Tukey’s multiple comparison tests (Wheeler 2010). A histogram of the tree diameters of the populations of *H. dulcis* was completed, and density (number of trees/ha) and basal area (m^2/ha) were calculated. Differences in values of density (number of trees/plot), basal area (cm^2/ha) and height (m) of *H. dulcis* trees were compared among vegetation types using permutation tests for one-way ANOVA with Tukey’s multiple comparison tests (Wheeler 2010). All the variance analysis tests with permutation followed by Tukey's tests were performed using the package 'lmPerm' (5000 iterations) of the R software (R Core Team 2014). Box-and-whisker plots were constructed for canopy openness and *H. dulcis* trees data using R software (R Core Team 2014).

The age estimates of sampled *H. dulcis* trees were based on regression equations generated from data on 506 trees cut down in October, 2012, in a parallel study (Dechoum et al., unpublished data) in which 35 trees originated from open areas, 318 in semi-open areas and 142 in closed areas. We measured the radius of each tree after cutting it and estimated the age by counting annual growth rings of each stump. The radius of each tree was measured from just inside the bark to the center of the trunk. Each year in age is represented by one annual growth ring. An annual ring is comprised of one layer of small vessels and one layer of large vessels, the former corresponding to the winter season and the latter to the summer season. The basal area of each tree was calculated by using the following equation: basal area = π (radius)^2. Regression models for the relationship between age and basal area were conducted using the Biostat 5.0 software (Ayres et al. 2007). The equations that describe those regressions are: $Y = 0.240 + 2.364*\ln X$ for the open vegetation type ($R^2=0.63$), $Y = 3.906*X\text{^}0.258$ for semi-open ($R^2=0.60$), and $Y = 5.213*X\text{^}0.238$ for closed ($R^2=0.54$), where Y = age and X = basal area. The age of the sampled trees was estimated through these equations, and histograms were plotted for each vegetation type.

The influence of soil characteristics and canopy openness on abundance and basal area of the native plant species sampled was assessed using canonical correspondence analysis (CCA) using CANOCO 4.5 software (ter Braak and Smilauer 2002; Leps and Smilauer 2003). In order to test the significance of the influence of environmental variables on species composition based on density and basal area, Monte Carlo permutation tests were carried out with 449 iterations. Ordination diagrams of the plots with isoclines of the "basal area" and "diversity" (Simpson Diversity Index) were produced in CANOCO 4.5, based on abundance and basal area (diversity isoclines only) of the sampled species to visualize the variation of these factors in relation to the plots.

Density, basal area, richness, Simpson Diversity Index (D), Shannon-Wiener diversity index (H'), Pielou evenness index (J), functional diversity index (FD) and functional diversity index weighted by abundance (wFD) (Casanoves et al. 2010; Pla et al. 2012) were compared between vegetation types and in plots with and without *H. dulcis*. The comparisons were made by applying permutation tests for two-way ANOVA with Tukey’s multiple comparison tests (Wheeler 2010), with vegetation type and presence/absence of *H. dulcis* included as factors. The tests were performed using the package 'lmPerm' (5000 iterations) of the R software (R Core Team 2014). Rarefaction curves were produced using 100 randomized orders and the Sobs Mau Tao estimators were calculated using EstimateS Software Version 8.2.0 (Colwell 2006). The mean values and confidence intervals (± 95%) obtained were graphically compared among vegetation types in areas with and without *H. dulcis*.

Functional diversity indices were calculated (FD and wFD) from a matrix composed by the absolute abundance of each species and presence/absence of the categories established for the selected parameters (dispersal syndrome, regeneration strategy, vertical stratification, and foliar phenology) per plot. The index value in each plot was estimated using the FDiversity Software (Casanoves et al. 2010). Correlations between FD, wFD and Shannon-Wiener Diversity Index values and the density of *H. dulcis* in each plot were evaluated using the STATISTICA 7.0 software package (Statsoft 2004).

Discriminant analyses were conducted for each vegetation type using the *stepwise* method of addition and removal of functional groups as discriminant variables in order to identify the functional groups that contributed more significantly and to detect differences in plots with and without the invasive species. A canonical correlation analysis was then performed to determine which functional groups were more relevant in forming the groups of the plots defined *a priori*. These analyses were carried out using the IBM SPSS Statistics 19.0 software (IBM Corp. 2010). The Chi Square test of association was performed using StatView 5.0.1 (SAS Institute Inc. 1998), in order to identify possible positive or negative associations among native species and *H. dulcis* in the plots.

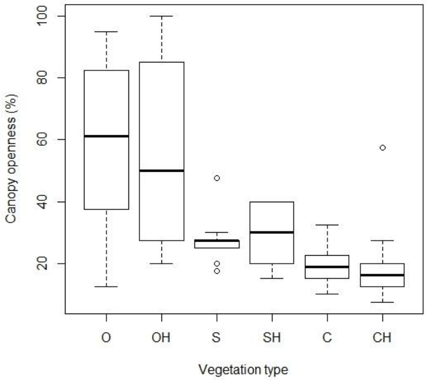
RESULTS

A total of 1976 trees belonging to 125 species and morphospecies and 40 families were recorded in the sampling plots. Nine of the species were not native. Among native species, 94 were identified at the species level and 22 as morphospecies at the genus or family levels. The list of all species, along with their native range, functional groups and number of trees recorded in each vegetation type is presented in Appendix I. The families with the largest numbers of species were Fabaceae, with 20 species (about 17%), Lauraceae, with 11 species (about 9%), Solanaceae, with eight species (about 7%), and Euphorbiaceae, with seven species (about 6%). There were native and alien species in Rutaceae, Moraceae, Myrtaceae, and Lauraceae, while Oleaceae, Cupressaceae, and Rhamnaceae were represented by alien species only.

COMPARISON OF CANOPY OPENNESS AMONG VEGETATION TYPES AND IN PLOTS WITH AND WITHOUT *H. dulcis*

"Vegetation type" was the only significant factor that allowed the differentiation of sampling plots with regard to canopy openness ($F_{(5,54)} = 15.41$; $p < 0.001$). As expected, canopy openness was greater in open than in semi-open and closed vegetation types (Figure 1).

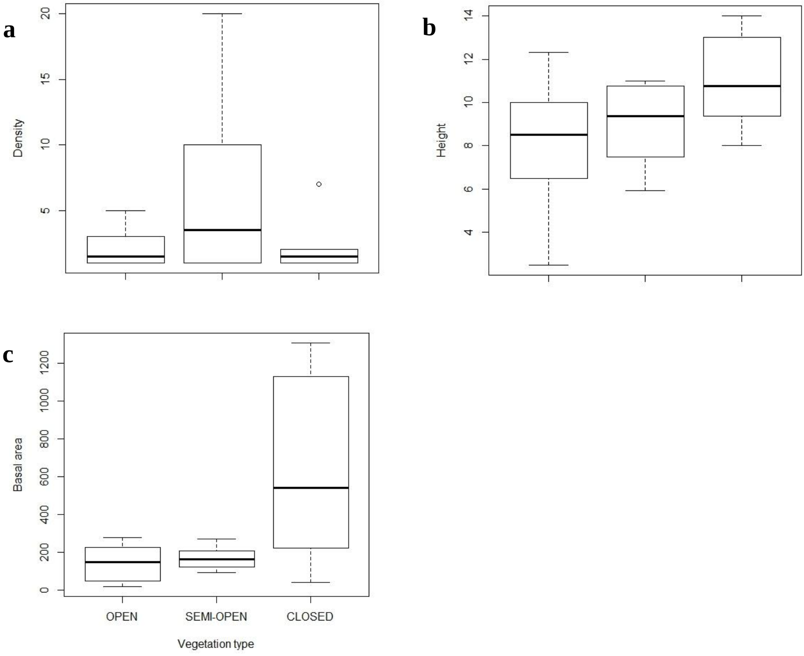
Figure 1 Box-and-whisker plot for canopy openness (%) compared among seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Concordia, SC, Brazil). Vegetation types - O: open without *H. dulcis*; OH: open with *H. dulcis*; S: semi-open without *H. dulcis*; SH: semi-open with *H. dulcis*; C: closed without *H. dulcis*; CH: closed with *H. dulcis*. Circles are outliers.



COMPARISON OF DENSITY, BASAL AREA, HEIGHT AND AGE OF *H. dulcis* TREES AMONG VEGETATION TYPES

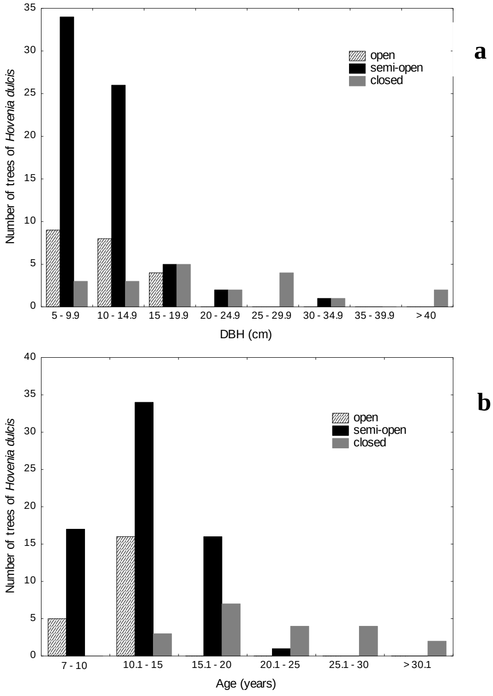
Of the 113 *H. dulcis* trees recorded, the largest number of individuals was present in the semi-open vegetation type (68; 60% of the total), with lower numbers in the closed (27; 24%) and open vegetation types (18; 16%) ($F_{(2,27)}=4.3$; $p=0.02$) (Figure 2). The numbers of trees did not differ between closed and open vegetation types (Figure 2). Average height differed among vegetation types ($F_{(2,27)}=3.7$; $p=0.04$), with taller trees in closed vegetation (Figure 2). The mean basal area was larger in closed vegetation than in open or semi-open types (($F_{(2,27)}=8.9$; $p=0.001$), not differing between semi-open and open types (Figure 2).

Figure 2 Box-and-whisker plot for density (a), height (b) and basal area (c) of *Hovenia dulcis* compared among seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Concordia, SC, Brazil). Vegetation types - OPEN: open; SEMI: semi-open; CLOSED: closed. Circles are outliers.



Overall, *H. dulcis* trees in semi-open and open vegetation types had smaller diameters than those in the closed vegetation type (Figure 3a). In semi-open vegetation, 96% (65 of 68) of *H. dulcis* tree diameters were below 20 cm, while all the trees in open vegetation were below 20 cm in diameter (Figure 3a). A larger variation in diameter was found in the closed vegetation type, with trees in the largest diameter class (>40 cm) found only in this type (Figure 3a). A similar pattern was observed in the age histogram of *H. dulcis*, with the majority of trees in the open and semi-open vegetation types belonging to the younger age classes, and greater age variation in the closed vegetation type (Figure 3b). The average age in the open vegetation type was 12 years (± 3.3), varying from 7 to 19 years (confidence interval 95%: $10.55 \leq \mu \leq 12.37$). In semi-open vegetation, the average age was 16.3 (± 6.3), varying between 9 and 23 years (confidence interval 95%: $12.28 \leq \mu \leq 13.72$). In the closed vegetation type, the average age was 21.4 (±6.5), varying from 9 to around 30 years (confidence interval 95%: $18.35 \leq \mu \leq 24.44$).

Figure 3 Diameter (a) and age (b) structure of *Hovenia dulcis* populations in open (slashed bars), semi-open (black bars) and closed (grey bars) seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Concordia, SC, Brazil)



ASSESSMENT OF THE INFLUENCE OF SOIL AND CANOPY OPENNESS ON NATIVE PLANT SPECIES

The cumulative variance of the CCA based on tree species density explained only 7.5% of the total variance when based on density (F=1.2; p=0.04). Ca, Mg and canopy openness were the variables that best explained the distribution of plots in the ordination space (Figure 4a). The Simpson Diversity Index (Figure 4b) and basal area isoclines (Figure 4c) showed lower diversity and smaller basal area in open vegetation plots. On the otherhand, there was a gradual increase in both measures in semi-open and closed vegetation types. The accumulated variance of the CCA based on tree species basal areas explained 33% of the total variance (F=1.4; p=0.004). Ca, Mg and K best explained the distribution of plots in the ordination (Figure 5a). The Simpson Diversity Index isoclines (Figure 5b) showed lower diversity in the open vegetation plots, and a gradual increase in semi-open and closed vegetation.

COMPARISON OF DENSITY, BASAL AREA, RICHNESS, DIVERSITY, EVENNESS AND FUNCTIONAL DIVERSITY AMONG VEGETATION TYPES AND IN PLOTS WITH AND WITHOUT *H. dulcis*

Structural parameters of the plant communities, density, basal area, richness, diversity by Shannon-Wiener diversity index, FD, and wFD varied significantly among habitat categories, while diversity by Simpson Diversity Index and evenness by Pielou Index did not vary significantly among plots (Table 1). Only the "vegetation type" factor was significant ($p < 0.0001$) among habitat categories for density, basal area, FD, and wFD (Table 1). Density was lower in the open vegetation type than in semi-open and closed vegetation (Table 1). Basal area, richness, Shannon-Wiener diversity index, FD, and wFD showed significantly higher values in the closed vegetation type when compared to semi-open and open vegetation (Table 1). There were no significant correlations between the density of *H. dulcis* and Shannon-Wiener diversity index ($y=1.9849-0.0063x$; $R^2=0.004$; $p=0.75$); the density of *H. dulcis* and FD ($y=5.2155-0.0416x$; $R^2=0.019$; $p=0.47$); and the density of *H. dulcis* and wFD ($y=4.0678-0.0196x$; $R^2=0.07$; $p=0.65$). Plots with

Figure 4 Canonical correspondence analysis (CCA) ordination biplot with plots and environmental variables (vectors) (a), isoclines of Simpson Diversity Index (b) and isoclines of basal area (c) based on density of the native tree species sampled in different seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Concordia, SC, Brazil). Environmental variables: Light - % canopy openness; TEXT - soil texture; pH; P - phosphorus; K - potassium; OM - % organic matter; Al - aluminum; Ca - calcium; Mg - magnesium; Na – sodium; CTC - cation exchange capacity; e V - base saturation. Vegetation types - empty squares: open without *H. dulcis*; full squares: open with *H. dulcis*; empty triangles: semi-open without *H. dulcis*, full triangles: semi-open with *H. dulcis*; empty circles: closed without *H. dulcis*; full circles: closed with *H. dulcis*

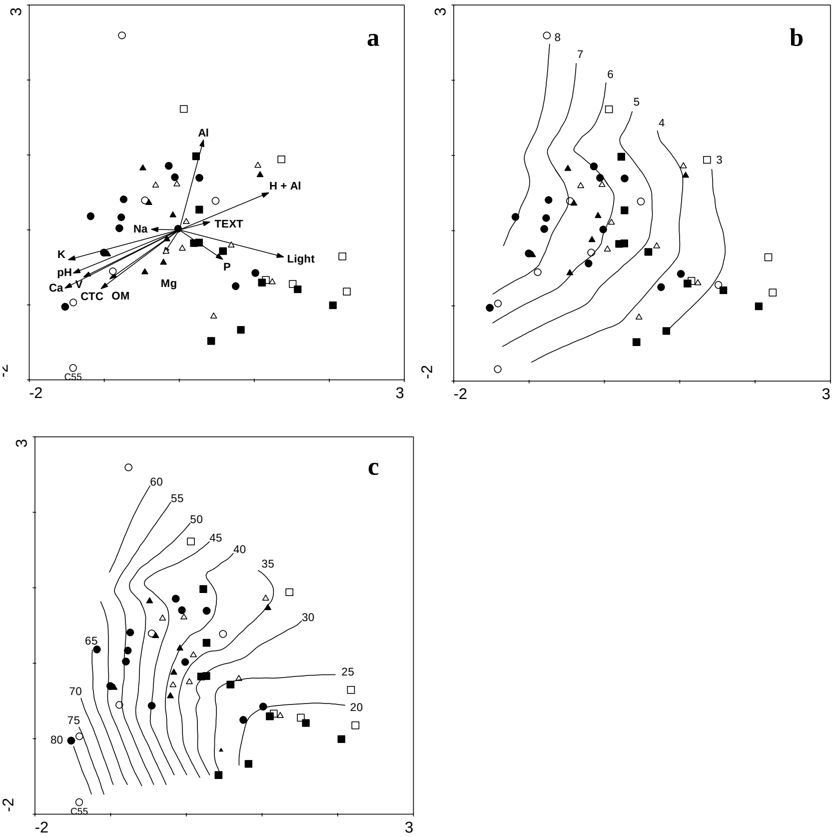
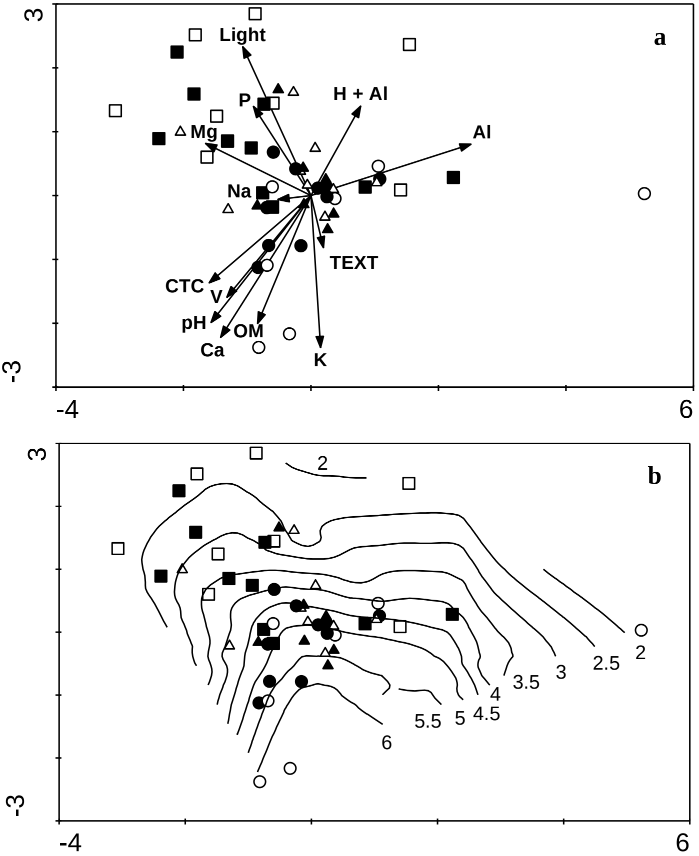


