UNIVERSIDADE FEDERAL DE SANTA CATARINA
CENTRO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA DE FUNGOS, ALGAS E PLANTAS

Amanda Angélica Carmes

Plantas lenhosas exóticas invasoras em florestas neotropicais: fatores que explicam a riqueza de espécies e potencial de invasão em *Schefflera* s.l.

Florianópolis
2024

Amanda Angélica Carmes

Plantas lenhosas exóticas invasoras em florestas neotropicais: fatores que explicam a riqueza de espécies e potencial de invasão em *Schefflera* s.l.

Tese submetida ao Programa de Pós-Graduação em Biologia de Fungos, Algas e Plantas da Universidade Federal de Santa Catarina para a obtenção do título de doutora em Biologia de Fungos, Algas e Plantas
Orientador: Prof. Dr. Pedro Fiaschi
Coorientadores: Profª Dra. Michele de Sá Dechoum, Dr. Rafael Barbizan Suhs

Florianópolis
2024

Ficha de identificação da obra

Carmes, Amanda Angélica
Plantas lenhosas exóticas invasoras em florestas neotropicais: fatores que explicam a riqueza de espécies e potencial de invasão em Schefflera s.l. / Amanda Angélica Carmes ; orientador, Pedro Fiaschi, coorientadora, Michele de Sá Dechoum, coorientador, Rafael Barbizans Suhs, 2024.
109 p.

Tese (doutorado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas, Programa de Pós-Graduação em Biologia de Fungos, Algas e Plantas, Florianópolis, 2024.

Inclui referências.

1. Biologia de Fungos, Algas e Plantas. 2. Deciduidade. 3. Germinação de sementes. 4. Plantas exóticas invasoras. 5. Tolerância a sombra. I. Fiaschi, Pedro. II. Dechoum, Michele de Sá. III. Suhs, Rafael Barbizans IV. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Biologia de Fungos, Algas e Plantas. V. Título.

Amanda Angélica Carmes

Plantas lenhosas exóticas invasoras em florestas neotropicais: fatores que explicam a riqueza de espécies e potencial de invasão em *Schefflera* s.l.

O presente trabalho em nível de doutorado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

Profª. Dra. Suzana Alcântara
Universidade Federal de Santa Catarina

Prof. Dr. Sérgio Zalba
Universidad Nacional Del Sur

Dra. Ana Boeira Porto
Universidade Federal do Rio Grande do Sul

Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de doutora em Biologia de Fungos, Algas e Plantas

ICP-Edu
Documento assinado digitalmente
Ana Claudia Rodrigues
Data: 29/10/2024 09:06:56-0300
CPF: ***.841.401-**
Verifique as assinaturas em https://v.ufsc.br

Profa. Dra. Ana Claudia Rodrigues
Coordenadora do Programa de Pós-Graduação

ICP-Edu
Documento assinado digitalmente
Pedro Fiaschi
Data: 28/10/2024 20:13:59-0300
CPF: ***.995.708-**
Verifique as assinaturas em https://v.ufsc.br

Prof. Dr. Pedro Fiaschi
Orientador

Florianópolis, 2024.

A Deus, por sempre me fortalecer e iluminar minha caminhada.

Ao meu companheiro e pais, pelo apoio e amor incondicional

AGRADECIMENTOS

Inicialmente gostaria de agradecer a mim mesma, por não ter desistido, mesmo diante das adversidades e dificuldades enfrentadas. A realização deste doutorado foi mais do que um crescimento profissional, foi pessoal também!

Agradeço também aos três amores da minha vida, meu companheiro André, e meus pais Rozana e Adison, obrigada pelo apoio de sempre e pela compreensão das ausências nas horas dispendidas ao estudo.

Aos meus orientadores, Michele Dechoum, Pedro Fiaschi e Rafael Barbizan Suhs, por todo conhecimento transmitido, pela paciência, pelo incentivo e por sempre estarem disponíveis para o esclarecimento de dúvidas ao longo destes pouco mais de quatro anos de convívio.

Aos meus colegas de laboratório e de vida Indiane Conti, Leticia Mesassaca e Luciana Silva, pelo auxílio nas saídas de campo. A Indiane Conti, pela grande ajuda na confecção do impecável mapa presente neste trabalho.

Às grandes amizades que fiz neste período, que me ajudaram, me ensinaram e me fortaleceram. Valeu a pena ter conhecido vocês, pessoal.

Ao Laboratório de Sistemática Vegetal da UFSC, pela infraestrutura oferecida, fundamentais à elaboração deste trabalho.

À equipe da RPPN Caraguatá, pela imporante ajuda para localizar e coletar sementes de indivíduos de *Didymopanax calvus*, localizados dentro dos limites desta Unidade de Conservação.

Ao Fernando Bruggemann, biólogo do Plaza Caldas da Imperatriz Resort e *Spa*, pela colaboração e autorização para entrarmos no Plaza para localização e coleta de sementes de indivíduos de *Didymopanax angustissimus.*

À Fundação de Amparo a Pesquisa de Santa Catarina – FAPESC, pela disponibilização da bolsa de estudos que permitiu minha total dedicação a este doutorado.

A todas as pessoas do meu convívio, que contribuíram, mesmo indiretamente, para a conclusão de mais esta etapa da minha vida. Meu muito obrigada!

“Por vezes sentimos que aquilo que fazemos não é senão uma gota de água no mar. Mas o mar seria menor se lhe faltasse uma gota”

(Madre Teresa de Calcutá)

RESUMO

O avanço da pressão antrópica em regiões tropicais tem levado à chegada de plantas exóticas invasoras em áreas de florestas inseridas em contextos de perda e fragmentação de hábitat. Florestas tropicais são historicamente consideradas menos suscetíveis à invasão do que outros tipos de vegetação, devido, principalmente, à baixa disponibilidade de luz, condição verificada principalmente nas fitofisionomias perenifólias. No entanto, estudos recentes têm mostrado que muitas espécies tolerantes à sombra conseguem sobreviver nessas condições. Diversos estudos têm mostrado que plantas exóticas invasoras apresentam atributos que ajudam a explicar o sucesso de invasão destas espécies comparado às nativas, inclusive sob diferentes condições de luminosidade. Os objetivos deste estudo foram: (Capítulo 1) identificar quais fatores explicam a riqueza de plantas lenhosas exóticas invasoras em florestas neotropicais com diferentes níveis de deciduidade foliar e, (Capítulo 2) quais atributos relacionados à germinação e crescimento diferem entre espécies exóticas invasoras e nativas de *Schefflera* s.l. No capítulo 1, foi realizada uma revisão sistemática de estudos que realizaram levantamento florístico em fitofisionomias florestais na região Neotropical. A partir da seleção dos artigos, foram obtidas variáveis climáticas, ambientais e antrópicas dos locais onde as espécies foram amostradas. Já no capítulo 2, sementes de duas espécies nativas e de duas espécies exóticas invasoras de *Schefflera* s.l. foram colocadas para germinar em duas condições de luz (100% e 50%), e monitoradas para obtenção de parâmetros de germinação, e sobrevivência e crescimento de plântulas. Os resultados do capítulo 1 mostraram que a riqueza de plantas exóticas invasoras aumentou com maior sazonalidade da temperatura, acessibilidade e Produto interno Bruto (PIB), e diminuiu com o aumento da cobertura florestal. Os resultados do capítulo 2 mostraram que as espécies exóticas invasoras germinaram mais rapidamente e em maior proporção em ambos os tratamentos de luz, quando comparadas às nativas. Além disso, as espécies invasoras mostraram maior taxa de sobrevivência sob 50% de luz. Os resultados obtidos neste estudo mostram que florestas de dossel fechado não limitam a ocorrência de espécies exóticas invasoras, como é o caso das espécies de *Schefflera* s.l. aqui estudadas. Somado a isto, a crescente pressão antrópica à qual as florestas neotropicais estão sujeitas contribuem para o aumento da riqueza das espécies exóticas invasoras, aumentando ainda mais a susceptibilidade destes ecossistemas à invasão por plantas.

Palavras-chave: crescimento; deciduidade; germinação de sementes; plantas exóticas invasoras; potencial de invasão; revisão sistemática; sobrevivência; tolerância à sombra.

ABSTRACT

The advance of anthropogenic pressure in tropical regions has led to the arrival of invasive non-native plants in forest areas in contexts of habitat loss and fragmentation. Tropical forests have historically been considered less susceptible to invasion than other vegetation types, mainly due to the low availability of light. However, recent studies have shown that many shade-tolerant species can survive in these conditions. Several studies have shown that invasive non-native plants have attributes that help explain their invasion success compared to native species, even under different light conditions. The objectives of this study were: (Chapter 1) to identify which factors explain the richness of invasive non-native woody plants in neotropical forests with different levels of leaf deciduousness and, (Chapter 2) which attributes related to germination and growth differ between invasive non-native and native species of *Schefflera* senso lato In Chapter 1, a systematic review was carried out of studies that carried out floristic surveys in forest phytophysiognomies in the Neotropical region. After selecting the articles, climatic, environmental and anthropogenic variables were obtained from the sites where the species were sampled. In Chapter 2, seeds from two native species and two invasive non-native species of *Schefflera* s.l. were allowed to germinate in two light conditions (100% and 50%) and monitored to obtain germination parameters and seedling survival and growth. The results of chapter 1 showed that the richness of invasive non-native plants increased with greater seasonality of temperature, accessibility and Gross Domestic Product (GDP), and decreased with increasing forest cover. The results of Chapter 2 showed that invasive non-native species germinated faster and in greater proportions in both light treatments when compared to native species. In addition, the invasive non-native showed a higher survival rate under 50% light. The results obtained in this study show that closed canopy forests do not limit the occurrence of invasive non-native species, as is the case with the *Schefflera* s.l. species studied here. In addition, the growing anthropogenic pressure to which Neotropical forests are subject contributes to the increase in the richness of invasive non-native species, further increasing the susceptibility of these ecosystems to plant invasion.

Keywords: growth; deciduousness; seed germination; invasive non-native plants; invasion potential; systematic review; survival; shade tolerance.

Resumo expandido

Introdução

Invasão biológica é um processo que envolve um contínuo de estágios separados por barreiras ecológicas que a espécie introduzida deve superar para se tornar uma invasora bem-sucedida. Três fatores-chave explicam o sucesso em processos de invasão biológica: características da espécie introduzida; características do ambiente invadido; e fatores relacionados aos esforços de introdução. Frequentemente, comparações experimentais entre espécies lenhosas filogeneticamente relacionadas mostram que a espécie invasora apresenta melhor desempenho com relação à proporção de sementes germinadas, altura da plântula, biomassa total e sobrevivência, quando comparada às nativas co-ocorrentes pertencentes ao mesmo gênero ou família. Características como tolerância à sombra e plasticidade fenotípica tem se mostrado importantes atributos para plantas exóticas invasoras de ecossistemas florestais. Recentemente, pesquisadores sugeriram a existência de um grupo de plantas invasoras denominadas 'superinvasoras', as quais crescem mais rapidamente do que a maioria das espécies nativas da área invadida quando a luz é abundante, e que também sobrevivem ao sombreamento, por precisarem de menor quantidade de luz para equilibrar a perda de carbono pela manutenção do indivíduo, quando comparadas às nativas. Com relação a plasticidade fenotípica, diversos estudos têm verificado o papel deste atributo no sucesso da invasão comparando a plasticidade de espécies invasoras com exóticas não invasoras ou nativas com relação a diferentes condições de luz, disponibilidade de nutrientes e de água, mostrando que de fato, as espécies invasoras apresentam maiores níveis de plasticidade fenotípica. As características do ambiente invadido também contribuem para determinar quais e quantas plantas introduzidas irão estabelecer populações viáveis e persistentes. Variáveis climáticas são importantes filtros para o estabelecimento de espécies exóticas invasoras e podem ser consideradas importantes preditores para a riqueza de exóticas invasoras. Os ambientes modificados por humanos contribuem como fonte de introdução de propágulos de espécies exóticas invasoras, bem como fonte de distúrbios. Variáveis que indicam atividade humana (*i.e.* PIB, alta proporção do uso do solo para agricultura, densidade populacional) relacionam-se positivamente com a riqueza de espécies exóticas invasoras em áreas não urbanizadas. Além dos distúrbios de origem antrópica, florestas também estão sujeitas a distúrbios naturais, como aberturas de clareiras promovidas pela queda de árvores e galhos, que são eventos estocásticos que podem ou não ser combinados com eventos determinísticos associados a ciclos de deciduidade foliar. A dinâmica de abertura do dossel em florestas pode ser um fator importante para a chegada e o estabelecimento de plantas exóticas invasoras, uma vez que dosséis florestais fechados, além de diminuírem a luminosidade, também podem funcionar como barreira física para a chegada de propágulos.

Objetivos

O objetivo geral desta tese é compreender quais fatores explicam a riqueza de plantas lenhosas exóticas invasoras em florestas neotropicais com diferentes níveis de deciduidade foliar, bem como avaliar quais atributos relacionados à germinação, sobrevivência e crescimento diferem entre espécies exóticas invasoras e nativas de *Schefflera* sensu lato (Araliaceae Juss.).

Metodologia

Para verificar quais fatores explicam a riqueza de plantas lenhosas exóticas invasoras em florestas neotropicais foi realizado uma revisão sistemática dos levantamentos florísticos realizados em florestas neotropicais, utilizando a base de dados *Web of Science*. A partir dos estudos selecionados, foram obtidas as coordenadas dos locais de amostragem, a área de amostragem, o número de espécies invasoras não nativas, o numero total de espécies registradas. Com base nas coordenadas de cada local de amostragem, foram obtidas variáveis climáticas, ambientais e antrópicas. A partir dos dados obtidos, foram construídos modelos lineares generalizado, e um foi selecionado para verificar quais variáveis influenciavam a riqueza de plantas lenhosas invasoras. Para avaliar quais atributos diferem entre espécies nativas e exóticas invasoras de *Schefflera* s.l., foram selecionadas quatro espécies de *Schefflera* s.l., duas das quais são exóticas invasoras (*Heptapleurum actinophyllum* (Endl.) Lowry & G.M. Plunkett; *Heptapleurum arborícola* Hayata) e duas são nativas (*Didymopanax angustissimus* Marchal e *D. calvus* (Cham.) Decne. & Planch.). As sementes coletadas foram utilizadas para a realização de testes de germinação, e as plântulas foram utilizadas para o acompanhamento do crescimento e da sobrevivência. Foram utilizados dois tipos de tratamentos: um com 100% de intensidade luminosa, e um com 50% de intensidade luminosa, com o uso de sombrite.

Resultados e discussão

Os resultados do presente estudo mostraram que as florestas neotropicais subtropicais são mais susceptíveis ao estabelecimento de plantas lenhosas exóticas invasoras, comparado à florestas tropicais. A deciduidade foliar que ocorre nestas florestas, como consequência da diminuição de temperatura, promove a diminuição da barreira física do dossel e aumento de luminosidade, favorecendo a chegada e o estabelecimento de propágulos de plantas invasoras. Ademais, verificamos que florestas com maior acessibilidade são mais susceptíveis à invasão por espécies lenhosas exóticas invasoras, devido à maior disponibilidade de propágulos de espécies cultivadas nas regiões do entorno. Com relação às comparações entre as espécies de *Schefflera* s.l. verificamos que as espécies exóticas invasoras mostraram maior proporção e velocidade de germinação quando comparadas às nativas, característica que contribui para o estabelecimento inicial, uma vez que espécies que germinam antecipadamente se beneficiam da competição reduzida. Verificamos também uma maior proporção de germinação de espécies invasoras sob 50% de luz, resultado que pode indicar que ambas as espécies invasoras possuem tolerância à sombra, conseguindo germinar mesmo sob condições mais escuras do subosque florestal. Sugerimos também que a espécie exótica invasora *Heptapleurum arboricola* possui atributos de uma ‘superinvasora’ em potencial (crescimento superior sob luz e persistência de plântulas sob sombra). Somado a isto, a maior plasticidade na alocação de biomassa raiz:parte aérea em condições de diferentes luminosidades contribui para o sucesso no estabelecimento e invasão de florestas.

Palavras-chave: crescimento; deciduidade; germinação de sementes; plantas exóticas invasoras; potencial de invasão; revisão sistemática; sobrevivência; tolerância à sombra.

LISTA DE FIGURAS

INTRODUÇÃO

CAPÍTULO 1

CAPÍTULO 2

LISTA DE TABELAS

CAPÍTULO 1

CAPÍTULO 2

LISTA DE ABREVIATURAS E SIGLAS

GLM:	Modelos lineares generalizdos
HII:	Índice global de influência humana
IDH:	Índice de desenvolvimento humano
IVG:	Índice de velocidade de germinação
NDVI:	Índice de vegetação com diferença normalizada
RREL-NDVI	Intervalo relativo do NDVI (Relative Range NDVI)
PIB:	Produto interno bruto
PIB PPC:	Produto interno bruto por paridade do poder de compra
TCRA:	Taxa de crescimento relativo em altura
VIF:	Valor de inflação da variância

SUMÁRIO

INTRODUÇÃO

As taxas de introdução de espécies têm aumentado nos últimos 200 anos, sendo que cerca de 40% dos primeiros registros de invasão foram relatados nos últimos 50 anos (SEEBENS *et al.*, 2017). Como consequência desse aumento, hoje as espécies exóticas invasoras representam grande ameaça à biodiversidade e à economia mundial (PYŠEK *et al.*, 2020; DIAGNE *et al.*, 2021). Invasão biológica é um processo que envolve um contínuo de estágios (introdução, estabelecimento e invasão) separados por barreiras ecológicas que a espécie introduzida deve superar para se tornar uma invasora bem-sucedida (RICHARDSON *et al.*, 2000; BLACKBURN *et al.*, 2011). Em síntese, três fatores-chave explicam o sucesso em processos de invasão biológica: (1) características biológicas e ecológicas da espécie introduzida (*invasiveness*); (2) características do ambiente invadido (*invasibility*); e (3) fatores relacionados aos esforços de introdução (pressão de propágulos) (PYŠEK *et al.*, 2020).