Figure 5 CCA ordination biplot with plots and environmental variables (vectors) (a) and isoclines of Simpson Diversity Index (b) based on the basal area of the native species sampled in different seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Concordia, SC, Brazil). (B) Environmental variables: Light - % canopy openness; TEXT - soil texture; pH; P - phosphorus; K - potassium; OM - % organic matter; Al - aluminum; Ca - calcium; Mg - magnesium; Na - sodium; CTC - cation exchange capacity; e V - base saturation. Vegetation types - empty squares: open without *H. dulcis*; full squares: open with *H. dulcis*; empty triangles: semi-open without *H. dulcis*, full triangles: semi-open with *H. dulcis*; empty circles: closed without *H. dulcis*; full circles: closed with *H. dulcis*



and without *H. dulcis* are not significantly different in estimated richness by rarefaction for the three vegetation types (open without *H. dulcis*=19±8; open with *H. dulcis*=36±10.3; semi-open without *H. dulcis*=42±10.7; semi-open with *H. dulcis*=40±10.4; closed without *H. dulcis*=63±12; closed with *H. dulcis*=63±11.9).

Table 1 Values (means ± 1 S.D.) for density (n of trees/hectare - Dens), basal area (m^2/ha - Basal), richness (number of species - Rich), Simpson diversity index (D), Shannon-Wiener diversity index (H'), Pielou evenness index (J), Functional diversity index (FD) and Functional diversity index weighted by abundance (wFD) compared between each single vegetation type in areas with and without *Hovenia dulcis*, in seasonal deciduous forest in the Fritz Plaumann State Park (Concordia, SC, Brazil). Vegetation types - O: open without *H. dulcis*; OH: open with *H. dulcis*; S: semi-open without *H. dulcis*; SH: semi-open with *H. dulcis*; C: closed without *H. dulcis*; CH: closed with *H. dulcis*

	O	OH	S	SH	C	CH	$F_{(5,54)}$	p
Dens	825^{a} ± 610.2	1100^{a} ± 467.2	1720^{b} ± 519.2	1720^{b} ± 500.6	1580^{b} ± 415.8	1850^{b} ± 322.3	7.2	<0.0001
Basal	10.9^{a} ± 7.6	18.8^{a} ± 5.9	33^{a} ± 8	40.2^{a} ± 9.1	70^{b} ± 16.3	61.2^{b} ± 21.9	32.6	<0.0001
Rich	4.5^{a} ± 2	7.2^{a} ± 3.2	10^{a} ± 3.8	10.8^{a} ± 3.2	13.6^{b} ± 3.1	14.9^{b} ± 2.4	17.2	<0.0001
D	4.4^{a} ± 2.8	5^{a} ±3.2	3.7^{a} ± 2.4	6.1^{a} ± 2.4	6.8^{a} ± 3.5	7.5^{a} ± 3.7	2.3	0.06
H'	1^{a} ± 0.5	1.6^{a} ± 0.4	1.8^{a} ± 0.6	1.9^{a} ± 0.4	2.2^{b} ± 0.3	2.4^{b} ± 0.2	14.6	<0.0001
J	0.6^{a} ± 0.3	0.7^{a} ± 0.1	0.6^{a} ± 0.2	0.7^{a} ± 0.1	0.7^{a} ± 0.1	0.8^{a} ± 0.1	2.2	0.07
FD	2.82^{a} ± 1.3	4.08^{a} ± 1.21	4.83^{a} ± 1.22	5.03^{a} ± 1.29	5.87^{b} ± 1.24	6.08^{b} ± 1.05	9.74	<0.0001
wFD	2.13^{a} ± 1	3.29^{a} ± 0.73	3.57^{a} ± 1.17	3.90^{a} ± 1.04	4.90^{b} ± 1.17	4.80^{b} ± 0.89	10.07	<0.0001

^{a,b}Different letters in each row indicate significant differences (Tukey-test, $p < 0.05$) for a single vegetation type in areas with and without *H. dulcis* and among vegetation types.

IDENTIFICATION OF FUNCTIONAL GROUPS THAT CONTRIBUTED MORE SIGNIFICANTLY TO THE SEPARATION OF PLOTS WITH AND WITHOUT *H. dulcis* FOR EACH VEGETATION TYPE

The functional groups containing zoochorous species showed higher abundance in all successional stages, with the group represented by zoochorous, pioneer, understory, evergreen species (FG11) containing the largest number of individuals (331). The group of zoochorous, non-pioneer, understory, and evergreen species (FG15) had the most species (16). A higher number of functional groups was present in the closed vegetation type (17) in comparison to the semi-open (16) and open (15) vegetation types (Appendix 1). *Hovenia dulcis* was the only alien species classified in the functional group composed by zoochorous, pioneer, canopy, deciduous species (FG14) (Carvalho 1994a). FG14 was represented by only four native species and 21 individuals.

The best discriminant analysis for open and semi-open vegetation types selected three of the 19 functional groups: 6, 13, and 17 for the open vegetation type, and 1, 13, and 17 for semi-open vegetation (Tables 2 and 3, respectively). The function DS= 0.436xFG17 + 0.345xFG6 + 0.168 xFG13 discriminated the two open vegetation type groups (with and without *H. dulcis*, $p < 0.001$), while the function DS= 0.517xFG17 + 0.343xFG1 - 0.22xFG13 discriminated the two semi-open vegetation groups ($p < 0.01$). The percentage of correctly allocated plots using the function obtained for the open vegetation type was 80% for plots with *H. dulcis* and 100% for plots without the species; the percentages were 70 and 100%, respectively, for semi-open vegetation with and without *H. dulcis*. The discriminant analysis showed the group composed by zoochorous, non-pioneer, canopy, evergreen species (FG17) was more important in separating plots with and without *H. dulcis* both in open and in semi-open vegetation types (Tables 2 and 3). The open vegetation type with *H. dulcis* contained 52 individuals from FG17 and the open vegetation type without *H. dulcis* had 13 individuals, while the semi-open type with *H. dulcis* contained 85 individuals from FG17 and the semi-open type without *H. dulcis* had 39 individuals.

Table 2 Discriminant analysis results for functional groups compared between open vegetation plots with and without *Hovenia dulcis*, in a seasonal deciduous forest in the Fritz Plaumann State Park (Concordia, SC, Brazil).

Variables	Standardized coefficients
FG6 (anemochorous, non-pioneer, canopy, evergreen)	0.999
FG13 (zoochorous, pioneer, canopy, evergreen)	0.888
FG17 (zoochorous, non-pioneer, canopy, evergreen)	1.16
Wilk's λ	0.329[a]
Canonical correlation coefficient	0.819

[a] $p < 0.001$

Table 3 Discriminant analysis results for functional groups compared between semi-open vegetation plots with and without *Hovenia dulcis*, in a seasonal deciduous forest at the Fritz Plaumann State Park (Concordia, SC, Brazil).

Variables	Standardized coefficients
FG1 (zoochorous, pioneer, understory, evergreen)	0.844
FG13 (zoochorous, pioneer, canopy, evergreen)	-0.696
FG17 (zoochorous, non-pioneer, canopy, evergreen)	1.101
Wilk's λ	0.484[a]
Canonical correlation coefficient	0.718

[a] $p < 0.001$

The best model for the closed vegetation type used seven of the 19 functional groups: FG3, FG4, FG6, FG9, FG11, FG15, and FG18 (Table 4). The function DS= 0.584xFG3 + 0.75xFG4 + 0.946xFG6 + 9.606xFG9 + 0.755xFG11 + 0.542xFG15 - 2.084xFG18 discriminated between the two groups, leading to the correct allocation of 100% of the plots with and without *H. dulcis* ($p < 0.001$). The discriminant analysis showed that the group composed by zoochorous, non-pioneer, canopy, deciduous species (FG18) was more important in separating the plots with and without *H. dulcis* (Table 4). The closed vegetation type with *H. dulcis* contained six individuals from FG18, while the closed vegetation type without *H. dulcis* had 17 individuals.

Table 4 Discriminant analysis results for functional groups compared between closed vegetation plots with and without *Hovenia dulcis*, in a seasonal deciduous forest at the Fritz Plaumann State Park (Concordia, SC, Brazil).

Variables	Standardized coefficients
FG3 (anemochorous, pioneer, canopy, deciduous)	2.292
FG4 (anemochorous, pioneer, emergent, deciduous)	0.989
FG6 (anemochorous, non-pioneer, canopy, evergreen)	2.443
FG9 (anemochorous, non-pioneer, understory, evergreen)	2.148
FG11 (zoochorous, pioneer, understory, evergreen)	1.806
FG15 (zoochorous, non-pioneer, understory, evergreen)	1.143
FG18 (zoochorous, non-pioneer, canopy, deciduous)	-3.126
Wilk's λ	0.051[a]
Canonical correlation coefficient	0.974

[a] $p < 0.001$

IDENTIFICATION OF ASSOCIATIONS AMONG NATIVE SPECIES AND *H. dulcis* IN PLOTS

Hovenia dulcis is positively associated with *Casearia sylvestris* ($\chi^2 = 6.67$; df = 1; p = 0.01), *Muellera campestris* ($\chi^2 = 5.93$; df = 1; p = 0.05), *Nectandra lanceolata* ($\chi^2 = 9.6$; df = 1; p = 0.01) and *Randia armata* ($\chi^2 = 5.45$; df = 1; p = 0.05), and negatively associated with *Actinostemon concolor* ($\chi^2 = -5.45$; df = 1; p = 0.05). Because of multiple comparisons, the significance of these results should be taken with caution. Three of the four species with which *H. dulcis* is positively associated are evergreen. *C. sylvestris* and *M. campestris* are more abundant in the semi-open and closed vegetation types, while *N. lanceolata* is very abundant in all the vegetation types (Appendix 1). On the other hand, *A. concolor* is deciduous and was more abundant in the closed vegetation type in plots without *H. dulcis* (Appendix 1).

DISCUSSION

Hovenia dulcis reached higher densities in intermediate stage, and lower densities in early and advanced stages. The species' colonization process took place 10 to 15 years ago in the forest now at an intermediate stage of succession, and at least 30 years ago in the forest now in advanced stage. In both cases, however, the forest probably had greater canopy openness when the colonization process occurred due to selective logging (Siminski et al. 2011). The colonization of the open vegetation type is more recent, and consequently, invasive trees are younger in early and older in more advanced successional stages. The estimated ages should be taken with caution because the R^2 values for the relationship between basal area and age were not very high. However, the clear pattern of more older-aged trees observed in closed vegetation when compared to semi-open and open vegetation should be considered. Contrary to the initial hypothesis, no differences were observed between plant communities invaded and non-invaded by *H. dulcis* in all successional stages. No negative relationship was found among species richness, diversity, functional diversity, and the species density in the successional stages.

Changes in structure and composition of plant communities due to *H. dulcis* presence were described for different types of subtropical forests (Bardall et al. 2004; Schaff et al. 2006; Boeni 2011). However, the results obtained in these studies should not be compared to our study, considering that Bardall et al. (2004) and Schaff et al. (2006) did not compare areas with and without the species' presence, but instead compared the same areas before and after the species' arrival. In turn, Boeni (2011) compared areas with dense forest in advanced successional stages with and without *H. dulcis*, but did not compare different successional stages. In our study, we did not observe differences in structure and composition between plant communities invaded and non-invaded by *H. dulcis*. The same results were observed for other invasive tree species (Martínez 2010; Siderhurst et al. 2012; Whitfield et al. 2014). One possible explanation for this result is that spatial and temporal variation in extrinsic factors, such as disturbance history and propagule pressure, could have been more important in determining the forest regeneration dynamics than the invasive species presence (Shea & Chesson 2002). Complementary, the low density of *H. dulcis* in most of the plots, especially in the open and closed vegetation types, would not be sufficient to reveal changes on the plant communities due to the species presence. Studies about *H. dulcis* influence on density and/or species richness of tree seedlings and herbaceous species below dense stands compared with non-invaded stands could shed light on identifying *H. dulcis* impacts in fragmented deciduous forest.

Hovenia dulcis colonized both disturbed and younger successional forests and may be unable to survive and persist as a forest matures, as described for other alien invasive shrubs and trees in temperate decidual forests (Johnson et al. 2006; Webster et al. 2006; Cunard and Lee 2009; Burnham and Lee 2010; Radtke et al. 2013). Because the species is described in literature as a pioneer (Carvalho et al. 1994), which suggests that it requires high levels of light to regenerate (Hartshorn 1978; Whitmore 1989), the high density of *H. dulcis* observed in the semi-open vegetation type was not expected. Although the forest had a greater canopy openness when the colonization process occurred due to selective logging (Siminski et al. 2011), those areas that presently are semi-open vegetation were not treeless in the past. Instead, aerial photographs from 1978 have provided evidence of the presence of some trees. This indicates that the species' may be tolerant to some shading, as has been observed for other invasive species in temperate, tropical and subtropical regions (Green et al. 2004; Martin and Marks 2006; Flory and Clay 2009; Martin et al. 2009; Godoy et al. 2011; Major et al. 2013).

On the other hand, the lower densities of *H. dulcis* in earlier and later successional stages could be a consequence of limited seed arrival and/or lack of suitable sites for seed germination and seedling establishment (Coutts et al. 2011; Schupp 2011). The low densities may be also due to biotic interactions that limited invasion in these successional stages. A possible biotic resistance mechanism through competition could be attributed to the higher abundance of individuals in the functional group composed by zoochorous, non-pioneer, canopy, deciduous species (FG18) in areas without *H. dulcis* in closed vegetation. This functional group is similar to the *H. dulcis* group (zoochorous, pioneer, canopy, deciduous species), and it is the most important one separating plots with and without *H. dulcis* in the closed vegetation type. Cunard and Lee (2009) showed a clear positive correlation between the invasive shrub *Frangula alnus* mortality, decreased light, decreased nutrients, and abundance in late successional species. According to the authors, this suite of relationships was explained by competition. Besides, reduced light levels promoted by evergreen species may also help explain the low densities of *H. dulcis* in the closed vegetation type (Silva 2012). The density of native trees is lower in open vegetation, when compared to semi-open and closed vegetation, making it less likely that biotic resistance through competition with similar species is a factor that is limiting population growth in these areas. Limitations imposed by abiotic and biotic factors in seed germination and seedling establishment are more prone to be responsible for the low density, besides the possibility of limited seed arrival in open vegetation. Assessments about seed arrival, seed predation, seedling herbivory, and the influence of factors such as herbaceous and shrub species cover, litter thickness and soil moisture on seed germination and seedling survival and growth could help to determine which factors are most important in limiting the species spread in open vegetation.