Identificar os atributos que contribuem para aumentar o potencial de invasão das espécies exóticas invasoras tem sido um dos objetivos centrais da ciência da biologia de invasões (MOODLEY *et al.*, 2013). Isto porque compreender os fatores que tornam as espécies invasoras capazes de colonizar uma ampla faixa de condições ambientais é importante para prever futuras invasões (GODOY *et al.*, 2011). Tem-se verificado um aumento no número de estudos experimentais que buscam comparar plantas exóticas invasoras e nativas co-ocorrentes; entretanto, muitos destes estudos não consideram a filogenia das espécies comparadas (YU e HE, 2021; PORTÉ *et al.*, 2011; MATHAKUTHA *et al.*, 2017). Espera-se que, ao comparar espécies filogeneticamente relacionadas, sejam encontradas características semelhantes devido à história evolutiva compartilhada (ANTÚNEZ *et al.*, 2001; LEICHT-YOUNG *et al.*, 2007). Ou seja, verificar a existência de diferentes características em plantas filogeneticamente próximas pode ajudar a explicar porque algumas espécies podem invadir com sucesso áreas previamente ocupadas por espécies nativas relacionadas (YU e HE, 2021). Frequentemente, comparações experimentais entre espécies lenhosas filogeneticamente relacionadas mostram que a espécie invasora apresenta melhor desempenho com relação à proporção de sementes germinadas, altura da plântula, biomassa total e sobrevivência, quando comparada às nativas co-ocorrentes pertencentes ao mesmo gênero ou família (LEICHT-YOUNG *et al.*, 2007; STRICKER e STILING 2013). Entretanto, tais estudos ainda são escassos, prevalecendo a maioria realizada com espécies herbáceas ou em florestas temperadas (YU e HE, 2021; PERGLOVA *et al.*, 2009; ASSAD *et al.*, 2021).

A tolerância à sombra também tem se mostrado um importante atributo para plantas exóticas invasoras de ecossistemas florestais (MARTIN *et al.*, 2009; JUNAEDI *et al.*, 2021). A habilidade de lidar com baixas condições de luz é um atributo importante para espécies exóticas invasoras conseguirem se estabelecer em florestas (POORTER, 1999; BLOOR e GRUBB, 2003; MARTIN *et al.*, 2010; JUNAEDI *et al.*, 2020). Um crescente número de estudos tem mostrado que plantas invasoras de florestas tropicais e subtropicais desenvolveram diferentes estratégias para lidar com diferentes condições de luminosidade (e.g.: MARTIN *et al.*, 2009; REJMANEK, 2014; MEDVECKÁ *et al.*, 2018; BERG *et al.*, 2016; FRIDLEY *et al.*, 2023). As espécies nativas tolerantes à sombra apresentam atributos que minimizam a respiração e renovação de tecidos; como consequência, há redução de crescimento e domínio competitivo nas condições de maior luz (LUSK e JORGENSEN, 2013; SENDALL *et al.*, 2016). Por outro lado, para algumas espécies exóticas invasoras tolerantes à sombra, há indícios de haver um *trade-off* entre os mecanismos de crescimento e sobrevivência nos períodos de maior e menor luz, onde há uma combinação de crescimento rápido em condições de luz intermediária a alta e crescimento lento em condições de luz baixa (MARTIN *et al.*, 2010). Recentemente, FRIDLEY *et al.* (2023) sugeriram a existência de um grupo de plantas invasoras denominadas 'superinvasoras', as quais crescem mais rapidamente do que a maioria das espécies nativas da área invadida quando a luz é abundante, e que também sobrevivem ao sombreamento, por precisarem de menor quantidade de luz para equilibrar a perda de carbono pela manutenção do individuo, quando comparadas às nativas (FRIDLEY *et al.*, 2023). Esta redução nos custos de carbono das 'superinvasoras' pode ser devida a mecanismos como redução/ausência de herbívoros, menor investimento em defesa, maior vida útil do tecido, menor estatura e menor investimento em raízes (FRIDLEY *et al.*, 2023).

A plasticidade fenotípica é frequentemente citada como um atributo que contribui para o sucesso de invasão, uma vez que permite à espécie expressar fenótipos vantajosos em uma ampla gama de ambientes (MATESANZ *et al.*, 2010; DAVIDSON *et al.*, 2011). Diversos estudos têm verificado o papel da plasticidade fenotípica no sucesso da invasão comparando a plasticidade de espécies invasoras com exóticas não invasoras ou nativas com relação a diferentes condições de luz, disponibilidade de nutrientes e de água, mostrando que de fato, as espécies invasoras apresentam maiores níveis de plasticidade fenotípica (FUNK, 2008;

DAVIDSON *et al*., 2011; MATESANZ *et al*., 2012; SKALOVÁ *et al*., 2012; MONTY *et al*., 2013; GRUNTMAN *et al*., 2020). Recentemente GRUNTMANN *et al*. (2020) compararam a plasticidade em populações na região nativa e na região introduzida de *Impatiens glandulifera* e mostraram que populações invasoras exibem maior plasticidade em diferentes condições de luminosidade. As respostas plásticas verificadas em diferentes condições de luminosidade incluem ajustes morfológicos e fisiológicos que promovem maior eficiência da captura de luz como tamanho da folha, área foliar específica, alocação de biomassa e taxa fotossintética (GRUNTMANN *et al*., 2020). A capacidade das plantas de capturar e utilizar a luz é um importante determinante do crescimento, recrutamento e aptidão das espécies, o que é de extrema importância para as plantas introduzidas que invadem os ecossistemas florestais (STANDISH *et al*., 2001).

Além dos atributos intrínsecos das espécies, as características do ambiente invadido também contribuem para determinar quais e quantas plantas introduzidas irão estabelecer populações viáveis e persistentes. Variáveis climáticas são importantes filtros para o estabelecimento de espécies exóticas invasoras e podem ser consideradas importantes preditores para a riqueza de exóticas invasoras. Em uma revisão global, SHI *et al*. (2010) mostraram relação positiva entre a riqueza de plantas invasoras e variáveis climáticas como temperatura e precipitação. Os autores concluíram que climas tropicais úmidos, i.e., com médias anual de temperatura entre 17-25°C e precipitação anual de 1.500 mm, apresentam condições ideais para a manutenção de uma maior riqueza de plantas exóticas invasoras (SHI *et al*., 2010). Apesar de sua importância para a riqueza de espécies invasoras, variáveis climáticas são pouco avaliadas em climas tropicais e subtropicais, a maioria dos estudos foram realizados em clima temperado (OHLEMÜLLER *et al*., 2006; MARINI *et al*., 2012; GALLARDO e VILÀ, 2019).

Os ambientes modificados por humanos contribuem como fonte de introdução de propágulos de espécies exóticas invasoras, bem como fonte de distúrbios (VILÀ *et al*., 2007; VICENTE *et al*., 2010; DIMITRAKOPOULOS *et al*., 2017; ESSL *et al*., 2019). O conceito de distúrbio utilizado foi proposto por SOMMER *et al*. (1993), no qual o distúrbio consiste em qualquer flutuação na disponibilidade de recursos. Esta definição difere de outras, uma vez que não considera apenas mudanças discretas, mas também mudanças contínuas ao longo de gradientes, bem como flutuações sazonais na disponibilidade de recursos (BATTISTI *et al*., 2016). Alguns estudos têm mostrado uma correlação positiva entre urbanização e/ou a presença de atividades antrópicas e níveis mais altos de chegada de propágulos via dispersão local nas comunidades naturais adjacentes (THUILLER *et al.*, 2005; CARBONI *et al.*, 2010). Variáveis que indicam atividade humana (*i.e.* PIB, alta proporção do uso do solo para agricultura, densidade populacional) relacionam-se positivamente com a riqueza de espécies exóticas invasoras em áreas não urbanizadas (SPEAR *et al.*, 2013; DIMITRAKOPOULOS *et al.*, 2017; ESSL *et al.*, 2019). Estradas também contribuem como meios de dispersão de espécies exóticas invasoras para áreas naturais adjacentes (JOLY *et al.*, 2011; DAR *et al.*, 2015; LEMKE *et al.*, 2019). Veículos atuam como vetores de dispersão, por meio dos quais propágulos podem ser dispersos a longas distâncias, mesmos sem adaptações específicas (TAYLOR *et al.*, 2012; VON DER LIPPE *et al.*, 2013; LEMKE *et al.*, 2019). Apesar disso, estudos mostrando a influência de estradas na dispersão de plantas exóticas invasoras em florestas tropicais ainda são escassos (DÖBERT *et al.*, 2018; PADMANABA e SHEIL, 2014; VELDMAN e PUTZ, 2010).

Em florestas, a ocupação humana promove a fragmentação e a formação de clareiras (VILÀ *et al.*, 2008; CHYTRÝ *et al.*, 2008; DIMITRAKOPOULOS *et al.*, 2017). O aumento da disponibilidade de luz promovida pela destruição de florestas é um dos fatores que explicam o maior número de espécies exóticas em bordas florestais ou em clareiras quando comparadas ao interior de florestas (GREEN *et al.*, 2004). Além dos distúrbios de origem antrópica, florestas também estão sujeitas a distúrbios naturais, como aberturas de clareiras promovidas pela queda de árvores e galhos, que são eventos estocásticos que podem ou não ser combinados com eventos determinísticos associados a ciclos de deciduidade foliar (GANDOLFI *et al.*, 2007; 2009). Clareiras, sejam elas estocásticas ou determinísticas, desempenham um importante papel na manutenção da riqueza de espécies nativas nesses ecossistemas, uma vez que diferentes condições de luminosidade abaixo das copas podem criar microhabitats que atuam como filtros para o estabelecimento de indivíduos regenerantes (GANDOLFI *et al.*, 2007; 2009). No entanto, a dinâmica de abertura do dossel em florestas também pode ser um fator importante para a chegada e o estabelecimento de plantas exóticas invasoras (SPEAR *et al.*, 2013; DECHOUM *et al.*, 2015), uma vez que dosséis florestais fechados, além de diminuírem a luminosidade, também podem funcionar como barreira física para a chegada de propágulos (HANSEN e CLEVENGER, 2005).

A Região Neotropical compreende áreas tropicais que se estendem da América do Sul ao México, e abriga a maior riqueza de espécies animais e vegetais do planeta, bem como um número significativo de hotspots de biodiversidade (MYERS *et al.*, 2000). No entanto, esta região apresenta as taxas mais altas do mundo de conversão de florestas em pastagens/monoculturas e abriga mais de 81% da população vivendo em áreas urbanas (WASSENAAR *et al*., 2007; MARIA *et al*., 2017, CURTIS *et al*., 2022). Como consequência, as florestas neotropicais têm sido impactadas negativamente por distúrbios antrópicos como o desmatamento, incêndios e invasões biológicas, bem como os efeitos combinados destes fatores com as mudanças climáticas (CARVALHO *et al*., 2001; MCDOWELL e ALLEN, 2015; ROWLAND *et al*., 2015; ESQUIVEL-MUELBERT *et al*., 2019; GOMES *et al*., 2019; FARIA *et al*., 2021; MELITO *et al*., 2021). Florestas tropicais são importantes componentes dos sistemas terrestres, uma vez que representam reservatórios de carbono, fornecem importantes serviços ecossistêmicos e abrigam uma considerável parte da biodiversidade terrestre (TAUBERT *et al*., 2018; FISCHER *et al*., 2021). Apesar de sua importância, as florestas têm sido ameaçadas por ações humanas como desmatamento, deposição de nitrogênio em excesso, perda de predadores que controlam herbívoros, mudanças climáticas e invasão por espécies exóticas (LIEBHOLD *et al*., 2017; DYDERSKI *et al*., 2018; ESQUIVEL-MUELBERT *et al*., 2019; GOMES *et al*., 2019).

Invasões bem-sucedidas podem ocorrer por muitas razões e, conforme já mencionado, podem envolver atributos que conferem vantagens competitivas a algumas espécies em comparação a outras (ORTEGA e PEARSON, 2005). Comparações realizadas entre espécies invasoras e não invasoras nos ajudam a compreender quais características podem contribuir para tornar uma espécie invasora (GERLACH e RICE, 2003). Alguns estudos demonstraram a importância de se considerar o parentesco filogenético de atributos biológicos entre espécies, isto porque espécies filogeneticamente relacionadas possuem características semelhantes, pois compartilham um ancestral comum relativamente recente (ANTÚNEZ *et al*., 2001; VAN KLEUNEM *et al*., 2010). O uso de espécies filogeneticamente relacionadas pode minimizar a confusão com relação às características adquiridas ao longo da história evolutiva, que podem diferir entre espécies filogeneticamente distantes (STRICKER e STILING, 2013). Apesar de nos últimos anos o número de estudos experimentais que buscam comparar plantas exóticas invasoras e nativas co-ocorrentes terem aumentado, muitas comparações não levam em conta a filogenia das espécies comparadas (PORTÉ *et al*., 2011; MATHAKUTHA *et al*., 2019; YU e HE, 2021).

Quatro espécies de árvores do gênero *Schefflera* sensu lato (Araliaceae Juss.) que ocorrem na área de estudo foram selecionadas para o estudo, duas das quais são exóticas invasoras (*Heptapleurum actinophyllum* (Endl.) Lowry & G.M. Plunkett; *Heptapleurum arborícola* Hayata) e duas são nativas (*Didymopanax angustissimus* Marchal e *D. calvus* (Cham.) Decne. & Planch.). Estudos recentes confirmam que *Schefflera* s.l. é um gênero polifilético representado por cinco clados distintos (Plunkett et al., 2005; Plunkett et al., 2019). As espécies anteriormente reconhecidas no clado asiático de *Schefflera* são atualmente tratadas como *Heptapleurum*, enquanto as espécies de *Didymopanax* fazem parte do clado neotropical, que também inclui outros quatro gêneros (Plunkett et al. 2019) (Figura 1).

Heptapleurum actinophyllum é nativa de Nova Guiné e Austrália, e *H. arboricola* da China e Taiwan (LOWRY e PLUKETT, 2020; INSTITUTO HÓRUS, 2022). Tais espécies são consideradas invasoras em diversos países do mundo (Singapura, Estados Unidos, Porto Rico, Cuba, Chile, Brasil, e ilhas do Pacífico) (INSTITUTO HÓRUS, 2022). Apesar disso, são amplamente utilizadas como plantas ornamentais nestas regiões (CHEN *et al*., 2003; LOWRY e PLUKETT, 2020). Ambas produzem uma grande quantidade de frutos e, nos locais onde são invasoras, seus frutos são ingeridos por aves nativas generalistas que habitam o entorno (MARCELINO, 2019; MARCINIAK *et al*., 2019). Somado a isto, ambas apresentam altas taxas de germinação, que permanecem elevadas mesmo após passar pelo trato digestivo de aves (MARCELINO, 2019; MARCINIAK *et al*., 2019). Por outro lado, *Didymopanax angustissimus* e *D. calvus* são nativas e endêmicas do Brasil, com distribuição limitada a florestas ombrófilas e semidecíduas da Mata Atlântica (FIASCHI e PLUNKETT, 2018; FIASCHI *et al*., 2020). Apesar de *D. angustissimus* produzir grande quantidade de sementes, ela não forma densas populações devido à competição intraespecífica de juvenis, que resultam em poucos indivíduos sobreviventes (ARMELIN, 2005). Além disso, ambas as espécies nativas apresentam baixa porcentagem de germinação, possivelmente devido à dormência tegumentar ou fisiológica ou à porcentagem de sementes danificadas por larvas de insetos (FRANCO e FERREIRA, 2002; ARMELIN, 2005; OHASHI e LEÃO, 2005; VILARINHO *et al*., 2019).

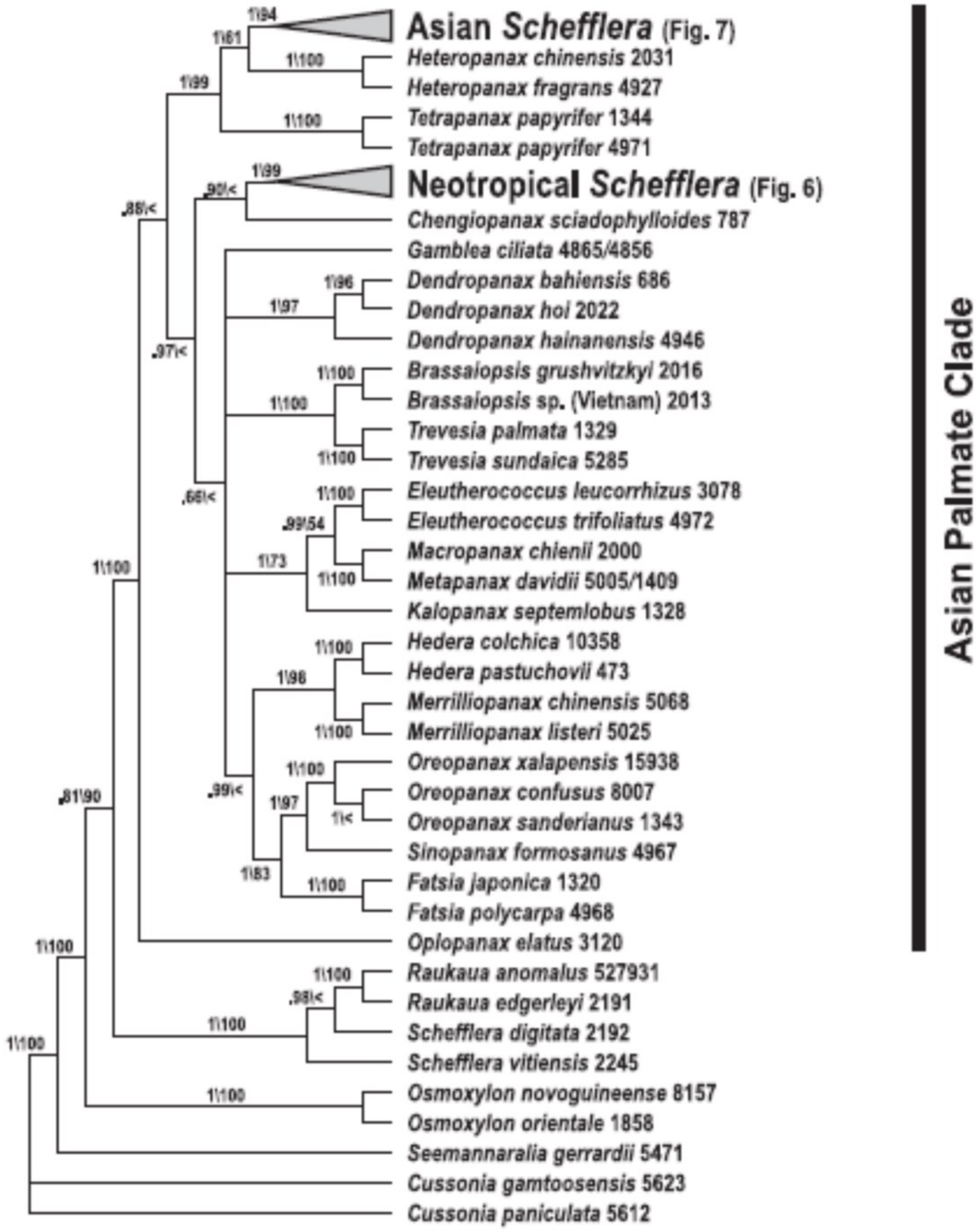

Figura 1. Filogenia do Clado "*Asian Palmate*" de Araliaceae, onde estão representadas as relações entre os clados Neotropical e Asiático de *Schefflera* s.l. (retirada de Plunkett *et al.* 2019).