Colonization by *H. dulcis* in younger successional forests may have been a consequence of landscape fragmentation and forest disturbance, as reported for other invasive plant species (Belote et al. 2008; Burnham and Lee 2010). In a fragmented landscape, disturbance can be a major factor interacting with fragment size to influence species richness and composition in forest fragments (dos Santos et al. 2007). This interaction can be explained by the increasing sensitivity to disturbance as fragments get smaller (increased edge:interior ratio) (dos Santos et al. 2007), and by the assumption that anthropogenic disturbance promotes the invasion of alien species in forest patches (Hobbs 2011). These factors can either impact forest composition regardless of land use history or can disproportionately affect forests with specific land use histories (Katz et al. 2010). Land use history remains a major determinant of forest composition and structure (Flinn and Marks 2007; Martínez 2010), and many studies have indicated that the history of use may increase the abundance of invasive plants in forest landscapes (Von Holle and Motzkin 2007; DeGasperis and Motzkin 2007; Martínez 2010; Siderhurst et al. 2012). The historic component of human occupation in the region was therefore decisive for forest fragmentation as well as essential for the increase of propagule pressure of *H. dulcis*, consequently optimizing the colonization by the species (Siderhurst et al. 2012), with the greatest benefits to the invasive species occurring in low competition, high disturbance sites (Bellingham et al. 2005).

Selective logging and other forest management activities can also favor the establishment of invasive species (Major et al. 2013; Radtke et al. 2013). The intensity of tree harvesting, for example, may influence the degree of invasion success (Rejmánek 1989) as large gaps receive more light and may provide more resources for recruiting plants (Radtke et al. 2013). Besides, selective logging of economically-valued species in fragments currently classified as closed vegetation may have led to the temporary or permanent impoverishment of specific functional groups, both in species richness and abundance. The biotic and abiotic changes caused by fragmentation may also have led to the loss of certain functional groups (Laurance et al. 2000; Michalski et al. 2007; Santos et al. 2008). Such differences in species richness and abundance among functional groups, and in functional diversity, caused by human activities, may change the invasibility of plant communities (Pokorny et al. 2005). The low species richness and low abundance of individuals in the functional group composed by zoochorous, pioneer, canopy, deciduous species (*H. dulcis* functional group) may be the result of fragmentation or logging leading to its rarefaction, or an intrinsic characteristic of the plant community. In the last case, opportunities for occupation of relatively open niches may have facilitated *H. dulcis* establishment (Funk et al. 2008; Byun et al. 2013).

Considering the context of intense forest fragmentation and the high susceptibility of young disturbed secondary forests to invasion by *H. dulcis*, a management strategy at different scales should be implemented, focusing on preventative and control work. At the local scale, control actions need to be conceived prioritizing small satellite or peripheral populations (Moody and Mack 1988) and populations in highly suitable habitat (Higgins et al. 2000), such as small and disturbed native vegetation patches, gaps and edges between closed and open vegetation types. A successful plan for reducing *H. dulcis* should also include management strategies to minimize disturbance (Whitfield et al. 2014) and subsequent reinvasion. One potential mechanism is to introduce native species assemblages that are highly competitive with the invasive species and can increase resistance to future invasion (Pywell et al. 2003). Successful resistance to invasion may be further strengthened if restored native species are functionally similar to and competitive with invading species, preempting available niche space for the invader (Pokorny et al. 2005; Funk et al. 2008; Ammondt and Litton

2011). In our study, *H. dulcis* showed a negative association with deciduous species, which could mean competitive exclusion or different habitat requirement by the native and the alien species. Although we cannot conclude which is the reason for the negative association; however, we can recommend that pioneer, deciduous and fast-growing species should be used in restoration efforts following removal of the invasive species.

Propagule availability is an extremely important determinant of the invasion extent in all habitats (Von Holle and Simberloff 2005; Eschtruth and Battles 2011). Any management strategy at the regional scale should include native species, which may replace *H. dulcis* for different purposes preferred by landowners and result in the reduction of the species' propagule pressure. Zoochorous, pioneer, and fast-growing species should be promoted by the local government in place of *H. dulcis*. Policies to both promote native species and restrict or prohibit the use of *H. dulcis* are essential for a strategy reaching the needed scale and providing opportunities for restoration of remaining forest fragments.

ACKNOWLEDGEMENTS

The expert help of Cassio Daltrini Neto, Tiago Barbosa and Daniel Falkenberg. Sílvia Ziller, Clare Aslan, Elaine Chow and Hugh Safford provided important suggestions and helped improve the language. Two anonymous referees whose comments and suggestions substantially improved the manuscript. Financial support came from Tractebel Energia S.A., from the Graduate Program in Ecology of the Federal University of Santa Catarina and from the Fundação de Apoio à Pesquisa Científica e Tecnológica do Estado de Santa Catarina, Brazil. MS Dechoum is supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brazil. N Peroni is supported by Conselho Nacional de Desenvolvimento Científico e Tecnólogico, Brazil. SM Zalba receives support of Universidad Nacional del Sur and CONICET, Argentina.

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Appendix I

List of tree species, origin information (native ou nonnative), functional group (FG) and number of individuals (N) of each species sampled in different vegetation types of seasonal deciduous forest at the Fritz Plaumann State Park (Concordia, SC, Brazil). Functional groups (FG): (1) anemochorous, pioneer, understory, evergreen; (2) anemochorous, pioneer, understory, deciduous; (3) anemochorous, pioneer, canopy, deciduous; (4) anemochorous, pioneer, emergent, deciduous; (5) anemochorous, non-pioneer, understory, deciduous; (6) anemochorous, non pioneer, canopy, evergreen; (7) anemochorous, non pioneer, canopy, deciduous; (8) autochorous, pioneer, understory, deciduous; (9) autochorous, non pioneer, understory, evergreen; (10) autochorous, non pioneer, understory, deciduous; (11) zoochorous, pioneer, understory, evergreen; (12) zoochorous, pioneer, understory, deciduous; (13) zoochorous, pioneer, canopy, evergreen; (14) zoochorous, pioneer, canopy, deciduous; (15) zoochorous, non pioneer, understory, evergreen; (16) zoochorous, non pioneer, understory, deciduous; (17) zoochorous, non pioneer, canopy, evergreen; (18) zoochorous, non pioneer, canopy, deciduous; (19) zoochorous, non pioneer, emergent, evergreen. Vegetation types - OH: open with *H. dulcis*; O: open without *H. dulcis*; SH: semi-open with *H. dulcis*; S: semi-open without *H. dulcis*; CH: closed with *H. dulcis*; C: closed without *H. dulcis*.

Botanical family	Species	Origin	FG	N/vegetation type						Total
				OH	O	SH	S	CH	C	
Acanthaceae	*Justicia* af. *brasiliana* Roth	native	-	0	0	0	0	4	0	4
Anacardiaceae	*Schinus terebinthifolius* Raddi	native	11	46	75	34	63	4	0	222
Annonaceae	*Annona neolaurifolia*H. Rainer	native	15	1	0	0	1	0	0	2
	Annona sylvatica A. St.-Hil.	native	18	0	0	0	0	1	0	1
	Annonaceae 1	native	-	0	0	0	0	1	0	1
	Annonaceae 2	native	-	0	0	0	0	1	0	1
	Guatteria nigrescens Mart.	native	17	3	0	2	0	0	1	6
Apocynaceae	*Aspidosperma* cf. *australe* Müll. Arg.	native	-	0	0	0	0	0	1	1

Botanical family	Species	Origin	FG	N/vegetation type						Total
				OH	O	SH	S	CH	C	
Apocynaceae	*Tabernaemontana catharinensis* DC.	native	11	1	0	1	5	4	1	12
Aquifoliaceae	*Ilex paraguariensis* A. St.-Hil.	native	15	16	38	20	59	1	0	134
Araliaceae	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin	native	14	0	0	0	0	2	0	2
Arecaceae	*Syagrus romanzoffiana* (Cham.) Glassman	native	13	3	1	5	17	5	3	34
Asteraceae	Asteraceae 1	native	-	0	0	0	0	0	1	1
	Baccharis caprariifolia DC	native	2	6	1	0	0	0	0	7
	Vernonanthura discolor (Spreng.) H.Rob.	native	1	0	0	1	0	0	0	1
Bignoniaceae	*Jacaranda micrantha* Cham.	native	3	0	0	1	0	1	3	5
Boraginaceae	*Cordia americana* (L.) Gottshling & J.E.Mill.	native	5	0	0	0	0	0	1	1
	Cordia ecalyculata Vell.	native	11	0	0	0	1	0	0	1
Cannabaceae	*Celtis ehrenbergiana* (Klotzsch) Liebm.	native	15	0	0	0	2	1	0	3
	Trema micrantha (L.) Blume	native	12	2	1	1	1	0	1	6
Celastraceae	*Pristimera andina* Miers	native	15	0	0	0	0	5	0	5
Cupressaceae	*Metasequoia* sp.	nonnative	-	0	0	0	1	0	0	1
Erythroxylaceae	*Erythroxylum deciduum* A. St.-Hil.	native	15	2	0	0	0	1	0	3
Euphorbiaceae	*Actinostemon concolor* (Spreng.) Müll. Arg	native	16	0	0	0	2	0	34	36
	Actinostemon klotzschii (Didr.) Pax	native	16	0	0	0	0	2	0	2

Botanical family	Species	Origin	FG	N/vegetation type						Total
				OH	O	SH	S	CH	C	
Euphorbiaceae	*Sapium glandulatum* (Vell.) Pax	native	13	0	0	1	0	0	1	2
	Sapium glandulosum (L.) Morong	native	15	0	0	3	1	0	0	4
	Sebastiania brasiliensis Spreng.	native	10	0	0	1	0	0	4	5
	Tetrorchidium dusenii Pax & K. Hoffm.	native	11	0	0	0	1	0	0	1
	Tetrorchidium rubrivenium Poepp. & Endl	native	13	0	0	0	0	1	0	1
Fabaceae	*Apuleia leiocarpa* (Vogel) J.F.Macbr.	native	4	0	0	0	0	0	4	4
	Bauhinia cf. *affinis*	native	-	0	0	1	0	0	0	1
	Bauhinia forficata Link	native	8	0	0	3	0	0	0	3
	Calliandra foliolosa Benth.	native	9	0	0	0	0	0	1	1
	Dalbergia frutescens (Vell.) Britton	native	5	0	0	7	0	6	22	35
	Inga marginata Willd.	native	11	0	0	0	0	5	0	5
	Lonchocarpus sp.	native	-	0	0	0	0	0	1	1
	Lonchocarpus subglaucescens Mart. ex Benth.	native	6	0	0	0	2	12	0	14
	Machaerium af. *acutifolium* Vogel	native	-	0	0	2	4	4	0	10
	Machaerium af. *brasiliense* Vogel	native	-	0	0	0	0	1	0	1
	Machaerium cf. *lanceolatum* (Vell.) J.F. Macbr.	native	-	0	0	0	4	0	0	4
	Machaerium lanceolatum (Vell.) J.F. Macbr.	native	5	0	0	0	3	4	8	15

Botanical family	Species	Origin	FG	N/vegetation type						Total
				OH	O	SH	S	CH	C	
Fabaceae	*Machaerium paraguariense* Hassl.	native	3	0	0	0	0	0	1	1
	Machaerium stipitatum (DC.) Vogel	native	3	0	0	0	1	0	0	1
	Muellera campestris (Mart. ex Benth.) M.J. Silva & A.M.G. Azevedo	native	6	7	0	23	18	28	3	79
	Myrocarpus frondosus Allemão	native	4	1	0	13	1	0	3	18
	Myroxylon balsamum (L.) Harms	native	1	0	0	0	0	1	0	1
	Parapiptadenia rigida (Benth.) Brenan	native	3	6	10	32	12	10	2	72
	Peltophorum dubium (Spreng.) Taub.	native	4	0	0	0	0	4	2	6
	Senegalia polyphylla (DC.) Britton	native	8	0	0	0	0	2	0	2
Lamiaceae	*Aegiphila brachiata* Vell.	native	11	9	0	0	0	0	0	9
	Vitex megapotamica (Spreng.) Moldenke	native	14	0	0	0	0	1	5	6
Lauraceae	*Aiouea saligna* Meisn.	native	17	11	5	6	7	1	13	43
	Cryptocarya saligna Mez	native	17	1	0	0	0	0	0	1
	Endlicheria paniculata (Spreng.) J.F. Macbr.	native	17	0	0	1	0	0	5	6
	Nectandra grandiflora Nees & C. Mart. ex Nees	native	17	0	0	0	3	0	0	3
	Nectandra lanceolata Nees	native	17	33	6	23	10	25	6	103

Botanical family	Species	Origin	FG	N/vegetation type						Total
				OH	O	SH	S	CH	C	
Lauraceae	*Nectandra megapotamica* (Spreng.) Mez	native	17	4	2	53	19	39	16	133
	Ocotea diospyrifolia (Meisn.) Mez	native	19	0	0	1	0	0	5	6
	Ocotea laxa (Nees) Mez	native	15	0	0	0	0	3	0	3
	Ocotea odorifera (Vell.) Rohwer	native	17	0	0	0	0	0	5	5
	Ocotea puberula (Rich.) Nees	native	13	0	0	9	7	13	6	35
	Ocotea teleiandra (Meisn.) Mez	native	15	0	0	0	1	3	0	4
	Persea americana Mill.	nonnative	-	0	0	0	0	1	0	1
Loganiaceae	*Strychnos brasiliensis* (Spreng.) Mart.	native	18	0	0	0	0	1	7	8
Malvaceae	*Luehea divaricata* Mart.	native	3	16	9	16	19	17	16	93
Meliaceae	*Cabralea canjerana* (Vell.) Mart.	native	13	1	2	14	5	16	12	50
	Cedrela fissilis Mell.	native	3	6	1	3	2	16	10	38
	Cedrela odorata L.	native	3	0	0	0	0	0	2	2
	Guarea macrophylla Vahl	native	15	0	0	0	0	0	2	2
	Thichilia claussenii C. DC.	native	17	0	0	0	0	0	8	8
	Trichilia cf. clausseni	native	-	0	0	0	0	0	1	1
	Trichilia elegans A. Juss.	native	15	0	0	0	0	2	10	12
Moraceae	*Brosimum glazioui* Taub.	native	18	0	0	0	0	1	0	1
	Ficus luschnathiana (Miq.) Miq.	native	19	1	0	0	0	1	3	5
	Maclura tinctoria (L.) Don ex Steud.	native	14	0	0	0	0	0	1	1
	Morus nigra L.	nonnative	-	2	2	10	0	0	0	14

Botanical family	Species	Origin	FG	N/vegetation type						Total
				OH	O	SH	S	CH	C	
Moraceae	*Sorocea bonplandii* (Baill.) W.C. Burger, Lanj. & Wess. Boer	native	15	0	0	0	0	7	10	17
Myrtaceae	*Campomanesia eugenioides* (Cambess.) D. Legrand	native	15	0	0	0	0	1	0	1
	Campomanesia guazumifolia (Cambess.) O. Berg	native	16	1	0	0	1	0	0	2
	Campomanesia reitziana D. Legrand	native	15	0	0	0	0	3	0	3
	cf. *Calyptranthes*	native	-	0	0	1	0	0	0	1
	cf. *Eugenia*	native	-	0	0	0	0	1	1	2
	Eugenia pyriformis Cambess.	native	15	0	0	0	0	1	0	1
	Psidium guajava L.	nonnative	-	0	0	4	0	0	0	4
Nyctaginaceae	*Pisonia zapallo* Griseb.	native	15	0	0	0	0	0	1	1
Oleaceae	*Fraxinus* cf. *americana* L.	nonnative	-	0	0	0	0	3	0	3
Primulaceae	*Myrsine umbellata* Mart.	native	13	11	4	4	21	25	3	68
Proteaceae	*Roupala brasiliensis* Klotzsch	native	5	0	0	0	0	0	1	1
Rhamnaceae	*Hovenia dulcis* Thunb.	nonnative	14	21	0	68	0	20	0	109
Rosaceae	*Prunus myrtifolia* (L.) Urb.	native	16	1	2	2	1	2	0	8
Rubiaceae	*Chomelia* af. *pubescens* Cham. & Schltdl.	native	-	1	0	0	0	0	0	1
	Psychotria sp.	native	-	0	0	0	0	0	1	1
	Randia armata (Sw.) DC.	native	16	2	0	1	0	4	0	7

Botanical family	Species	Origin	FG	N/vegetation type						Total
				OH	O	SH	S	CH	C	
Rutaceae	*Balfourodendron riedelianum* (Engl.) Engl.	native	7	0	0	0	0	1	0	1
	Citrus reticulata Blanco	nonnative	-	0	0	2	0	0	0	2
	Citrus reticulata x sinensis	nonnative	-	0	0	0	4	0	0	4
	Citrus sp.	nonnative	-	0	0	4	0	0	0	4
	Zanthoxylum monogynum A. St.-Hil.	native	16	0	0	0	0	0	2	2
	Zanthoxylum rhoifolium Lam.	native	14	1	1	3	4	2	1	12
Salicaceae	*Casearia decandra* Jacq.	native	18	1	0	2	2	0	6	11
	Casearia gossypiosperma Briq.	native	18	0	0	0	6	0	3	9
	Casearia obliqua Spreng.	native	11	0	0	0	0	3	0	3
	Casearia sylvestris Sw.	native	11	6	1	22	16	28	3	76
	Xylosma ciliatifolia (Clos) Eichler	native	16	0	0	0	0	1	0	1
Sapindaceae	*Allophylus guaraniticus* Radlk.	native	12	10	3	21	8	8	12	62
	Allophylus petiolulatus Radlk.	native	12	1	1	0	0	1	6	9
	Cupania vernalis Cambess.	native	13	4	0	4	7	20	19	54
	Matayba elaeagnoides Radlk.	native	13	0	1	3	2	3	2	11
Sapotaceae	*Chrysophyllum gonocarpum* (Mart. & Eichler ex Miq.) Engl.	native	16	1	0	0	0	0	0	1
	Chrysophyllum marginatum (Hook. & Arn.) Radlk.	native	18	0	0	0	0	3	1	4
Solanaceae	*Acnistus arborescens* (L.) Sendtn.	native	11	0	0	0	1	0	0	1
	Cestrum cf. *amictum*	native	-	0	0	0	0	1	0	1

Botanical family	Species	Origin	FG	N/vegetation type						Total
				OH	O	SH	S	CH	C	
Solanaceae	*Solanum argenteum* Dunal	native	12	0	0	2	1	1	0	4
	Solanum cf. *concinnum*	native	-	0	0	0	0	0	1	1
	Solanum mauritianum Scop.	native	12	2	0	2	2	0	0	6
	Solanum pseudoquina A. St.-Hill.	native	12	0	0	0	1	1	0	2
	Solanum sanctaecatharinae Dunal	native	11	0	0	0	0	0	1	1
	Solanum sp.	native	-	1	0	0	0	0	1	2
Styracaceae	*Styrax leprosus* Hook. & Arn.	native	17	0	0	0	0	0	3	3
Symplocaceae	*Symplocos* sp.	native	-	0	0	0	0	1	0	1
Urticaceae	*Boehmeria macrophylla* Hornem.	native	1	0	0	0	0	0	1	1
	Urera baccifera (L.) Gaudich.	native	12	0	0	0	0	2	5	7
Verbenaceae	*Aloysia virgata* (Ruiz & Pav.) Pers.	native	1	1	0	1	0	0	0	2
	Dead trees		-	9	3	17	13	15	18	75

CAPÍTULO 2 - LIMITED SEED DISPERSAL MAY EXPLAIN DIFFERENCES IN FOREST COLONIZATION BY AN INVASIVE TREE IN SOUTHERN BRAZIL

ABSTRACT

Short-distance dispersal by frugivorous birds can create patterns of expansion from patches of invasive alien species. Different management strategies may be required to prevent the arrival of propagules of such species in uninvaded sites. *Hovenia dulcis*, a tree native to East Asia, invasive in forests in South America, produces capsuled fruits attached to peduncles that grow thick and fleshy when ripe. Birds can carry infructescences of *H. dulcis* to perches on other trees, to peck at the fleshy peduncles, facilitating its dispersal. The spread of *H. dulcis* propagules to uninvaded sites from invaded patches was evaluated at a local spatial scale in this study. The arrival of seeds carried by birds was compared between sites in open and closed vegetation in heterogeneous habitats at different distances from invaded patches. The arrival of seeds was also compared between control plots, where no management action was carried out, and plots where trees were felled in a 30 meter radius around each plot. Limited seed dispersal was observed for *H. dulcis* in the study area, especially occurring in open vegetation sites. There was a negative exponential relationship between number of seeds and distance from *H. dulcis* trees to non-invaded sites and the number of seeds found in traps increased exponentially in relation to the basal area of *H. dulcis*. Finally, in closed vegetation, the felling of *H. dulcis* trees was effective in reducing the arrival of seeds in uninvaded sites, resulting in a significantly smaller number of seeds in managed plots than in control plots.

KEYWORDS: *Hovenia dulcis;* deciduous forest*;* dispersal foci*;* propagule pressure*;* bird dispersal*;* invasive tree management.

INTRODUCTION

Tree species have been moved among regions of the world in the last centuries to provide services in forestry and agroforestry, food production, erosion control, and for horticulture (Dickie et al., 2014; Rejmánek, 2014). A large effort in introducing alien trees has occurred in the last decades due to the intensification of international commerce, resulting in more introductions both in terms of numbers of species and the extent of new plantations (Fonseca et al., 2013; van Wilgen and Richardson, 2014). Many of these species have established in and invaded natural areas, and biological invasion is therefore considered one of the worst environmental threats to ecosystems (Richardson and Rejmánek, 2011; van Wilgen and Richardson, 2014). Rejmánek and Richardson (2013) listed 434 tree species behaving as invasive species in at least one geographical region.

Plant invasions occur as a result of appropriate biological traits of introduced species, characteristics of the communities where they arrive, local abiotic environments, and propagule pressure (Richardson and Pysek, 2006; Fridley, 2011). Propagule pressure is an essential mechanism for the success of invasions at different scales (Lockwood et al., 2005; Simberloff, 2009), and can be defined by its two major components: the number of individuals released in each introduction effort, and the number of introduction efforts (Simberloff, 2009). There is also a genetic component, entitled propagule diversity, which refers to the number of genetically different source populations in a certain area (Lockwood et al., 2005). The more intense the propagule pressure and the larger the genetic diversity of source populations, the larger the chance of establishment success of alien species (Crawford and Whitney, 2010; Zenni and Simberloff, 2013).

Once a species has naturalized at a local scale, i.e., is capable of surviving and producing reproductive descendants in the new habitat (Richardson et al., 2000), dispersal mechanisms will determine the magnitude and speed of propagules arrival onto new sites, and, consequently, may influence invasion success (Schupp, 2011). Species with fleshy fruits, attractive for animal seed dispersers, are often considered potentially highly invasive (Rejmánek and Richardson, 1996; Daehler et al., 2004; Richardson and Rejmánek, 2011) because vertebrate dispersal leads to quick spread at different spatial scales, often increasing seed germination and seed deposition in sites favorable for seedling establishment (Panetta and McKee, 1997; Wenny, 2001; Verdú and Traveset, 2004).

The attraction of frugivores to patches of invasive plants depends on the local abundance of fruit, which may primarily depend upon density, size, age structure, and spatial distribution of invasive plants (Nathan and Muller-Landau, 2000; Aslan, 2011; Amodeo and Zalba, 2013). Characteristics such as color, fruit or infructescence size, nutritional content, and pulp/seed ratio are also important determinants of frugivore attraction (Debussche and Isenmann, 1989; Whelan and Willson, 1994; Herrera, 1998; Levey and Martínez del Río, 2001). Different groups of animals may act as long- or short-distance dispersers of invasive species (Richardson et al., 2000b; Shupp, 2011). While short-distance dispersal determines local population dynamics, long-distance dispersal induces the establishment of new populations and their connection in metapopulations (Schupp, 2011). In general, local dispersal fills the gaps left by the advance of new invasions. Understanding growth patterns of existing patches, distance and intensity of propagule arrival in different habitats may be important information needed to constrain the spread of invasive plants.

Hovenia dulcis Thunb. (Rhamnaceae) is a deciduous tree species native to East Asia (Kopachon et al., 1996), invasive in forests in South America and in Tanzania (Hyun et al., 2010; Zenni and Ziller, 2011; Rejmánek and Richardson, 2013). It is a fast growing pioneer species that reaches 10 to 25 meters in height, and reproduces sexually by seeds (Carvalho, 1994). It bears fruit in winter, between March and October in Brazil (Carvalho, 1994), with more intense fructification between June and July (Dechoum, unpublished data). It produces dark, dry globular infructescences measuring 6-7mm in diameter which contain two to four seeds connected to brown peduncles rich in carbohydrates that become thick and fleshy when ripe (Carvalho, 1994; Zhou et al., 2013). Intact seeds are consumed both in its native range and in South American forests and dispersed over short and long distances in mammal feces (Takatsuki, 1988; Mottajunior et al., 1994; Cáceres and Monteiro-Filho, 2001; Hirsch, 2009; Tsuji et al., 2011; Hendges et al., 2014; Lima, 2014). In both regions, birds feed on the fleshy peduncles but do not swallow or carry the seeds to long distances. The infructescences are in general carried by the peduncles to short distances, so their transport and seed droppings are incidental (Zhou et al., 2013; Lima, 2014). Forest dwelling birds *Trogon surrucura*, *Penelope obscura*, and *Pyroderus scutatus* have been observed feeding on *H. dulcis* pseudofruits in tree crowns in the study area (FATMA, 2005; Lima, 2014). The first species is quite common in the region, and is adapted to high levels of anthropogenic disturbance; the other two species occur in more preserved forests in higher density vegetation and have had their populations reduced due to hunting and deforestation (Rosário, 1996; FATMA, 2005).

Hovenia dulcis occurs in patches of different sizes at the study area, in a vegetation mosaic resulting from fragmentation caused by logging until the first half of the 20th century (Silva, 2008). While habitat fragmentation may create barriers to animal dispersal in some situations in a landscape scale (Hutchinson and Vankat, 1998), it may increase invasion rates in others (Gosper et al., 2005). Vegetation fragments may serve as stepping stones for frugivorous birds and, consequently, function as seed dispersal foci for invasive plants (sensu nascent foci, Moody and Mack, 1988). In this study, our assumption was that the local spread of *H. dulcis* from invaded patches is mediated by frugivore birds that use the infructescences as a food source. The main objective of this study was to characterize the arrival of *H. dulcis* propagules in uninvaded sites from invaded patches at a local spatial scale (within areas of ca. 0.01 ha). The specific objectives were to (1) compare the arrival of *H. dulcis* propagules by local bird seed dispersal in uninvaded sites in different vegetation types, and establish the relation of propagule pressure to age, distance, and abundance of potential seed sources; and (2) assess the effect of management practices in the reduction of propagule arrival in different vegetation types by felling adult *H. dulcis* trees. The major hypotheses were: (1) local dispersal of propagules of the invasive species from invaded patches will be related to the density and distance of propagule sources, and that (2) the local dispersal pattern will change significantly when the seed source trees are felled.

MATERIALS AND METHODS

STUDY AREA

This study was carried out in remnants of seasonal deciduous forest in the Fritz Plaumann State Park, Santa Catarina, Brazil (27° 16’18” e 27° 18’ 57” S, e 52° 04’ 15” e 52° 10’ 20” W), in Cfa (subtropical) climate according to the Köppen-Geiger classification system. The seasonal deciduous forest is nowadays highly fragmented and restricted to 16% of its original area in Santa Catarina state, with 90% of the remnants smaller than 50 ha (Vibrans et al., 2012). The park was established in 1998 and covers 740 hectares in the Atlantic forest domain, containing the threatened species *Ocotea odorifera* (Vell.) Rohwer (Lauraceae) (Brasil, 2008). The vegetation is currently composed by forest fragments in different successional stages, in this paper defined as "closed vegetation," interspersed with herbaceous-shrubby vegetation in early regeneration stages, in this paper defined as "open vegetation." The area was formerly occupied by rural properties used for agriculture, cattle ranching, and wood exploitation (Silva 2008). The vegetation has been regenerating since the park was established.

Hovenia dulcis was introduced in the study region in the second half of the 20th Century (Vibrans et al., 2012), and more intensively cultivated after the 1980s, when agroindustries in the region promoted its use in pig and chicken farms (Selle, 2009). Since its introduction, *H. dulcis* has been extensively planted in rural properties for wood (Selle, 2009), shade for cultivation and pasture areas, hedges, and energy production (Carvalho, 1994).

DATA COLLECTION

Sixty 10 x 10 m plots were set up in sites without *H. dulcis,* forty of them in closed vegetation, and twenty in open vegetation in different forest fragments. A minimum distance of 100 meters was kept between plots. The number of plots set up in open and closed vegetation was different because the closed vegetation forest fragments are the main vegetation types in the area, covering about 65% of the park surface (FATMA 2005). All *H. dulcis* trees with diameter at breast height (DBH) over 5 cm located outside the plots in a 30 meter radius from the central points of each plot were marked, measured, and their heights estimated. These trees were considered potentially reproductive adults (Carvalho 1994). The distance from each tree to the center of the plot was measured, and the surrounding vegetation was classified as open or closed.

Five 0.6 x 0.6 m seed traps were set up in each plot 0.5 m above the ground, one in the center and the other four at 2.5m from each corner towards the center. The number of trees functioning as perch poles was counted inside each plot. All trees higher than four meters with at least one branch were considered potential perch poles for birds. The material accumulated in the seed traps was collected every fortnight during the species fructification period (May to September, 2012), and the *H. dulcis* seeds were counted.

In October 2012 the adult *H. dulcis* trees located within a 30 meter radius of 50% of the plots in each vegetation type were felled. These plots were selected at random. Between May and September 2013 the collection of seeds was repeated in all the plots (managed and not managed). The age of the felled trees was determined from the growth rings, generating data that were used for the estimation of the age of the remaining trees in the plots.

DATA ANALYSIS

In order to relate propagule arrival to *H. dulcis* tree abundance, distance and age, the age of trees had to be estimated. Regression equations generated from the data of the 506 trees felled in October 2012 were used to estimate the age of the remaining *H. dulcis* trees using Biostat 5.0 software (Ayres et al., 2007). The equations that best described the correlations were: $\mathbf{y=0.24 + 2.36*\ln(x)\ (R^2=58.4)}$ for trees growing in open vegetation, and $\mathbf{y=4.01*x\text{^}0.26\ (R^2=62.5)}$ for trees in closed vegetation, where $\mathbf{y}$ equals age and $\mathbf{x}$ is basal area. Propagule arrival was estimated by the potential seed rain index (PSRI), which is a single parameter calculated in order to estimate propagule production and arrival in non-invaded sites. The formula $\sum\mathbf{(BA/d^2)}$ was used to estimate PSRI, in which **BA** stands for basal area, and **d** is the distance in meters from the plot center to each mature tree in a 30 meter radius (modified from Rejmánek et al., 2013). This calculation was made for the years 2012 and 2013 for each vegetation type (open and closed).

Differences in the mean number of *H. dulcis* trees in 2012, as well as the mean basal area, age and height of plants sampled in the 30 meter radius around open and closed vegetation sites were compared via t tests with permutation (5000 iterations; Wheeler, 2010) because the distribution of data was not normal and did not result in homogeneity of variance. The mean distance between each tree and the center of the respective plot, the mean PSRI values and the number of perch trees in 2012 were compared between closed and open vegetation sites using the same test. Frequency histograms were constructed using the age data from sampled trees for comparison between those growing in open and closed vegetation. These histograms were based on five 8-year interval age classes, where the first class was comprised of trees that started to grow after the Park was established (between six and 14 years), or rather, when logging interventions in the forest were no longer taking place.

The numbers of seeds collected in the five seed traps in each plot were added up over all the field visits made in each year, resulting in the total number of seeds per plot per year (2012 and 2013). One plot in which branches of an *H. dulcis* tree were found hanging over the seed collector was excluded from the analysis. The number of seeds found in closed vegetation in 2012 was used to assess the relation between propagule arrival in sites where *H. dulcis* was not present (response variable) and three explanatory variables: PSRI in each plot, total number of perch poles in each plot, and mean age of *H. dulcis* trees sampled in a 30 meter radius around the plots. The analysis was carried out only for closed vegetation, as no seeds were found in the traps set up in the open vegetation plots (see Results). A collinearity analysis among the variables was performed *a priori* using variance inflation factors (VIF). However, no variable was excluded as all VIF values were lower than 3, indicating no collinearity among variables (Zuur et al., 2007). A generalized linear model (GLM) was used assuming the Poisson distribution for the number of seeds and the log link function for the relationship between seed number and explanatory variables. The inclusion or exclusion of variables was based on AIC (Akaike´s Information Criterion) values calculated using maximum likelihood. As data overdispersion was detected (overdispersion = variance > mean in response variable), a correction of standard errors was made using a quasi-GLM model in which variance is the result of **f × μ**, where **f** is the dispersion parameter, and **μ** the mean (Zuur et al., 2012 The estimate of the dispersion parameter **f** was 9.59, which led to all standard errors being multiplied by 3.1 (the square root of 9.59).