Considerando: (1) a importância e subrepresentação de estudos em biologia da invasão em florestas tropicais e subtropicais, especialmente nos neotrópicos, e (2) a importância e subrepresentação de estudos comparativos entre espécies exóticas invasoras e nativas filogeneticamente relacionadas, o objetivo geral desta tese é compreender quais fatores explicam a riqueza de plantas lenhosas exóticas invasoras em florestas neotropicais com diferentes níveis de deciduidade foliar, bem como avaliar quais atributos relacionados à germinação, sobrevivência e crescimento diferem entre espécies exóticas invasoras e nativas de *Schefflera* s.l. A tese está dividida em dois capítulos, sendo que, no capítulo 1, a questão a ser respondida é: quais fatores antrópicos, climáticos e ambientais melhor explicam a riqueza de plantas lenhosas exóticas invasoras em florestas neotropicais com diferentes níveis de deciduidade foliar. Já no capítulo 2 as questões a serem respondidas são (1) As diferenças nos atributos biológicos relacionados à germinação de sementes e ao desenvolvimento de plântulas entre espécies exóticas invasoras e nativas filogeneticamente próximas podem ajudar a explicar o potencial de invasão biológica em florestas subtropicais? (2) A expressão destes atributos varia de acordo com as diferentes condições de luz?

REFERÊNCIAS

ANTÚNEZ, I., RETAMOSA, E.C., VILLAR, R. Relative growth rate in phylogenetically related deciduous and evergreen woody species. **Oecologia**, 128, 172–180, 2001.

ARMELIN, R.S. **As dinâmicas de *Schefflera angustissima* (March.) Frodin (Araliaceae) e de *Andira anthelmia* (Vell.) March. (Fabaceae) na Reserva de Morro Grande, São Paulo.** Tese (Doutorado em Ecologia), Universidade de São Paulo, São Paulo. 2005

ASSAD, R.; RASHID, I.; RESHI, Z.A.; SOFI, I.A. Invasiveness traits help Amaranths to invade Kashmir Himalaya, India. **Tropical Ecology**, 62, 209-217, 2021.

BATTISTI, C.; POETA, G.; FANELLI, G. The concept to f disturbance. In: BATTISTI, C.; POETA, G.; FANELLI, G. (eds.). **An introduction to disturbance ecology**. Switzerland: Springer, 2016, p. 7-11.

BERG, C.; DRESCHER, A.; WAGNER, V.; ESSL, F. Temporal trends in the invasions of Austrianwoodlands by alien trees. **Preslia**, v. 88, n. 2, p. 185-200. 2016.

BLACKBURN, T.M.; PYŠEK, P.; BACHER, S.; CARLTON, J. T., DUNCAN, R.P., JAROŠÍK, V.; RICHARDSON, D. M. A proposed unified framework for biological invasions. **Trends in ecology & evolution**, v. 26, n. 7, p. 333-339. 2011.

BLOOR, J.M.G.; GRUBB, P.J. Growth and mortality in high and low light: trends among 15 shade tolerant rain forest tree species. **Journal of Ecology**, v. 91, p. 77–85. 2003.

CARBONI, M.; SANTORO, R.; ACOSTA, A.T. Are some communities of the coastal dune zonation more susceptible to alien plant invasion? **Journal of Plant Ecology**, v. 3, n. 2, p. 139-147. 2010.

CARVALHO, G., BARROS, A.C., MOUTINHO, P., NEPSTAD, D. (2001). Sensitive development could protect Amazonia instead of destroying it. *Nature*, 409, 131.

CHEN, J.; HENNY, R.J.; MCCONNELL, D.B. Development of New Foliage Plant Cultivars. In: JANICK, J.; WHIPKEY, A. (Eds.), **Trends in new crops and new uses**. Alexandria: ASHS press, p. 466-472. 2003.

CHYTRÝ, M.; MASKELL, L.C.; PINO, J.; PYSEK, P.; VILÁ, M.; FONT, X.; SMART, S.M. Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. **Journal of Applied Ecology**, v. 45, n. 2, p. 448–458. 2008.

CURTIS, J.R.; ROBINSON, W.D.; ROMPRÉ, G.; AUSTIN, S.H. Urbanization is associated with unique community simplification among birds in a neotropical landscape. **Landscape Ecology**, 1-23, 2022.

DAR, P.A.; RESHI, Z.A.; SHAH, M.A. Roads act as corridors for the spread of alien plant species in the mountainous regions: A case study of Kashmir Valley, India. **Tropical Ecology**, v. 56, n. (2), p. 183–190. 2015.

DAVIDSON, A.M.; JENNIONS, M.; NIKOTRA, A.B. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. **Ecology Letters**, v. 14, p. 419–431. 2011.

DECHOUM, M.S.; CASTELLANI, T.T.; ZALBA, S.M.; REJMÁNEK, M.; PERONI, N.; TAMASHIRO, J.Y. Community structure, succession and invasibility in a seasonal deciduous Forest in southern Brazil. **Biological Invasions**, v. 17, n. 6, p. 1697-1712. 2015.

DIAGNE, C.; LEROY, B.; VAISSIÈRE, A.C.; GOZLAN, R.E.; ROIZ, D.; JARIĆ, I.; ... & COURCHAMP, F. High and rising economic costs of biological invasions worldwide. **Nature**, v. 592, n. 7855, p. 571-576. 2021.

DIMITRAKOPOULOS, P.G.; KOUKOULAS, S.; GALANIDIS, A.; DELIPETROU, P.; GOUNARIDIS, D.; TOULOUMI, K.; ARIANOUTSOU, M. Factors shaping alien plant species richness spatial patterns across Natura 2000 Special Areas of Conservation of Greece. **Science of the Total Environment**, v. 601, p. 461-468. 2017.

DÖBERT, T.F.; WEBBER, B.L.; SUGAU, J.B.; DICKINSON, K.J.; DIDHAM, R.K.. Logging, exotic plant invasions, and native plant reassembly in a lowland tropical rain forest. **Biotropica**, v. 50, n. 2, p. 254-265. 2018.

DYDERSKI, M.K.; PAZ, S.; FRELICH, L.E.; JAGODZINSKI, A.M. How much does climate change threaten European forest tree species distributions? **Global Change Biology**, v. 24, p. 1150–1163. 2018.

ESQUIVEL-MUELBERT, A.; BAKER, T.R.; DEXTER, K.G.; LEWIS, S.L.; BRIENEN, R.J.; FELDPAUSCH, T.R.; PHILLIPS, O.L. Compositional response of Amazon forests to climate change. **Global change biology**, v. 25, n. 1, p. 39-56. 2019.

ESSL, F.; DAWSON, W.; KREFT, H.; PERGL, J.; PYŠEK, P.; VAN KLEUNEN, M.; WINTER, M. Drivers of the relative richness of naturalized and invasive plant species on Earth. **AoB Plants**, v. 11, n. 5, p. plz051. 2019.

FARIA, B.L.; STAAL, A.; SILVA, C.A.; MARTIN, P.A.; PANDAY, P.K.; DANTAS, V.L. Climate change and deforestation increase the vulnerability of Amazonian forests to post-fire grass invasion. **Global Ecology and Biogeography**, 30(12), 2368-2381, 2021.

FIASCHI, P.; PLUNKETT, G.M. Revision of the *Didymopanax* group of Neotropical *Schefflera* (Araliaceae). (2018) **Annals of the Missouri Botanical Garden**, v. 103, n. 1, p. 24-105.

FIASCHI, P.; LOWRY, P.P.; PLUNKETT, G.M. Studies in Neotropical Araliaceae. III. Resurrection of the New World genus *Didymopanax* Decne. & Planch., previously included in *Schefflera* (Araliaceae). **Brittonia**, v. 72, n. 1, p. 16-22. 2020.

FISCHER, R.; TAUBERT, F.; MÜLLER, M.S.; GROENEVELD, J.; LEHMANN, S.; WIEGAND, T.; HUTH, A. Accelerated forest fragmentation leads to critical increase in tropical forest edge area. **Science Advances**, v. 7, n. 37, p. eabg7012. 2021.

FRANCO, E.T.H.; FERREIRA, A.G. Tratamentos pré-germinativos em sementes de *Didymopanax morototoni* (Aubl.) Dcne. et Planch. **Ciência Florestal**, v. 12, n. 1, p. 1-10. 2002.

FRIDLEY, J.D.; BELLINGHAM, P.J.; CLOSSET-KOPP, D.; DAEHLER, C.C.; DECHOUM, M.S.; MARTIN, P.H.; MURPHY, H.T.; ROJAS-SANDOVAL, J.; TNG, D. A general hypothesis of forest invasions by woody plants based on whole-plant carbon economics. **Journal of Ecology**, v. 111, n. 1, p. 4-22, 2023.