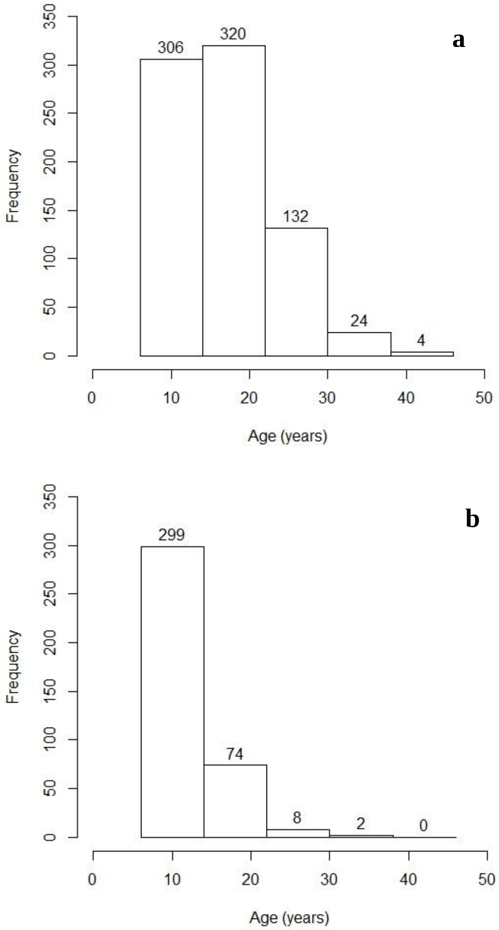
To assess the effect of *H. dulcis* felling, the total number of collected seeds was compared between managed and unmanaged plots in closed vegetation. The analysis was made using generalized linear mixed modeling (GLMM) assuming the Poisson distribution for the number of seeds and the log link function for the relationship between seed number and explanatory variables. The variables year (2012 or 2013), treatment (control or felling), and the interaction between year and treatment were considered fixed effects, while the plots were considered repeatedly measured replicates, and therefore considered random effects. All statistical analyses and figures were produced with R software (R Development Core Team, 2014), using the lmPerm package for parametric tests with permutation, the lme4 package for GLM and GLMM, and the Sciplot package for the bar plots.

RESULTS

A total of 1,169 *H. dulcis* trees were recorded around the plots, 383 in closed vegetation, and 786 in open vegetation. *H. dulcis* was absent in the 30 m radius area of eight plots, six of them in closed vegetation, and two in open vegetation. The age range in closed vegetation varied from six to 44 years, with about 39% (n=306) of the plants in the first age class (6 to 14 years), and 40% (n=320) in the second age class (Figure 1a). In open vegetation, 78% (n=299) of the trees fell into the first age class, while the age range varied between six and 37 years (Figure 1b). Of all sampled trees, 43.3% (506) were felled in association with plots selected for management, with 422 (83.4%) located near plots in closed vegetation, and 84 (17.6%) near plots in open vegetation.

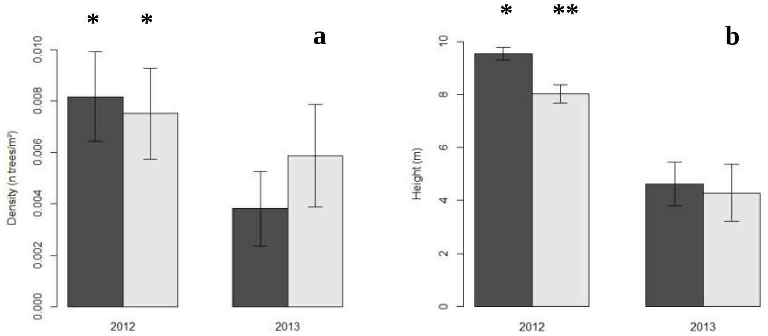
In 2012, average height (t=3.6, df=32.6, p=0.001), average basal area (t=3.0, df=42.3, p=0.004), and average age (t=6.1, df=47.1, p<0.0001) of *H. dulcis* trees were higher around closed vegetation plots than in open vegetation (Figure 2).The number of perch poles (t=2.4, df=43.5, p=0.01) and PSRI (t=2.8, df=40.8, p=0.007) were also higher in closed vegetation. Only average distance (t=-0.9, df=35.4, p=0.4) and average density (t=0.3, df=44.6, p=0.8) of *H. dulcis* trees did not differ

Figure 1 Age frequency histograms of *Hovenia dulcis* trees sampled within a 30 meter radius around plots in closed vegetation (a) (n=985) and in open vegetation (b) (n=184) in the Fritz Plaumann State Park, Brazil. The numbers above the bars refer to the number of plants in each age class. Age classes (years): (1) 6 - 14; (2) >14 - 22; (3) >22 - 30; (4) >30 - 38; (5) >38 - 46.

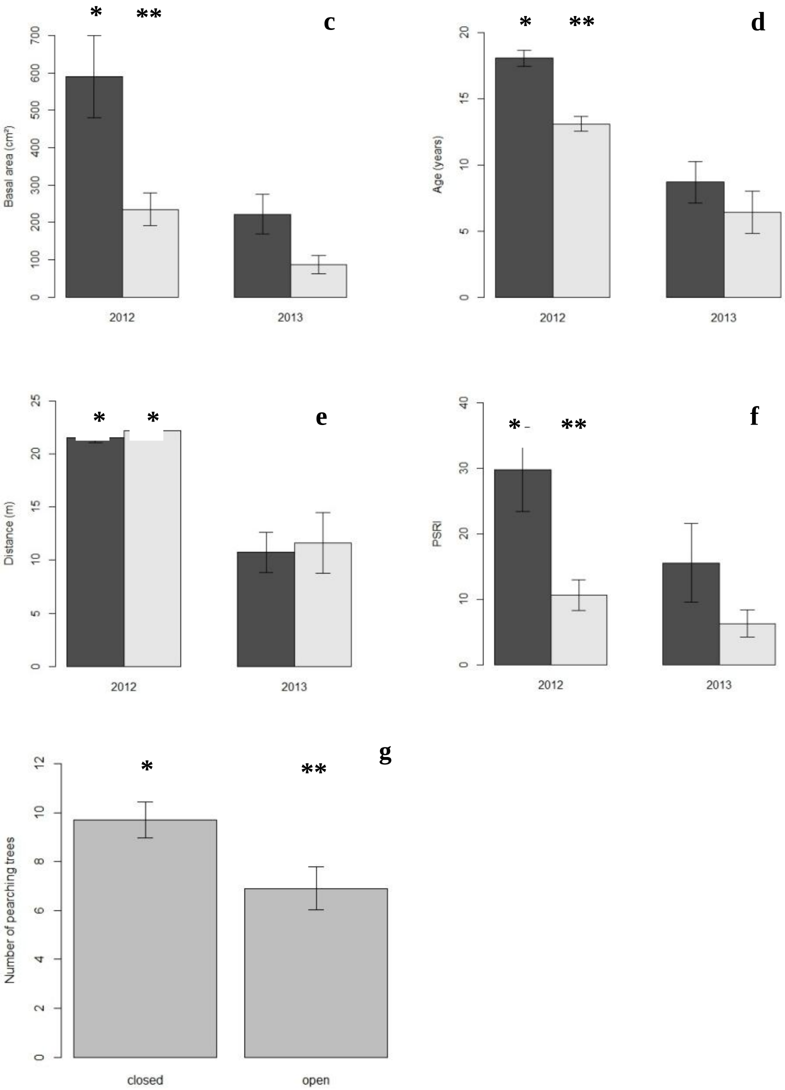


between vegetation types (Figure 2). A reduction in value of the parameters evaluated in 2013 was observed due to the felling of *H. dulcis* trees in 50% of the plots in each vegetation type (Figure 2).

Figure 2 Parameters evaluated in plots (n=60) set up in closed vegetation (dark bars) and open vegetation sites (light bars) in the Fritz Plaumann State Park, Brazil, in 2012 and in 2013. Average density (a), height (b), basal area (c), and age (d) (± standard deviation) refer to *Hovenia dulcis* trees present in a 30 m radius around plots. Distance (e) = average distance of *H. dulcis* trees around plots. PSRI (f) - *potential seed rain index* = $\sum (BA/d^2)$, where **BA** stands for basal area, and **d** stands for distance from the center of a plot to a mature tree, in meters, within a 30 m radius. Perch poles (g) indicate the average number of woody plants with a minimum height of four meters and at least one stem bifurcation. The 2013 data refer to the same plots after the felling of *H. dulcis* trees around 50% of the plots (n=30 plots). The number of perch poles (g) was compared between closed and open vegetation in 2012 only. Parameters represented by bars with different symbols differed between closed and open vegetation types in 2012.



(continuation - Figure 2)



No seeds accumulated in the seed traps in open vegetation in 2012 or in 2013. The numbers of seeds collected in closed vegetation did not differ between control and (pre) felling plots in 2012 (Z=0.97, p=0.33), but were different between seed collection years (Z=21.2, p<0.0001) and between control and felling plots in 2013 (Z=-7.5, p<0.0001) (Tables 1 and 2).

Table 1 Numbers of seeds found in plots (n=40) in closed vegetation sites in the Fritz Plaumann State Park, Brazil, in 2012 and in 2013. Seeds were collected before and after felling *Hovenia dulcis* trees in a 30 meter radius around half the plots. Felling = plots where *H. dulcis* trees were cut down in a 30 meter radius after seed trap monitoring in 2012; No felling = plots in which *H. dulcis* trees were not cut down after seed trap monitoring in 2012.

Number of	2012		2013	
	Felling	No felling	Felling	No felling
plots with seeds	2	6	1	7
traps with seeds	4	9	2	18
seeds	11	44	2	1268

Table 2 Statistics for the models analyzed for differences in number of seeds of *Hovenia dulcis* between 2012 and 2013, and between control and felling plots in closed vegetation sites in the Fritz Plaumann State Park, Brazil.

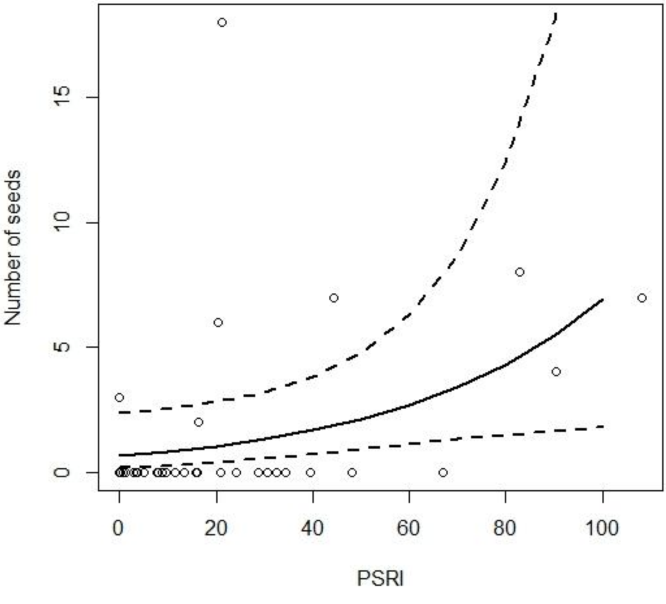
Fixed effects	Estimate	Std error	Z value	df	p
Intercept	-9.211	1.8871	-4.881		<0.0001
Control x felling 2012	2.0059	2.067	0.97	1	0.332
2012 x 2013	3.5327	0.1668	21.181	1	<0.0001
Control x felling 2013	-5.7299	0.7638	-7.502	1	<0.0001

PSRI showed a significant effect of the number of seeds collected in closed vegetation sites in 2012 (*Explained deviance*=19.86, p<0.0001) (Figure 3, Table 3). The variables "perch poles" and "age" were stepwise excluded as they were not significant (p>0.05). The distribution of the number of seeds is best represented by the exponential function in relation to PSRI, which minimizes variance dispersion (Figure 3). The confidence interval increases significantly when PSRI is higher than 60 due to the small number of existing points higher than that value (Figure 3). No clear standard was observed in the residues generated from the model (Figure 2A).

Table 3 Statistics of the model analyzed for number of seeds of *Hovenia dulcis* in seed traps (response) and potential seed rain index (PSRI) (factor) in closed vegetation in the Fritz Plaumann State Park, Brazil. PSRI - *potential seed rain index* = ∑ (BA/d^2), where **BA** stands for basal area, and **d** stands for distance from the center of a plot to a mature tree, in meters, within a 30 m radius.

Parameter	Estimate	Std error	t value	df	p
Intercept	-0.43514	0.65648	-0.0663	38	0.51
PSRI	0.02369	0.0165	2.223	37	0.0324

Figure 3 Relationship between seed number and potential seed rain index (PSRI) of *Hovenia dulcis* in closed vegetation sites in the Fritz Plaumann State Park, Brazil, in 2012. PSRI - *potential seed rain index*=∑ (BA/d^2), where BA stands for basal area, and **d** stands for the distance from the center of each plot to a mature tree, in meters, in a 30 meter radius around plots. Full line = model prediction; dotted lines = confidence intervals (±1.96 standard error).



DISCUSSION

Dispersal of *H. dulcis* seems to be relatively rare at the local scale in the study area. This limitation seems to occur both in open vegetation, where no seeds accumulated in the seed traps, and in closed vegetation, where the numbers of seed traps with seeds as well as the numbers of seeds found in the traps were low in relation to the sampling effort (the maximum number of seed traps with seeds was 18, equivalent to 6% of the 300 seed traps set up in the area) and to the number of fruits produced per plant in the study site (which varied between 22.2 and 40.2 fruits/tree/month/m² crown projection - Lima, 2014). Limited seed dispersal of exotic woody plants at similar scales was observed in several other studies (Mazia et al., 2001; Siemann and Rogers, 2003; Manning et al., 2004; McCay and McCay, 2009).

A lower frequency of bird visitation in the open vegetation type may be one of the causes of limited seed dispersal in this habitat. Patches of *H. dulcis* trees in the open vegetation were formed by smaller (smaller basal area and height) and younger plants than in the sites in closed vegetation. Considering the positive relationship between basal area and age found in this study (age = f(basal area) function presented in Material and Methods), and positive correlation between fecundity and basal area, height, and age (Deckers et al., 2005; Perglová et al., 2006; Boulant et al., 2008; Burnham and Lee, 2010), it is certain that younger and smaller plants produce fewer fruits than older and larger trees (Debain et al., 2003; Burnham and Lee 2010). Lower fruit yield likely leads to lower bird attraction for foraging, which would also reduce the amount of consumed fruit and seed dispersal, as demonstrated by Amodeo and Zalba (2013).

According to Deckers et al. (2005), landscape structures acting as perches seem to especially promote dispersal by frugivorous birds. The perch pole effect may be defined as the increase of seed deposition under perch trees or under structures serving as perches for birds (Holl, 1998; Wenny, 2001), which are of fundamental importance for invasive species dispersal (Ferguson and Drake, 1999). A smaller number of perch poles in open vegetation plots may lead birds to a lower use of these areas in comparison with closed vegetation sites (Holl, 1998; Deckers et al., 2005), reducing seed arrival. However, in our study, perch poles seemed to be of lower importance as a predictor variable of seed numbers arriving in closed vegetation sites.

It is important to highlight that this study considered the primary short distance dispersal of *H. dulcis* seeds associated with frugivorous birds in order to explain spread from already established patches. However, it is important to stress that apart from birds *H. dulcis* is also dispersed by the terrestrial mammals such as *Cerdocyon thous* in the studied area (Lima, 2014). *Cerdocyon thous* is recognized as an efficient seed dispersal agent as it feeds on large quantities of seed and is capable of covering long distances even in heterogeneous landscapes (Cheida et al., 2006). Seeds of *H. dulcis* were also observed in *Atta sexdens* ant nests (Lima, 2014). Although frequently ignored, secondary dispersal of seeds may greatly affect seed shadow and dispersal distances (Nathan and Muller-Landau, 2000). Secondary dispersal by ants, for example, may result in seeds displaced to sites with higher light intensity, rich in nutrients and protected from predators (Bond and Stock, 1989), facilitating new invasion foci in the landscape (Richardson et al., 2000). This foci may then accelerate invasion (Moody and Mack, 1988). Understanding the relevance of secondary dispersal to invasion over short and long distances seems essential, therefore, to selection of management strategies for the invasive species under study.