FUNK, J.L. Differences in plasticity between invasive and native plants from low resource environment. **Journal of Ecology**, v. 96, p. 1162–1173, 2008.

GALLARDO, B.; VILÀ, L. La influencia humana, clave para entender la Biogeografía de especies invasoras en el Antropoceno. **Cuadernos de investigación geográfica/Geographical Research Letters**, v. 45, p. 61-86. 2019.

GANDOLFI, S.; JOLY, C.A.; RODRIGUES, R.R. Permeability-impermeability: canopy trees as biodiversity filters. **Scientia Agricola**, v. 64, p. 433-438. 2007.

GANDOLFI, S.; JOLY, C.A.; LEITÃO-FILHO, H.D.F. "Gaps of deciduousness": cyclical gaps in tropical forests. **Scientia Agricola**, v. 66, p. 280-284. 2009.

GERLACH, J.D.; RICE, K.J. Testing life history correlates of invasiveness using congeneric plant species. **Ecological Applications**, v 13, p. 167–179. 2003.

GODOY, O.; SALDAÑA, A.; FUENTES, N.; VALLADARES, F.; GIANOLI, E. Forests are not immune to plant invasion: phenotypic plasticity and local adaptation allow *Prunella* *vulgaris* to colonize a temperate evergreen rainforest. **Biological Invasions**, v. 13, p. 1615-1625, 2011.

GOMES, V.H.F.; VIEIRA, I.C.G.; SALOMÃO, R.P. Amazonian tree species threatened by deforestation and climate change. **Nature Climate Change**, v. 9, p. 547–553. 2019.

GREEN, P.T.; LAKE, P.S.; O'DOWD, D.J. Resistance of island rainforest to invasion by alien plants: influence of microhabitat and herbivory on seedling performance. **Biological Invasions**, v. 6, n. 1, p. 1–9. 2004.

GRUNTMAN, M.; SEGEV, U.; TIELBÖRGER, K. Shade-induced plasticity in invasive *Impatiens glandulifera* populations. **Weed Research**, v. 60, n. 1, p. 16-25. 2020.

HANSEN, M.J.; CLEVENGER, A.P. The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. **Biological Conservation**, v. 125, n. 2, p. 249–259. 2005.

INSTITUTO HÓRUS DE DESENVOLVIMENTO E CONSERVAÇÃO AMBIENTAL. **Base de dados de espécies exótica invasoras**, 2020. Disponivel em: http://i3n.institutohorus.org.br/www. Accesso em: jan. 2020.

JOLY, M.; BERTRAND, P.; GBANGOU, R.Y.; WHITE, M.C.; DUBÉ, J.; LAVOIE, C. Paving the way for invasive species: Road type and the spread of common ragweed (*Ambrosia artemisiifolia*). **Environmental Management**, v. 48, n. 3, p. 514–522. 2011.

JUNAEDI, D.I.; GUILLERA-ARROITA, G.; VESK, P.A.; MCARTHY, M.A.; BURGMAN, M.A.; CATFORD, J.A. Traits explain invasion of alien plants into tropical rainforests. **Ecology and evolution**, v. 11, n. 9, p. 3808-3819. 2021.

LEICHT-YOUNG, S.A.; SILANDER, J.A.; LATIMER, A.M. Comparative performance of invasive and native *Celastrus* species across environmental gradients. **Oecologia**, 154, 273-282, 2007.

LEMKE, A., KOWARIK, I., VON DER LIPPE, M. How traffic facilitates population expansion of invasive species along roads: the case of common ragweed in Germany. **Journal of applied Ecology**, v. 56, n. 2, p. 413-422. 2019.

LIEBHOLD, A.M., BROCKERHOFF, E.G., KALISZ, S., NUÑEZ, M.A., WARDLE, D.A., WINGFIELD, M.J. Biological invasions in forest ecosystems. **Biological Invasions**, v. 19, n. 11, p. 3437-3458. 2017.

LOWRY, P.P.; PLUNKETT, G.M. Resurrection of the genus *Heptapleurum* for the Asian clade of species previously included in *Schefflera* (Araliaceae). **Novon**, v. 28, n. 3, p. 143-170. 2020.

LUSK, C.H.; JORGENSEN, M.A. The whole-plant compensation point as a measure of juvenile tree light requirements. **Functional Ecology**, v. 27, n. 6, p. 1286–1294. 2013.

MARCELINO, P.G. **O papel das aves na dispersão de sementes da espécie exótica *Schefflera actinophylla* (Apiales, Araliaceae): potencial de invasibilidade**. Dissertação (Mestrado em Profissional em Conservação da Fauna) – Programa de Pós-Graduação em Conservação da Fauna, Universidade Federal de São Carlos, Sorocaba, 2019.

MARIA, A.; ACERO, J.L.; AGUILERA, A.I.; LOZANO, M.G. (Eds.). **Central America urbanization review: making cities work for Central America**. World Bank Publications, 2017.

MARCINIAK, B.; DECHOUM, M.D.S.; CASTELLANI, T.T. The danger of non-native gardens: risk of invasion by *Schefflera arboricola* associated with seed dispersal by birds. **Biological Invasions**, v. 22, n. 3, p. 997-1010. 2020.

MARINI, L.; BATTISTI, A.; BONA, E.; FEDERICI, G.; MARTINI, F.; PAUTASSO, M.; HULME, P.E. Alien and native plant life-forms respond differently to human and climate pressures. **Global ecology and biogeography**, v. 21, n. 5, p. 534-544, 2012.

MARTIN, P.H.; CANHAM, C.D.; MARKS, P.L. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. **Frontiers Ecological Environment**, v. 7, p. 142–149. 2009.

MARTIN, P.; CANHAM, C.; KOBE, R. Divergence from the growth-survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. **Journal of Ecology**, v. 98, p. 778–789. 2010.

MATHAKUTHA, R.; STEYN, C.; LE ROUX, P.C.; BLOM, I.J.; CHOWN, S.L.; DARU, B.H.; GREVE, M. Invasive species differ in key functional traits from native and non-invasive alien plant species. **Journal of Vegetation Science**, v. 30, n. 5, p. 994-1006, 2019.

MATESANZ, S.; GIANOLI, E.; VALLADARES, F. Global change and the evolution of phenotypic plasticity in plants. **Annual NY Academic Science**, v. 1206, p. 35–55. 2010.

MATESANZ, S.; HORGAN-KOBELSKI, T.; SULTAN, S.E. Phenotypic plasticity and population differentiation in an ongoing species invasion. **PlosOne**, v. 7, n. 9, p. e44955. 2012.

MCDOWELL, N.G.; ALLEN, C.D. Darcy's law predicts widespread forest mortality under climate warming. **Nature Climate Change**,v. 5, p. 669–672, 2015.

MEDVECKÁ, J., JAROLÍMEK, I., HEGEDÜŠOVÁ, K., ŠKODOVÁ, I., BAZALOVÁ, D., BOTKOVÁ, K., ŠIBÍKOVÁ, M. Forest habitat invasions – Who with whom, where and why. **Forest Ecology and Management**, v. 409, p. 468-478. 2018.

MELITO, M.; ARROYO-RODRÍGUEZ, V.; METZGER, J.P. Landscape forest loss decreases aboveground biomass of Neotropical forests patches in moderately disturbed regions. **Landscape Ecology**, v. 36, p. 439–453, 2021.

MONTY, A.; BIZOUX, J.P.; ESCARRÉ, J.; MAHY, G. Rapid plant invasion in distinct climates involves different sources of phenotypic variation. **PlosOne**, v. 8, n. 1, p. e55627. 2013.

MOODLEY, D.; GEERTS, S.; RICHARDSON, D.M.; WILSON, J.R.U. Different Traits Determine Introduction, Naturalization and Invasion Success in Woody Plants: Proteaceae as a Test Case. **PLoS ONE**, v. 8, p. 1–8, 2013.

MYERS, N.; MITTERMEIER, R.A.; MITTERMEIER, C.G.; DA FONSECA, G.A.; KENT, J. Biodiversity hotspots for conservation priorities. **Nature**, v. 403, n. 6772, p. 853-858, 2000.

OHASHI, S.T.; LEÃO, N.V.M. Morototó *Schefflera morototoni* (Aubl.) Maguire, Steyern. & Frodin. **Informativo Técnico Rede de Sementes da Amazônia**, n. 12. 2005.

OHLEMÜLLER, R.; WALKER, S.; BASTOW WILSON, J. Local vs regional factors as determinants of the invasibility of indigenous forest fragments by alien plant species. **Oikos**, 112(3), 493-501, 2006.

ORTEGA, Y.K.; PEARSON, D.E. Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. **Ecological Applications**, v. 15, p. 651–661. 2005

PADMANABA, M.; SHEIL, D. Spread of the invasive alien species *Piper aduncum* via logging roads in Borneo. **Tropical Conservation Science**, v. 7, n. 1, p. 35-44, 2014.

PERGLOVA, I.; PERGL, J.; SKALOVA, H.; MORAVCOVA, L.; JAROŠÍK, V.; PYŠEK, P. Differences in germination and seedling establishment of alien and native Impatiens species. **Preslia**, v. 81, n. 4, p. 357-375, 2009.

PLUNKETT, G.M., LOWRY II, P.P., FRODIN DG, WEN J. Phylogeny and geography of *Schefflera*: Pervasive polyphyly in the largest genus of Araliaceae. **Annual Missouri Botanical Garden**, 92, p. 202–224, 2005.

PLUNKETT, G.M., LOWRY II, P.P., FIASCHI, P., FRODIN, D.G., NICOLAS, A.N. Phylogeny, biogeography, and morphological evolution among and within the Neotropical and Asian clades of *Schefflera* (Araliaceae). **Taxon,** 68, p. 1278–1313, 2019.

POORTER, L. Growth responses of 15 rain forest tree species to a light gradient: The relative importance of morphological and physiological traits. **Functional Ecology**, v. 13, p. 396–410. 1999.

PORTÉ, A.J.; LAMARQUE, L.J.; LORTIE, C.J.; MICHALET, R.; DELZON, S. Invasive *Acer negundo* outperforms native species in non-limiting resource environments due to its higher phenotypic plasticity. **BMC ecology**, v. 11, p. 1-13, 2011.

PYSEK, P.; BACHER, S.; KUHN, I.; NOVOA, A.; CATFORD, J.A.; HULME, P.E.; PERGL, J.; RICHARDSON, D.M.; WILSON, J.R.U.; BLACKBURN, T.M. Macroecological Framework for invasive aliens (MAFIA): disentangling large-scale context dependence in biological invasions. **NeoBiota**, v. 62, p. 407-461. 2020.

REJMÁNEK, M. Invasive tree and shrubs: wher do they como from and what we should expect in the future? **Biological Invasions**, v. 16, p. 483-498. 2014.

RICHARDSON, D.M.; PYŠEK, P.; REJMANEK, M.; BARBOUR, M.G.; PANETTA, F.D.; WEST, C.J. Naturalization and invasion of alien plants: concepts and definitions**. Diversity and Distributions**, v. 6, p. 93–107. 2000.

ROWLAND, L.; DA COSTA, A.C.L.; GALBRAITH, D.R.; OLIVEIRA, R.S.; BINKS, O.J.; OLIVEIRA, A.A.; MEIR, P. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. **Nature**, v. 528, p. 119–122, 2015.

SEEBENS, H.; BLACKBURN, T. M.; DYER, E. E.; GENOVESI, P.; HULME, P. E.; JESCHKE, J. M.; ESSL, F. No saturation in the accumulation of alien species worldwide. **Nature Communications**, v. 8, n. 1, p. 14435, 2017.

SENDALL, K.M.; LUSK, C.H.; REICH, P.B. Trade-offs in juvenile growth potential vs.Shade tolerance among subtropical rain forest trees on soils of contrasting fertility. **Functional Ecology**, v. 30, n. 6, p. 845–855. 2016.

SHI, J.; LUO, Y.Q.; ZHOU, F.; HE, P. The relationship between invasive alien species and main climatic zones. **Biodiversity and Conservation**, v. 19, p. 2485-2500, 2010.

SKÁLOVÁ, H., HAVLÍČKOVÁ, V., PYŠEK, P. Seedling traits, plasticity and local differentiation as strategies of invasive species of *Impatiens* in central Europe. **Annals of Botany**, v. 110, p. 1429–1438. 2012.
SOMMER, U.; PADISAK, J.; REYNOLDS, C.S.; PUHÁSZ-NAGY, P. Hutchinson' heritage: the diversity-disturbance relationship in phytoplankton. **Hydrobiologia**, v. 249, p. 1–7. 1993.

SPEAR, D., FOXCROFT, L.C., BEZUIDENHOUT, H., MCGEOCH, M.A. Human population density explains alien species richness in protected areas. **Biological Conservation**, v. 159, p. 137-147. 2013.

STANDISH, R.J.; ROBERTSON, A.W.; WILLIAMS, P.A. The impact of an invasive weed *Tradescantia fluminensis* on native forest regeneration. **Journal of Applied Ecology**, v. 38, n. 6, p. 1253-63. 2001.

STRICKER, K.; STILING, P. Seedlings of the introduced invasive shrub *Eugenia uniflora* (Myrtaceae) outperform those of its native and introduced non-invasive congeners in Florida. **Biological invasions**, v. 15, p. 1973-1987, 2013.

TAUBERT, F.; FISCHER, R.; GROENEVELD, J.; LEHMANN, S.; MULLER, M.S.; RODIG E.; WIEGAND T.; HUTH, A. Global patterns of tropical forest fragmentation. **Nature**, v. 554, p. 519–522. 2018.

TAYLOR, K.; BRUMMER, T.; TAPER, M.L.; WING, A.; REW, L.J. Human-mediated long-distance dispersal: An empirical evaluation of seed dispersal by vehicles. **Diversity and Distributions**, v. 18, p. 942–951. 2012.

THUILLER W.; RICHARDSON D.; PYSEK P.; et al. Niche-based modeling as a tool for predicting the risk of alien plant invasions at a global scale. **Global Change Biology**, v. 11, p. 2234–50. 2005.

VAN KLEUNEN, M.; WEBER, E.; FISCHER, M. A meta-analysis of trait differences between invasive and non invasive plant species. **Ecology Letters**, v. 13, n. 2, p. 235–245. 2010.

VELDMAN, J.W.; PUTZ, F.E. Long-distance dispersal of invasive grasses by logging vehicles in a tropical dry forest. **Biotropica**, v. 42, n. 6, p. 697-703, 2010.

VICENTE, J.; ALVES, P.; RANDIN, C.; GUISAN, A.; HONRADO, J. What drives invasibility? A multi-model inference test and spatial modelling of alien plant species richness patterns in northern Portugal. **Ecography**, v. 33, n. 6, p.1081-1092. 2010.

VILÀ, M.; PINO, J.; FONT, X. Regional assessment of plant invasions across different habitat types. **Journal of Vegetation Science**, v. 18, n. 1, p. 35–42. 2007.

VILA, M.; SIAMANTZIOURAS, A.D.; BRUNDU, G.; et al. Widespread resistance of Mediterranean island ecosystems to the establishment of three alien species. **Diversity and Distribuitions**, v. 14, p. 839–51. 2008.

VILARINHO, M.K.; SALES, V.H.; NASCIMENTO, J.; CALDEIRA, D.; SOUZA, W. Quebra de dormência em sementes de *Schefflera morototoni* (Aubl.) Maguire et al. **Enciclopédia Biosfera**, v. 16, n. 29. 2019.
VON DER LIPPE, M.; BULLOCK, J.M.; KOWARIK, I.; KNOPP, T.; WICHMANN, M. Human-mediated dispersal of seeds by the airflow of vehicles. **PLoS One**, v. 8, n. 1, p. 1–10. 2013.

WASSENAAR, T.; GERBER, P.; VERBURG, P.H.; ROSALES, M.; IBRAHIM, M.; STEINFELD, H. Projecting land use changes in the Neotropics: The geography of pasture expansion into forest. **Global Environmental Change**, v. 17, p. 86-104, 2007.

YU, H.W.; HE, W.M. Congeneric invasive versus native plants utilize similar inorganic nitrogen forms but have disparate use efficiencies. **Journal of Plant Ecology**, v. 14, n. 2, p. 180-190, 2021.

CAPÍTULO 1

Factors explaining species richness of invasive plants in Neotropical forests

Original article

Factors explaining species richness of invasive plants in Neotropical forests

Amanda Angélica Carmes[1,*] (Orcid ID: http://orcid.org/0000-0002-0766-9845)

Rafael Barbizan Sühs[2] (Orcid ID: https://orcid.org/0000-0001-5921-7181)

Gabriela Moraes da Silva[3] (https://orcid.org/0009-0009-4431-593X)

Pedro Fiaschi[4] (Orcid ID: https://orcid.org/0000-0002-5457-6369)

Michele de Sá Dechoum[2,3] (Orcid ID: http://orcid.org/0000-0002-3484-2498)

[1] Universidade Federal de Santa Catarina, Programa de Pós-Graduação em Biologia de Fungos, Algas e Plantas, Campus Universitário Reitor João David Ferreira Lima, Trindade, 88040-900, Florianópolis, Santa Catarina, Brazil.

[2] Universidade Federal de Santa Catarina, Departamento de Ecologia e Zoologia, Programa de Pós-Graduação em Ecologia, Campus Universitário Reitor João David Ferreira Lima, Trindade, 88040-900, Florianópolis, Santa Catarina, 88040-900, Brazil

[3] Universidade Federal de Santa Catarina, Departamento de Ecologia e Zoologia, Centro de Ciências Biológicas, Campus Universitário Reitor João David Ferreira Lima, Trindade, 88040-900, Florianópolis, Santa Catarina, 88040-900, Brazil

[4] Universidade Federal de Santa Catarina, Departamento de Botânica, Campus Universitário Reitor João David Ferreira Lima, Trindade, 88040-900, Florianópolis, Santa Catarina, Brazil.