The presence of plants younger than ten years old in closed vegetation is evidence that the species is regenerating in the study area (Dechoum et al., 2014). This result was unexpected, given that the species is considered a pioneer (Carvalho, 1994), and may be an indicator of shade tolerance in the seedling stage, as already demonstrated for other invasive plants (Martin and Canham, 2010; Godoy et al., 2011). Seed germination may occur in winter, when more light reaches the forest floor due to leaf loss by deciduous trees, and *H. dulcis* reaches the peak of fruit production. Studies on seed viability in the soil and shade tolerance in the seedling establishment phase can provide complementary information about possible invasion opportunity associated with deciduous forests, and consequently, for prioritizing control efforts.

In closed vegetation areas the variable that best explained the numbers of *H. dulcis* seeds was PSRI, with a positive exponential relation between variables. The graphic representation of this relationship is very similar to the exponential curve proposed in the theoretical model describing the dose-response relation between propagule pressure and establishment probability of an introduced species (Ruiz and Carlton, 2003). In this theoretical model, the exponential relationship means that the saturation value of propagule pressure that would result in maximum establishment success for the species has not yet been reached, so management efforts to reduce the arrival of the species propagules may be beneficial (Lockwood et al., 2005). Following similar logic as the dose-response model (Ruiz and Carlton 2003), management strategies may be directed at keeping PSRI lower than 60 by removing the largest basal area trees from the borders of invaded patches occurring at short distances from uninvaded sites. Complementarily, outlying isolated trees or low density patches of invasive trees must be the primary target of management (Moody and Mack, 1988; Zhu et al., 2007; Chaplat et al., 2014), given that isolated trees are more fertile than trees in patches (Debain et al., 2003). In this management strategy directed at reducing or containing invasion (Buckley et al., 2006), habitat heterogeneity must also be considered for defining priority sites for control, and control efforts must primarily target higher invasibility sites (Chaplat et al., 2014).

Even at a small scale, short distance bird dispersal may facilitate the establishment of *H. dulcis* in closed vegetation sites. Felling adult *H. dulcis* trees in a 30 meter radius around uninvaded closed vegetation sites was sufficient to reduce the arrival of seeds in these areas. Therefore, we recommend that a minimum distance of 30 meters from forest fragment borders should be considered a priority for eradication of *H. dulcis* individuals and continuous monitoring and control activities, in order to reduce the intensity of seed arrival in protected areas and in other sites of high conservation value. This can help prevent the establishment of new invasion foci or the aggravation of already existing invasions.

ACKNOWLEDGEMENTS

Financial support was received from Tractebel Energia S.A., the Graduate Program in Ecology of the Federal University of Santa Catarina (Brazil) and the Fundação de Apoio à Pesquisa Científica e Tecnológica do Estado de Santa Catarina (FAPESC-Brazil). Sílvia

Ziller, Rafael Zenni and Clare Aslan provided important suggestions on different versions of the manuscript, and also helped improve the language. Michele Dechoum is supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES-Brazil). Sergio Zalba receives support from the Universidad Nacional del Sur and CONICET, Argentina.

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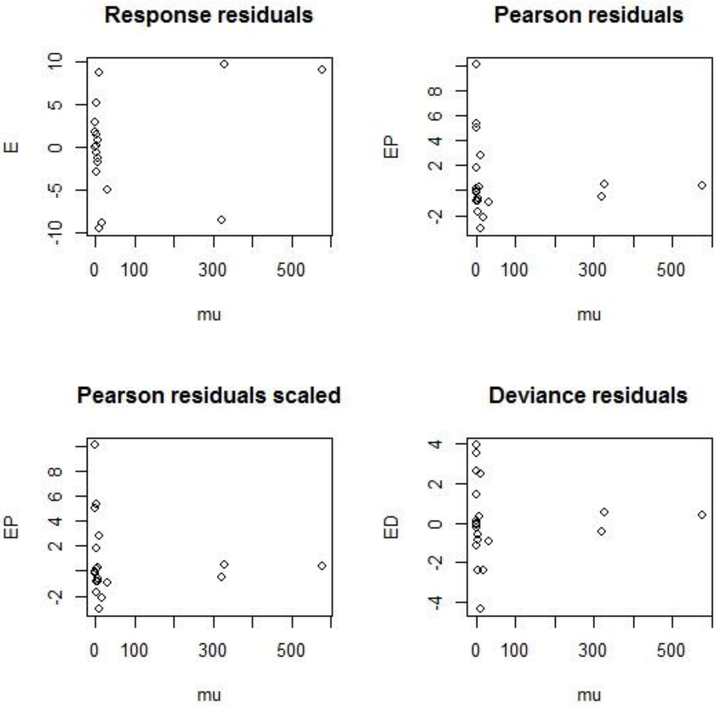


Figure 1A Residuals for number of seeds compared between the years 2012 and 2013, and between control plots and management plots where *Hovenia dulcis* trees were felled in a 30m radius in closed vegetation sites in the Fritz Plaumann State Park, Brazil.

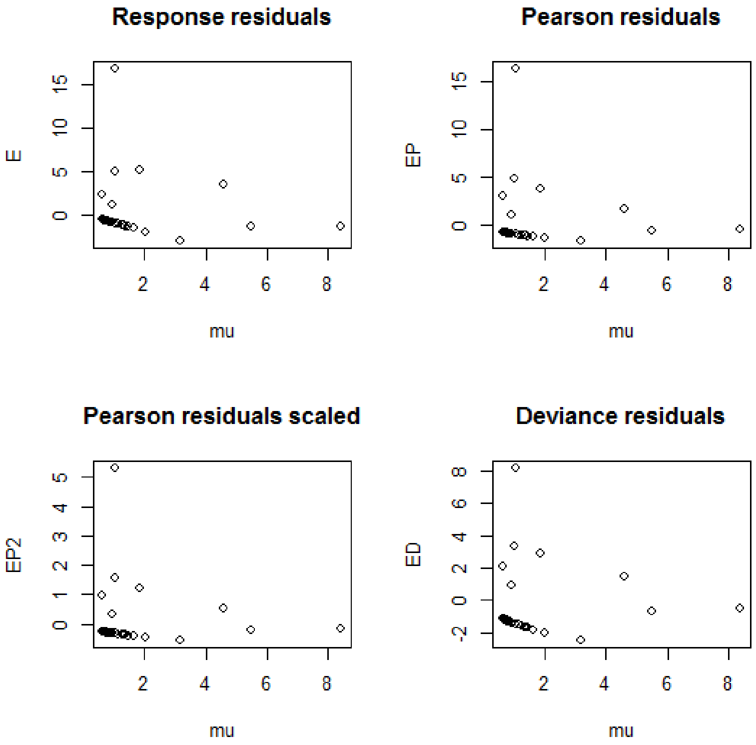


Figure 2A Residuals of the relationship between seed number and Potential Seed Rain Index (PSRI) in 2012 in closed vegetation sites in the Fritz Plaumann State Park, Brazil.

CAPÍTULO 3 - INVASIONS ACROSS SECONDARY FOREST SUCCESSIONAL STAGES: EFFECTS OF LOCAL PLANT COMMUNITY, SOIL, LITTER, AND HERBIVORY ON *Hovenia dulcis* SEED GERMINATION AND SEEDLING ESTABLISHMENT

ABSTRACT

Species abilities for seed germination and seedling survival under a broad range of conditions are good predictors of their capacity to colonize a broad range of habitats. The main objective of this study was to evaluate seed germination, seedling survival, and growth of the invasive tree *Hovenia dulcis* under experimental field conditions in three successional stages of a fragmented seasonal deciduous forest in southern Brazil. Our hypothesis was that *H. dulcis* seed germination, seedling survival, and seedling growth decrease along a successional gradient from initial to advanced secondary forest succession, and are dependent on understory cover, soil moisture, and litter thickness. We also tested the hypothesis that frequency of herbivory on *H. dulcis* was different among successional stages. Our main finding was that *H. dulcis* is able to germinate and establish along all forest successional stages because it is relatively shade tolerant. There was a positive relationship between soil moisture and seed germination, while litter thickness negatively influenced seed germination. The percentage of bare soil negatively influenced seedling survival. Higher germination rates were observed in closed vegetation, while seedling survival was higher in semi-open vegetation, and growth rates were higher in open vegetation. There was no difference in herbivory frequency among successional stages. The results of our study show that intermediate forest succession stages congregate the most favorable conditions for *H. dulcis* establishment, therefore making them more susceptible to invasion. Abiotic conditions were more important than biotic factors in determining *H. dulcis* naturalization success.

KEYWORDS: growth; survival; regeneration; biotic resistance; shade tolerance; deciduous forest.

INTRODUCTION

One fundamental but difficult question to answer over the last decades of biological invasion studies has been which biological attributes make some plants more invasive. Within a wide range of woody plant taxa, populations invading disturbed landscapes tend to have short juvenile periods (< 10 years), short intervals between large seed crops, small seed masses (< 50 mg) and wide native ranges (Rejmánek and Richardson 1996; Pyšek et al. 2009; Hui et al. 2011). Invasiveness, however, is not equal among all invasive plant populations, but determined by different biological attributes depending on where a species is introduced (Rejmánek et al. 2013) and on the characteristics of the introduction events. Propagule pressure, genetic pool, residence time, and human assistance can be determinants for success (Rejmanek et al. 2013; Zenni and Simberloff 2013; Zenni et al. 2014), while different traits may be important in each invasion stage (Dawson et al. 2009; Bufford and Daehler 2011; Moodley et al. 2012). For instance, seed size was an important predictor of naturalization and invasion for Proteceae species, albeit in contrasting ways. During the naturalization stage, large seeds were important for holding greater nutrient reserves, favoring establishment; conversely, small seeds facilitate long-distance dispersal and favor spread (Bufford and Daehler 2011; Moodley et al. 2012). Among woody plants, biological attributes correlated with invasiveness also vary with the taxa (Richardson et al. 2011; Moodley et al. 2012).

Traits related to reproduction and dispersal are crucial for the naturalization and invasion of species in new environments (Richardson et al. 2011). However, no matter how prolific a species, or how efficient its dispersal , it will not invade unless the seeds reach suitable habitat, germinate and establish (Coutts et al. 2011). Understanding the factors that limit or promote seed germination and seedling establishment is critical in determining if and where a plant species can invade (McAlpine and Jesson 2008). Consequently, the local abundance of an invasive population may be defined by the magnitude of local seed supplies with seedling requirements acting as an additional, subsequent filter (Levine 2000; Mazia et al. 2001). Reaching high rates of germination, seedling survival, and growth can be challenging for many introduced plants because seeds and seedlings are exposed to numerous risks during establishment, including resource limitation, loss of viability in the soil, predation, herbivory, pathogens, and competition (Moles 2006; Boulant et al. 2009). Biotic and abiotic factors can act in isolated or aggregated ways, which can be extremely relevant for invasion success. Litter, for instance, may have positive or negative effects on seed germination and seedling recruitment (Baskin and Baskin, 2014). Litter usually reduces soil temperature amplitude and water evaporation, thereby increasing soil moisture and promoting better conditions for seed germination (Eriksson 1995; Scariot 2000). On the other hand, litter can act as a physical barrier to seedling root penetration and can also inibit seed germination by the antagonistic chemical interaction of allelopathy (Eriksson 1995; Scariot 2000; Baskin and Baskin 2014). For biotic interactions, for example, generalist and specialist herbivores are expected to interact differently with introduced plants. Whereas generalists feed on a wide range of plants, possibly including introduced species, specialists are not expected to feed on them (Morrisson and Hay 2011; Jacquemart et al. 2013). Whereas some biotic and abiotic factors may hinder the naturalization of introduced species (Zenni and Nuñez 2013), other factors can facilitate it. These factors may fluctuate and have distinct effects on the survival of introduced plants over time.

In addition to the factors cited above, disturbance can also influence invasion success. Regeneration dynamics in neotropical forests are largely determined by natural disturbance (Hubbel et al. 1999). However, when human disturbance generates forest fragmentation, significant changes in the natural disturbance regime occur, which may favor invasive species (Hyatt 2008; Moles et al. 2012). Forest fragmentation may facilitate invasion because of increased resource availability, especially in clearings and along the edges between original and converted areas (Fine 2002; Hobbs 2011). Consequentially, invasions are more frequent in small fragments and along edges (Vilà and Ibáñez 2011; Radtke et al. 2013; González-Muñoz et al. 2014). Furthermore, given that invasive alien species are often good colonizers, early stages of secondary forest succession should be more susceptible to invasion (Catford et al. 2012). However, fragmentation can also indirectly influence the success of invasive species through changes to native species that can potentially establish interactions with introduced species. In a recent meta-analysis of the effect of fragmentation on herbivorous insects, Guimarães et al. (2014) showed that edge formation had a positive effect on herbivore abundance and richness, and that edge plants exhibited 70% more damage than interior plants. The effects of environmental heterogeneity (uneven distribution of resources in space and time) may, however, increase or decrease invasion success, depending on the capacity of species establishment under different environmental conditions (Melbourne et al. 2007). Species seed germination and seedling survival under a broad range of conditions are good predictors of their capacity to colonize novel habitats, and consequently to spread in a heterogeneous landscape.

Seasonal deciduous forests originally covered 8% (7,671 km²) of Santa Catarina state in southern Brazil (Klein 1978), but are now highly fragmented and restricted to 16% of their original area. About 90% of forest fragments are smaller than 50 ha (Vibrans et al. 2012). *Hovenia dulcis* Thunb. (Rhamnaceae) was introduced to southern Brazil in the second half of the 20th century (Vibrans et al. 2012). Although described in literature as a pioneer species (Carvalho 1994), it is currently present in fragments in different successional stages. *Hovenia dulcis* can change the structure and composition of plant communities in seasonal, dense, and mixed ombrophilous forests (Bardall et al. 2004; Schaff et al. 2006; Boeni 2011). Determining patterns of invasion across fragmented habitats is necessary for effective invasive species management and the conservation of native species (Flory and Clay 2009).

The main objective of this study was to evaluate seed germination, seedling survival and growth of *H. dulcis* under experimental field conditions in three successional stages in a seasonal deciduous forest. Our hypothesis was that *H. dulcis* seed germination, seedling survival, and seedling growth decrease along a successional gradient from initial to advanced secondary forest succession, and are dependent on understory vegetation cover, soil moisture, and litter thickness. We also tested the hypothesis that frequency of herbivory on *H. dulcis* would decrease along the successional gradient.

MATERIAL AND METHODS

THE STUDY SYSTEM

This study took place in remnants of seasonal deciduous forest in the Fritz Plaumann State Park, Santa Catarina, Brazil (coordinates 27°16’18” - 27°18’57” S, and 52°04’15” - 52°10’20” W), in subtropical climate, Cfa type in the Köppen-Geiger classification system. The 740 hectares of the Park comprises secondary forest fragments in different successional stages that have been regenerating since the Park was created in 1998. The area was formerly used for agriculture, cattle breeding, and logging (Silva 2008).

Hovenia dulcis is a deciduous tree native to East Asia, invasive in forests in South America and Tanzania (Kopachon et al. 1996; Hyun et al. 2010; Zenni and Ziller 2011; Rejmánek and Richardson 2013). It is described as a fast growing, pioneer plant commonly regenerating in clearings, disturbed forests, and open areas (Carvalho 1994). It reproduces sexually by seed (Carvalho 1994) and bears fruit between March and October in Brazil (Carvalho 1994). The number of fruits produced per plant in the study site varies between 22.2 and 40.2 $\text{fruits.tree}^{-1}.\text{month}^{-1}.\text{m}^2$ of crown projection (Lima 2014). Intact seeds are consumed and dispersed by birds and mammals both in its native range and in South American forests (Zhou et al. 2013; Hendges et al. 2014; Lima 2014). Although there is no consensus about seed dormancy, freshly harvested seeds are successfully germinated in nurseries with percentages up to 50%, suggesting no dormancy (Carvalho 1994; Blakesley et al. 2002). Moderate levels of shade (8 - 40% of sunlight) are the most suitable conditions for the germination of *H. dulcis* seeds, whereas deep shade and full sunlight are less favorable under experimental conditions (Kopachon et al. 1996). *Hovenia dulcis* plants have food bodies which attract insectivorous ants, and secondary compounds in its leaves that most likely serve as protection against herbivory (Kimura et al. 1981; Buono et al. 2008).

EXPERIMENTAL DESIGN

The forest fragments in the Park were classified as open, semi-open, or closed vegetation based on the physiognomy at the time of the study, time since abandonment, and history of use (aerial photographs from 1978, 2005, 2008 and 2011, and Siminski et al. 2011). Open areas had a herbaceous or herb-shrub cover and few isolated small-size trees, while semi-open areas were characterized by open forest with a more dense layer of trees. Open and semi-open areas were formerly used for agriculture and/or grazing. Closed areas were under selective logging, which enabled the tree layer not to be totally suppressed and the physiognomy of a closed forest with a higher tree layer to be preserved, with a greater vertical stratification compared to the other vegetation types (Dechoum et al. 2014). The three vegetation types were considered as distinct successional stages. In each type, ten 10 x 10 m plots were established without *H. dulcis*. A minimum distance of 100 meters was kept between plots. Five 1 x 1 m subplots were delimited inside each plot, one in the center and four at 2.5 m from the four corners towards the center (seedling subplots, hereafter).

Hovenia dulcis seeds were collected in the area between June and August 2012 from fallen infructescences under the canopy trees in all vegetation types. The seeds were mixed and kept in plastic bags under refrigeration until March 2013, then taken to a greenhouse for germination. After immersion in water at room temperature for 12 hours (following Carvalho 1994), the seeds were sowed into 34 x 125 cm pots on vermiculite substrate. The pots were irrigated once a day. After 73 days, 900 seedlings were transplanted to the field. Six seedlings were planted in each seedling subplot, totaling 30 seedlings per plot and 300 per forest type. Each seedling subplot was divided into two rows and three columns, with distances of 25 cm between columns and 50 cm between rows; the seedlings were planted at the intersections. All seedlings were labeled on the day of planting, the number of leaves and height were recorded (time 0 = day 0 = 04-Jun-2013). Average height was 4 cm (SD = 0.9 cm), and 90% of the seedlings had at least one leaf besides the cotyledons. We monitored the seedlings monthly during 12 months (time 12 = day 400 = 02-Jul-2014).

For the germination experiment, four 0.5 x 0.5 m subplots were delimited inside each plot (seed subplots, hereafter). Fifty *H. dulcis* seeds were sowed in each seed subplot, which was paired with a control seed subplot. The control seed subplots were necessary to verify the seed bank contribution to germination. We monitored seed subplots monthly during nine months until March 2014, when a new seed crop was ripe.

DATA COLLECTION

Litter thickness, soil moisture, percentage of bare soil, percentage of grass cover, and percentage of non-grass cover were measured in each plot at the beginning of the experiment. Measurements were taken in five quadrats per plot, which were set next to the seed and seedling subplots. Litter thickness was measured with a tape from the litter surface to the top of the mineral soil. Soil moisture was determined with an electronic soil moisture meter (HidroFarm HFM2010/HFM2030, Falker S.A., Brazil) that calculates the percentage of volumetric soil moisture from zero to 10 cm depth with a 3% error. Percentages of cover were visually estimated to fit the following classes: 0, 1 (1-5%), 2 (5 - 25%), 3 (25 - 50%), 4 (50 - 75%), 5 (75 - 95%), and 6 (95 - 100%). The mean values of each class were used for the analysis.

During the monthly monitoring efforts for seed germination, each emerging *H. dulcis* seedling was labeled, and the number of new seedlings was recorded. The same counting procedure was applied to control seed subplots. Life status (alive or dead) and herbivory evidence on leaves were recorded for each seedling. Plant height and number of leaves was recorded again at the end of the experiment (time = 12), when all seedlings and seeds were removed from the plots to prevent further invasion.

DATA ANALYSIS

Survival functions were estimated for each vegetation type using the Kaplan-Meyer method for censored data, a discrete stepped survivorship curve that adds information as each death occurs. The Mantel-Haenszel test was used to test differences between vegetation types. A Cox proportional hazards regression model considering vegetation type, percentages of grass and non-grass cover, percentage of bare soil, litter thickness, and soil moisture was used in order to verify which variables were determinant for seedling survival. A likelihood ratio test was used to quantify the relation of the group of covariates with survival. Vegetation type was considered a strata variable, which means that each stratum is allowed to have a different baseline hazard function, while the coefficients of the remaining covariates are assumed to be constant across strata.

Generalized linear mixed-effects models (GLMM) for nested data were used to test the hypotheses related to seed germination, seedling growth, and herbivory. For seed germination, the Poisson distribution was assumed for the response variable and the log link function for the relationship between the response and explanatory variables. The response variable was the sum of germinated seeds in each subplot from time 0 to time 12. The explanatory variables (vegetation type, litter thickness, soil moisture, percentage of grass cover, percentage of non-grass cover, and percentage of bare soil), as well as the interactions between all variables, were initially considered fixed effects. As many of the variables were highly correlated, a less complex model was obtained considering vegetation type, litter thickness, soil moisture, and the interaction between them as fixed effects. Seed subplots were spatially dependent, while plots were considered replicates of each vegetation type and inserted into the model as a random effect. A GLMM was fitted using maximum likelihood and Adaptive Gauss-Hermite Quadrature to the deviance. Data from 17 subplots were excluded, where the number of germinated seeds in paired control seed subplots was larger than zero, in order to neutralize the effect of the seed bank in the analysis.

Seedling height and number of leaves were correlated (Spearman $r = 0.56$, $p < 0.0001$). Thus, only the height measurement data were used to test the hypothesis that seedling growth varied between vegetation types. The response variable for each seedling was the difference between height at the end and at the beginning of the experiment (Δheight = height in time 12 - height in time 0). Three seedlings were excluded from the analysis because their Δheight was negative, probably as a consequence of herbivory. A GLMM was fitted using maximum likelihood and Laplacian approximation to the deviance, and gamma distribution for the response variable. Vegetation type was inserted into the model as a fixed effect. Plots and seedling subplots were considered repeatedly measured replicates, therefore random effects.

To test the hypothesis that herbivory varied between successional stages, the response variable was defined as the sum of herbivory records along the experiment period for each seedling with a minimum of zero for no herbivory and a maximum of 12 (the total number of observations) for monthly occurring herbivory. Vegetation type was considered a fixed effect and plots and seedling subplots, random effects. Data from all seedlings were considered in the model, including those that died before the end of the experiment. As a consequence, a new random effect was included in the model, which was a binomial variable related to seedling condition at the end of the experiment (alive or dead). A GLMM was fitted using maximum likelihood and Laplacian approximation to the deviance, assuming the Poisson distribution for the response variable and the log link function for the relationship between the response and explanatory variables. All statistical analyses and figures were done with R version 3.0.3 (R Development Core Team 2014), using the 'lme4' package for GLMM, and the 'survival' package for survival analysis.

RESULTS

Seedling survival curves differed between vegetation types (χ^2 = 40.7, df = 2, $p < 0.0001$; Fig. 1). Survival rate was higher in semi-open vegetation during the whole experiment compared to open and closed vegetation. Survival rate was higher for closed vegetation compared to open vegetation in the first month, but after the second month until the end of the experiment, survival in open vegetation overcame survival in closed vegetation (Fig. 1). The mean age at death for *H. dulcis* seedlings was 133.22 days (SE = 6.87) in open, 169.72 days (SE = 7.74) in semi-open, and 112.26 days (SE = 5.12) in closed vegetation. The numbers of transplanted seedlings still alive at the end of the experiment (time 12 = day 400) were 50 in open vegetation (16.67%), 64 in semi-open (21.33%), and 14 in closed vegetation (4.67%). The percentage of bare soil was determinant for seedling survival in all vegetation types (Z = 2.781, p = 0.005; Table 1). There was a slightly negative relationship between age at death and bare soil percentage (Fig. 2).

Figure 1 Survival rates for *Hovenia dulcis* seedlings transplanted to open (full line), semi-open (dashed line) and closed (dotted line) vegetation types for a period of 400 days in seasonal deciduous forest in the Fritz Plaumann State Park (Brazil). Crosses represent censored data

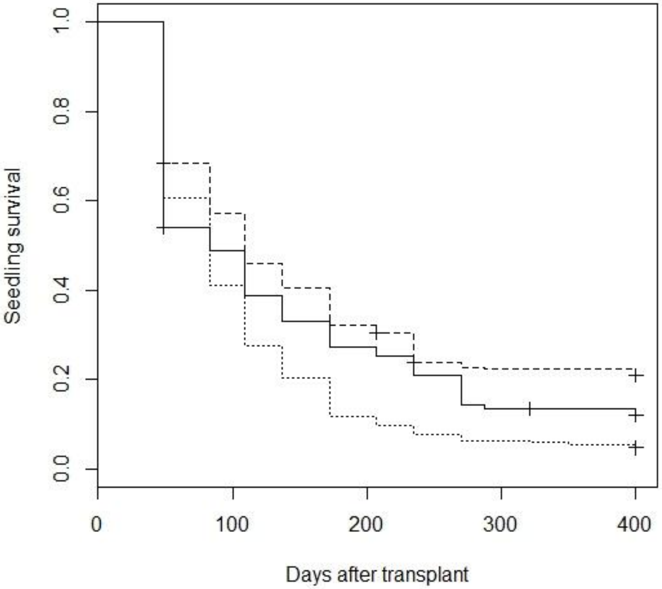
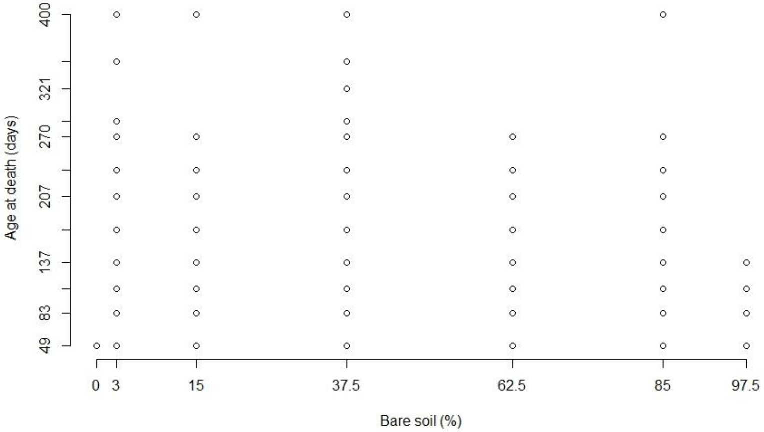


Table 1 Cox proportional hazards regression model for *Hovenia dulcis* seedling survival in three vegetation types in the Fritz Plaumann State Park, Brazil. $R^2 = 0.126$. Likelihood ratio test= 121.6 on 4 df, $p < 0.0001$. Significant p values are in bold.

Variable	Coefficient	se (coefficient)	Z value	p
Grass cover	0.003949	0.003819	1.03	0.3
Non-grass cover	0.001	0.00429	0.326	0.7
Bare soil	0.00995	0.003578	2.78	**0.005**
Litter thickness	0.01125	0.029	0.385	0.7
Soil moisture	0.00958	0.006856	1.398	0.16

Figure 2 Age at death of *Hovenia dulcis* seedlings in relation to percentage of bare soil in sampling units in the Fritz Plaumann State Park (Brazil). Bare soil percentage was visually estimated. The values on the x-axis are the means for the following classes: 1 (0-5%), 2 (5 - 25%), 3 (25 - 50%), 4 (50 - 75%), 5 (75 - 95%), and 6 (95 - 100%)



A total of 1,014 seeds germinated in the three vegetation types (16.9%). The total numbers of germinated seeds were 127 in open, 253 in semi-open, and 634 in closed vegetation. Seed germination varied among vegetation types (Table 2, Fig. 3), while soil moisture, litter thickness, and the interaction between these factors were all relevant for seed germination (Table 2, Fig. 3). Higher numbers of germinated seeds were observed in subplots with thinner litter layers and wetter soils (Fig. 4).

Table 2 Statistics for fixed effects of a generalized linear mixed model for seed germination in three vegetation types in the Fritz Plaumann State Park, Brazil. AIC = 262.2. Significant p values are in bold.

Variable	Estimate	Std error	Z value	p
Intercept (open vegetation type)	2.988956	0.46829	6.38	< **0.0001**
Semi-open vegetation type	0.697767	0.22267	3.1	**0.002**
Closed vegetation type	1.318778	0.261659	5.0	< **0.0001**
Litter	-0.635125	0.126425	-5.0	< **0.0001**
Moisture	-0.1055	0.02287	-4.6	< **0.0001**
Litter x moisture	0.03466	0.00639	5.4	< **0.0001**

Figure 3 Box-and-whisker plot for seed germination compared among seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Brazil). Bold central lines represent the median, box line limits the 25% and 75% quartiles, whisker the quartiles ± 1.5 interquartile range. Circles are outliers

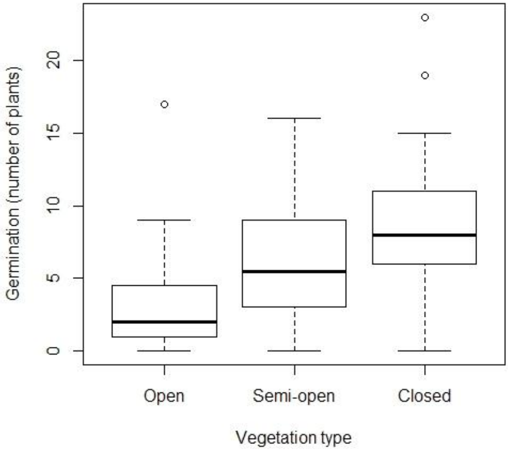
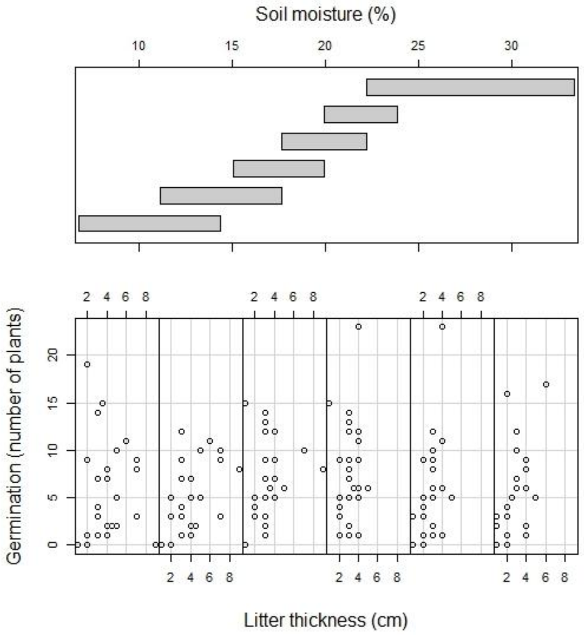


Figure 4 Number of germinated *Hovenia dulcis* seeds in relation to litter thickness (cm), soil moisture (%) and the interaction between them, compared among seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Brazil). (a) Intervals for soil moisture (%) measured in plots; (b) each scatterplot showing relationship between germination (number of plants) and litter thickness (cm) was generated for one of the intervals of soil moisture (from left to right in (a))



Seedling Δheight average was 13.1 cm (SE = 2.1) in open, 7.99 cm (SE = 0.7) in semi-open and 6.9 cm (SE = 1.1) in closed vegetation (Fig. 5; Δheight = height in time 12 - height in time 0). The difference in seedling Δheight between vegetation types was significant, according to GLMM (Table 3).

Figure 5 Box-and-whisker plot for *Hovenia dulcis* seedling Δheight (cm) compared among seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Brazil). Δheight = height in time 12 - height in time zero. Bold central lines represent the median, box line limits the 25% and 75% quartiles, whisker the quartiles ± 1.5 interquartile range. Circles are outliers

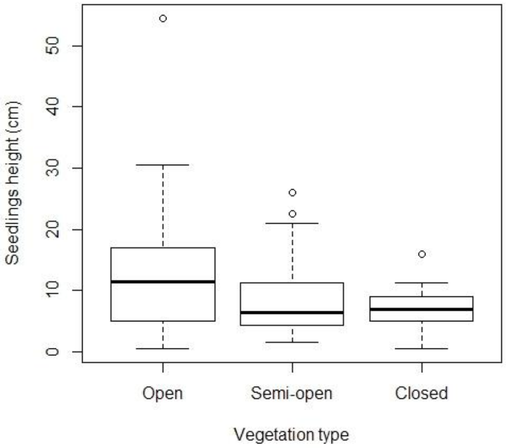


Table 3 Fixed effects of a generalized linear mixed model statistics for *Hovenia dulcis* seedling height in three vegetation types in the Fritz Plaumann State Park, Brazil. AIC = 681.3. Significant p values are in bold.

Variable	Estimate	Std error	t value	p
Intercept (open vegetation type)	0.08964	0.01948	4.601	**< 0.0001**
Semi-open vegetation type	0.04703	0.01559	3.017	**0.002**
Closed vegetation type	0.0742	0.0303	2.449	**0.01**

The percentage of alive seedlings with evidence of herbivory at the end of the experiment was 64% (n = 32) in open, 93.75% (n = 60) in semi-open, and 85.71% (n = 12) in closed vegetation. There was a higher variation in herbivory frequency in semi-open vegetation compared with open and closed vegetation (Fig. 6), but herbivory frequency did not differ significantly between vegetation types (Fig. 6, Table 4).

Figure 6 Box-and-whisker plot for herbivory frequency on *Hovenia dulcis* seedlings transplanted to three vegetation types in seasonal deciduous forest in the Fritz Plaumann State Park (Brazil). Bold central lines represent the median, box line limits the 25% and 75% quartiles, whisker the quartiles ± 1.5 interquartile range. Circles are outliers

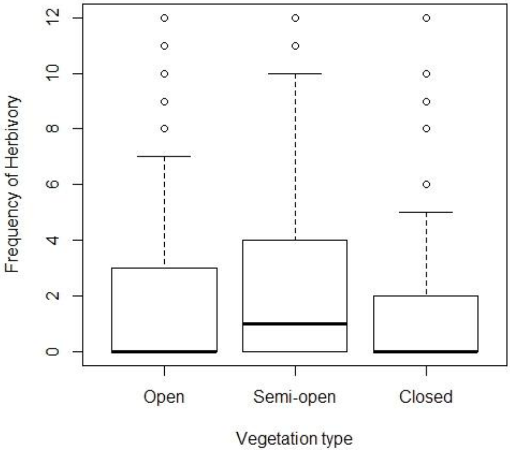


Table 4 Statistics for fixed effects of generalized linear mixed model for herbivory frequency on *Hovenia dulcis* seedlings transplanted to three vegetation types in the Fritz Plaumann State Park, Brazil. AIC = 3439.9.

Variable	Estimate	Std error	Z value	p
Intercept (open vegetation type)	0.6759	0.68215	0.99	0.3
Semi-open vegetation type	0.2295	0.40765	0.56	0.57
Closed vegetation type	0.0367	0.408	0.09	0.9

DISCUSSION

Our results partially support the hypothesis that *H. dulcis* seed germination, seedling survival, and seedling growth would decrease along a successional gradient from initial to advanced secondary forest succession. Higher germination rates were observed in closed vegetation, seedling survival was higher in semi-open vegetation, and growth rates were higher in open vegetation. Once seeds germinate, seedling survival and growth are not limitant for the species' establishment in semi-open and closed vegetation types, confirming its tolerance to varying environmental conditions. Our main finding that *H. dulcis* is relatively shade tolerant and thus able to germinate and establish seedlings along a gradient of forest succession suggests that *H. dulcis* is able to establish and invade all successional stages of secondary forests. This has been observed for other shade-tolerant invasive species in temperate, tropical and subtropical regions (Green et al. 2004; Martin and Marks 2006; Martin et al. 2009; Major et al. 2013).

Different environmental conditions influenced seed germination, seedling survival and seedling growth, with abiotic conditions being more important than biotic factors. Whereas soil moisture and litter thickness were important for seed germination, the percentage of bare soil was a determinant for seedling survival. In tropical and subtropical forests, litter may play a significant role in preventing seed germination due to effects on light quality or as a physical barrier that prevents root growth into the soil (Baskin and Baskin 2014). The litter layer also influences soil moisture, which in turn can influence seed germination. Small-seeded species are especially responsive to soil moisture, as water stress greatly reduces germination in small-seeded species, but it is not so with large-seeded species (Baskin and Baskin 2014). Thin litter layer and high soil moisture favor the germination of *H. dulcis* seeds, suggesting that reduced physical barriers and water stress are important for establishment success. Thin litter layers are usually observed in early successional stages, while high soil moisture is more commonly observed in late successional stages as a consequence of denser vegetation cover and thicker litter layers (Baskin and Baskin, 2014). Therefore, appropriate conditions for *H. dulcis* seed germination were observed in both successional stages, corroborating what was observed in previous work by Dechoum et al.

(2014), who showed that *H. dulcis* is able to colonize plant communities in early and in more advanced successional stages. On the other hand, less bare soil led to higher seedling survival, suggesting that ground cover by non-woody plants is beneficial. These results contradict our initial expectations that disturbed sites would be invasible by *H. dulcis*. Disturbance usually generates prevalence of bare ground and open spaces, and is often considered the best invasibility predictor in vegetation studies (Fridley 2011). However, the positive relationship between disturbance and forest invasibility is not straightforward for all invasive species, as some forest invaders are shade-tolerant. It seems clear that some ground cover is beneficial for *H. dulcis* because it helps maintain adequate soil moisture and light intensity while offering low levels of competition for these resources.

Higher germination percentages were observed in closed vegetation, where canopy openness varied from 5 to 32.5%, a range similar to the best light conditions for seed germination and seedling growth under controlled conditions (Kopachon et al. 1996). Conversely, in our experiment the closed vegetation type combined the worst conditions for *H. dulcis* seedling survival and growth, whereas semi-open and open vegetation, respectively, conferred the best overall conditions for seedlings. The disparate patterns between successional stages are evidence of a growth-survival trade-off resulting from *H. dulcis* physiological plasticity (Martin et al. 2010). *Hovenia dulcis* combines rapid growth at high-light with intermediate survivorship at low-light conditions, traits that are typical of early and mid-successional species (Bazzaz 1979). Similar evidence for such trade-off plasticity has been reported for other invasive trees and shrubs (Reinhart et al. 2006; Ridenour et al. 2006; Martin et al. 2010).

Herbivory frequency on *H. dulcis* seedlings did not differ between successional stages. Herbivory is highly context-dependent in natural landscapes, with a variety of biotic and abiotic factors modulating its incidence and intensity, including host plant density and life stages, existence and density of understory vegetation, and canopy openness (Lewis et al. 2006; Cipollini and Lieurance 2012; Giffard et al. 2012; Dostál et al. 2013; Biswas et al. 2014). The effects of environmental conditions on herbivory however, may be masked by spatial and temporal heterogeneity (Biswas et al. 2014). Further studies on herbivory and its importance in life stages of *H. dulcis* seedlings should include spatial and temporal heterogeneity to explain the observed patterns.

Herbivory was high considering the number of plants with herbivory vestiges during the experiment, especially in semi-open and closed vegetation. In our case, even though this highly invasive species escaped its native range herbivores, the enemy release hypothesis (identified by the absence of herbivory damage) seems to be inconsistent (Biswas et al. 2014). Conversely, *H. dulcis* has special structures and chemical defenses in the form of food bodies and secondary compounds likely to help repel herbivores (Kimura et al. 1981; Buono et al. 2008). Additionally, its seedlings resprout vigorously after injury by herbivores, which may reduce the relevance of any damage (Biswas et al. 2014). Further studies on interactions between ant species, herbivores and *H. dulcis* plants will clarify the role of biotic interactions in invasion failure or success.

The results of this study show that both biotic and abiotic factors are important for explaining *H. dulcis* invasion. Whereas there is some degree of biotic resistance hindering the naturalization process, the abiotic conditions of the site facilitate the invasion. The intermediate forest succession stage, or semi-open vegetation type, combines the most favorable conditions for *H. dulcis* establishment, deeming it more invasible. Initial and advanced successional stages, however, should not be assumed resistant to invasion. Given that alien plant populations grow and propagule pressure increases outside or within such areas, invasions may well start or increase in any of the successional stages (Foster 2001; Duncan 2011). The prevalence of a natural disturbance regime in deciduous forests in southern Brazil can also directly influence *H. dulcis* invasion dynamics (Dechoum et al. 2014). Seasonal canopy openness forms small temporary gaps that may benefit *H. dulcis* regeneration and spread to non-invaded areas. Our results suggest that the most effective means of controlling *H. dulcis* in the study area would be to fell individual *H. dulcis* trees in closed and semi-open vegetation types, which would reduce propagule pressure, and persist with follow-ups to eliminate regeneration until the seed bank is exhausted. If *H. dulcis* invasions in seasonal deciduous forests are left unattended they will increase in area and severity, potentially causing negative impacts on the regional biodiversity.

ACKNOWLEDGEMENTS

Financial support was received from Tractebel Energia S.A., PPGECO/UFSC and FAPESC. M. S. D. is supported by CAPES, Brazil. R. D. Z. acknowledges support from CNPq-Brazil. S. M. Z. receives support from the Universidad Nacional del Sur and CONICET, Argentina. Sílvia Ziller and Clark Richter helped improve the language.

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CONCLUSÃO GERAL

A introdução de *Hovenia dulcis* no estado de Santa Catarina foi simultânea à conversão de florestas estacionais deciduais para agricultura e pecuária e à exploração de recursos madeiráveis nessas florestas. O plantio de *Hovenia dulcis* para diversos fins em propriedades rurais resultou em uma intensa pressão de propágulos da espécie em remanescentes florestais. Neste cenário de paisagem heterogênea, composta por fragmentos florestais degradados pela exploração e conversão históricas, a espécie estabeleceu-se com sucesso e atualmente invade florestas estacionais deciduais secundárias em diferentes estágios sucessionais. As principais conclusões obtidas neste trabalho estão listadas abaixo:

1. *Hovenia dulcis* é claramente uma espécie tolerante à sombra na fase de plântula, o que a torna uma invasora em potencial mesmo no interior de florestas com menor abertura de dossel. Os processos de germinação de sementes e estabelecimento de plântulas de *H. dulcis* ocorrem nos três estágios sucessionais estudados. As condições ambientais existentes em florestas em estágio intermediário de regeneração são as mais adequadas para o estabelecimento de *H. dulcis*, sendo estas mais suscetíveis à invasão pela espécie.
2. Uma maior densidade de árvores adultas foi observada em áreas que hoje estão em estágio intermediário de sucessão, mas a espécie é capaz de colonizar áreas em estágio inicial e de persistir em comunidades vegetais em estágio avançado. A deciduidade natural da floresta é um fator que provavelmente facilitou a colonização e a permanência da espécie nos estágios mais avançados de regeneração.
3. A maior chegada de propágulos em formações em estágios sucessionais mais avançados parece ocorrer como consequência de uma maior densidade e idade mais avançada dos indivíduos de *H. dulcis* que existem nessas áreas, o que faz com que haja uma maior oferta de infrutescências e, consequentemente, uma maior atração de aves potencialmente dispersoras da espécie. O mesmo processo poderia explicar a menor densidade de árvores adultas da espécie em áreas em estágios iniciais de regeneração detectada neste estudo.

Destaca-se que iniciativas de controle de *H. dulcis* no Parque Estadual Fritz Plaumann devem ser imediatamente implementadas, priorizando-se: (1) a eliminação de indivíduos com maior área basal isolados ou nas bordas de manchas de invasão da espécie e que estejam a uma menor distância de áreas não invadidas e; (2) a eliminação de indivíduos de maior porte que estejam presentes em fragmentos em estágios intermediário e avançado de sucessão, levando à formação de grandes clareiras, comparáveis às condições existentes em áreas em estágio inicial de sucessão. Essas estratégias de manejo poderiam auxiliar na redução da pressão de propágulos e da germinação de sementes nessas áreas; entretanto, como as plântulas da espécie sobrevivem e crescem relativamente bem em áreas em estágio inicial de regeneração, ações de monitoramento e repasse são fundamentais no sentido de eliminar a regeneração da espécie até que o banco de sementes seja esgotado.

Medidas complementares de restauração ambiental no sentido de aumentar a resistência de ecossistemas naturais contra reinvasões por *H. dulcis* são fundamentais. O plantio de espécies nativas funcionalmente semelhantes a *H. dulcis* pode aumentar a resistência de florestas em estágios sucessionais intermediário e avançado à invasão pela espécie, por meio do mecanismo de resistência biótica via competição. Espécies zoocóricas, não pioneiras e decíduas devem ser utilizadas em iniciativas de restauração, também no sentido de enriquecer essas áreas e de torná-las mais atrativas à fauna. Esta nova, mais diversificada e mais abundante oferta de recursos alimentares provida por meio de espécies zoocóricas pode também aumentar a diversidade de animais que visitam essas áreas, possibilitando o aumento do consumo e da dispersão das espécies nativas plantadas e consequentemente reduzindo o consumo e a dispersão de *H. dulcis*. Alguns exemplos de espécies que poderiam ser utilizadas são: *Annona sylvatica*, *Brosimum glazioui*, *Casearia decandra*, *Casearia gossypiosperma*, *Chrysophyllum marginatum* e *Strychnos brasiliensis*. Já em florestas em estágio inicial de regeneração, espécies pioneiras e de rápido crescimento são recomendadas no sentido de ocupar rapidamente o espaço, tais como: *Trema micranta, Cedrela fissilis, Parapiptadenia rigida, Cabralea canjerana, Cupania vernalis, Matayba elaeagnoides*, *Myrsine umbellata*, *Zanthoxylum rhoifolium*, *Ocotea puberula, Sapium glandulatum, Syagrus romanzoffiana, Tetrorchidium rubrivenium, Maclura tinctoria, Schefflera morototoni* e *Vitex megapotamica*.

Em um contexto mais amplo, o controle de espécies exóticas invasoras em áreas protegidas será inócuo caso essas espécies continuem sendo intensamente utilizadas no entorno dessas áreas, para diferentes fins. Consta no recente Inventário Florístico Florestal de Santa Catarina, publicado em 2012, que *H. dulcis* é uma das espécies exóticas que pode ser encontrada na forma de indivíduos adultos e de regenerantes no interior de fragmentos em sucessão secundária de Floresta Ombrófila Densa e Floresta Ombrófila Mista, além da Floresta Estacional Decidual. Destaca-se também que as formações florestais de Santa Catarina encontram-se com cobertura bastante reduzida com relação à sua cobertura original, com mais de 70% dos fragmentos remanescentes sendo menores do que 50 hectares nas três formações (74% para Floresta Ombrófila Densa, 82% para Floresta Ombrófila Mista e 90% para Floresta Estacional Decidual). Considerando-se a capacidade de *H. dulcis* de colonizar e invadir florestas secundárias, especialmente aquelas em estágio intermediário de regeneração, a condição na qual atualmente se encontram as florestas catarinenses seria o cenário ideal para a invasão pela espécie. A suscetibilidade dessas florestas à invasão por *H. dulcis* pode ser ainda maior em virtude do plantio difuso da espécie em propriedades rurais para fins diversos, resultando em uma intensa pressão de propágulos em fragmentos florestais.

Considerando o exposto, faz-se urgente e necessária a regulamentação para uso e manejo da espécie prevista na legislação estadual que instituiu a lista estadual de espécies exóticas invasoras de Santa Catarina. Neste sentido, recomenda-se que a utilização da espécie seja proibida em projetos de recuperação e restauração ambiental, assim como seu plantio para qualquer fim em unidades de conservação e em suas zonas de amortecimento. Recomenda-se, ainda, que uma faixa mínima de 30 metros de distância de bordas de fragmentos florestais seja priorizada para erradicação de indivíduos de *H.dulcis*, mesmo quando esta faixa estiver localizada em propriedades privadas. Essa distância reduziria a chegada de sementes em bordas de fragmentos florestais por meio da dispersão local por aves frugívoras. Complementarmente seria necessário que ocorressem nessas faixas monitoramentos e repasses de controle anuais permanentes, tendo em vista que: (1) a distância de 30 metros seria suficiente para reduzir mas não para eliminar por completo a chegada de sementes trazidas por aves frugívoras e; (2) *H. dulcis* pode também ser dispersa por mamíferos terrestres, o que possivelmente implicaria em maiores distâncias de dispersão. Estudos sobre distância de dispersão de *H. dulcis* em diferentes formações florestais do estado poderiam prover medidas mais acuradas e precisas para plantio da espécie em propriedades rurais, considerando-se diferenças regionais na composição de espécies, abundância e distribuição de agentes dispersores.

O uso de espécies nativas em substituição a *H. dulcis*, por meio de políticas públicas e programas de incentivo, é também fundamental para a conservação dos fragmentos remanescentes da Floresta Estacional Decidual de Santa Catarina. As espécies arbóreas nativas *Zanthoxylum rhoifolium*, *Maclura tinctoria*, *Schefflera morototoni*, *Cabralea canjerana*, *Cupania vernalis* e *Myrsine umbellata* devem ser promovidas pelo poder público para substituir *H. dulcis* em seu uso madeireiro. Deve-se também estimular o uso de espécies decíduas, zoocóricas e de rápido crescimento, tais como *Z. rhoifolium*, *M. tinctoria* e *S. morototoni*, nas granjas de suínos e aves para substituir *H. dulcis* no provimento de sombra. Além disso, *M. umbellata* poderia também ser utilizada como fonte alternativa de lenha em propriedades rurais.