[*] Corresponding author: amandacarmes@hotmail.com

Abstract

Despite the biological relevance of tropical forests, increasing pressure from human activities in tropical regions has led to the introduction of invasive non-native plants. However, much of the scarce literature about plant invasions in tropical forests places a greater emphasis on Old World forests as well as on grasses, while Neotropical forests are neglected in the scientific literature. To fill this gap, we aimed to understand patterns of woody invaders in forest ecosystems in neotropical forests as well as to identify the factors that explain the richness of invasive non-native woody plants in neotropical forests with different levels of leaf deciduousness. We conducted a systematic review of floristic surveys in neotropical forests. Climate, environmental, and anthropogenic variables were obtained for the surveyed sites across the Neotropics. The richness of invasive non-native plants increased with higher temperature seasonality, accessibility, and per capita Gross Domestic Product, and decreased with the increase of canopy cover. In synthesis, higher temperature seasonality and accessibility positively affected invasive non-native plant richness. Closed canopy forests do not limit the occurrence of some invasive non-native plants. In addition, aside from growing human pressure from deforestation and climate change, neotropical forests are subject to natural disturbance that contributes to invasive species richness, further increasing the susceptibility of these ecosystems to plant invasions.

Keywords: The Caribbean, Central America, deciduousness, forest invasion, South America, systematic review, tropical forest, woody invaders

Introduction

Climatic variables are important filters for the establishment of non-native species. Positive relationships between temperature and precipitation and invasive plant richness were shown in a global review (Shi et al. 2010). In this study, climates with a mean annual temperature between 17 and 25°C and mean annual precipitation of 1,500 mm seem to provide ideal conditions for higher invasive plant richness. Such conditions are found in humid tropical climates. Other studies demonstrated that mild temperature regions often present a higher richness of invasive non-native plants (Ohlemüller et al. 2006; Marini et al. 2012; Gallardo & Vilà 2019).

Human influence, however, can change or override climatic variables. For example, biomes characterized by limiting environmental conditions, such as periods of rain scarcity, may host higher invasive non-native species richness when in proximity to areas densely populated (Spear et al. 2013; Dimitrakopoulos et al. 2017). In addition, human-modified habitats function both as sources of disturbance (Dimitrakopoulos et al. 2017) and of introduction and spread of invasive non-native species propagules (Vilà et al. 2007; Vicente et al. 2010; Essl et al. 2019).

Socioeconomic variables that indicate the existence of human activities, such as *per capita* gross domestic product (GDP), a high proportion of land use for agriculture, and population density, are positively related to the presence and/or richness of non-native invasive species in non-urbanized areas worldwide (Essl et al. 2019). Anthropogenic disturbance promotes increases in the richness and abundance of invasive plants in tropical forests, including grasses (*e.g. Megathyrsus maximus*, *Urochloa brizantha*) and trees (*Artocarpus heteroplyllus*) (Abreu & Rodrigues 2010; Veldman & Putz 2011). In temperate regions, roads function as pathways that allow invasive non-native species to reach adjacent natural areas (Joly et al.

2011; Lemke et al. 2019), as vehicles are long-distance vectors of propagule spread despite the lack of specific adaptations in seeds or fruits for dispersal in this way (Taylor et al. 2012; Von der Lippe et al. 2013; Lemke et al. 2019). Studies showing the influence of roads on the spread of invasive non-native plants in tropical forests are scarce (Döbert et al. 2018 - but see Padmanaba & Sheil 2014; Veldman & Putz 2010). Furthermore, human occupation in forest regions often leads to fragmentation and gap formation, resulting in changes in local environmental conditions. The increase in light availability due to forest degradation is one of the factors that explains the higher number of invasive non-native species along forest edges or in forest gaps compared with the forest interior (Laurance et al. 2002; Green et al. 2004).

In addition to anthropogenic disturbances, forests are also affected by natural disturbance such as gap openings caused by falling trees and branches. These stochastic events may or may not be combined with deterministic events associated with deciduousness cycles (Gandolfi et al. 2007; 2009). Stochastic and deterministic gaps both play an important role in maintaining native species richness in these ecosystems, as light conditions under the canopy create microhabitats that function as filters in the establishment of regenerating plants (Gandolfi et al. 2007; 2009). The dynamics of canopy openness in forests may also, however, be an important factor affecting the arrival and establishment of non-native invasive plants (Spear et al. 2013; Dechoum et al. 2015), as dense forest canopies not only reduce the incidence of light but act as physical barriers to the entry of propagules (Hansen & Clevenger 2005).

Tropical forests are historically considered less susceptible to invasion than tropical open ecosystems or temperate forests (Rejmánek 1996; Teo et al. 2003). This perception is due to few studies documenting biological invasions in these regions and a recent history of species introductions and habitat loss compared with temperate forests (Denslow & DeWalt 2008; Chong et al. 2021). Additionally, low light availability may be a limiting factor for the establishment of non-native invasive species, although some of them can establish and survive in the understory (Fine 2002; Martin et al. 2009; Dechoum et al. 2015). Deciduousness in tropical forests varies with climatic characteristics (Pennington & Lavin 2016). Some closed-canopy forests occur in humid climates (Fine et al. 2005), while seasonal forests are found in areas with extended dry periods in tropical or subtropical regions characterized by low temperatures in winter (Malhi et al. 2009).

The Neotropical region comprises the area from the south of South America to the central region of Mexico, including moist and dry broadleaf forests, grasslands and savannas, deserts and xeric shrublands (Olson et al. 2001). It harbors the highest richness of animal and plant species on the planet, as well harbors five of the world's 24 biodiversity hotspots (Myers et al. 2000). Neotropical forests have been negatively impacted by anthropogenic disturbances, such as deforestation, fire, and biological invasions, as well as by the combined effects of these factors and climate change (extended drought periods, increase in temperature) (*e.g.* Carvalho et al. 2001; Rowland et al. 2015; Gomes et al. 2019; Faria et al. 2021). The Neotropics are one of the fastest developing areas in the world, with over 81% of the population living in urban areas, and one of the highest global rates of forest conversion to pasture/monoculture (Wassenaar et al. 2007; Curtis et al. 2022). Anthropogenic disturbance is reported as one of the major determinants for the establishment and invasion by invasive non-native species in both tropical and temperate natural areas (Brooks 2007; Vicente et al. 2010).

This study aimed to fill a knowledge gap resulting from the underrepresentation of invasion biology studies in tropical and subtropical forests, especially in the neotropics. The scarce literature on plant invasions in tropical forests places a greater emphasis on Old World forests (Africa and Asia) as well as on herbaceous species (grasses) (Fine et al. 2002; Chong et al. 2021). This study is the first focused on patterns of woody invaders in Neotropical forests. Our main aim was to uncover the factors (anthropogenic, climatic, and environmental) that explain the presence of invasive non-native plants in neotropical forests with different levels of deciduousness. In other words, the questions guiding this study were: which anthropogenic, climatic, and environmental factors best explain the richness of invasive non-native woody plants in different types of neotropical forests?

Material and methods

Data search and selection criteria

We conducted a systematic review of floristic surveys carried out in neotropical forests between 1945 and 2019 using the *Web of Science* database. The terms used in the search were combined for (a) study type: *floristic* OR *phytosociology* OR *flora* AND; (b) forest type: *deciduous forest* OR *semideciduous forest* OR *evergreen forest* OR *rain forest* AND; (c) country where the study was carried out: *Argentina* OR *Belize* OR *Bolivia* OR *Brazil* OR *Chile* OR *Colombia* OR *Cuba* OR *Costa Rica* OR *Dominican Republic* OR *Ecuador* OR *El Salvador* OR *French Guiana* OR *Guatemala* OR *Guyana* OR *Haiti* OR *Honduras* OR *Jamaica* OR *Mexico* OR *Nicaragua* OR *Panama* OR *Paraguay* OR *Peru* OR *Puerto Rico* OR *Suriname* OR *Trinidad and Tobago* OR *Uruguay* OR *Venezuela*. The search terms had to appear in the publication title, abstract, or keywords.

The mention of invasive non-native shrubs or trees in the articles was verified by a search for the words exotic, non-native, non-indigenous, invasive, alien, naturalized throughout the text. In the absence of such words, a search of the species lists was conducted to verify whether the species were non-native and invasive or native in the region where the survey was carried out. Global and national databases were used to verify this information (CABI - Invasive Species Compendium 2020; GISD - Global Invasive Species Database 2020; I3N - Brazil National Invasive Alien Species Database Base 2020; CONABIO - Mexico

Commission for the Knowledge and Use of Biodiversity 2020). Author names for the species listed (Supplementary Table 2) were checked on The Plant List (2020). The names of the invasive non-native species were checked on World Flora Online (WFO 2019).

We considered the articles that mentioned the size of the sampling area and complete species lists. The data obtained from these articles were coordinates of the sampling sites, sampling area (in hectares), number of invasive non-native species, and total number of species recorded.

Articles covering more than one site, more than 5 km apart, with separate species lists for each site, were considered as individual surveys. Articles with surveys in more than one site that did not provide separate species lists were discarded. The location of the sampling area in articles with more than one sampling site less than 5km apart was marked as the centroid of the group of sampling areas. The centroid was calculated using QGIS *Development Team* software (2020).

Explanatory variables – climatic, environmental and anthropogenic

Based on the coordinates of the sampling sites we defined eight climatic variables (mean annual temperature, temperature seasonality, maximum temperature of the hottest month, minimum temperature of the coldest month, annual rainfall, rainfall of the wettest month, rainfall of the driest month, rainfall seasonality); two environmental variables (canopy cover; relative range of normalized difference vegetation index - NDVI); and seven anthropogenic variables (accessibility, population density, index of human influence, Gross Domestic Product *per capita* (GDP), parity of purchasing power – GDP-PPP, human development index - HDI, and night light development index - NLDI) (Table 1). The variables were obtained from matrix files (raster) available from global databases. The QGIS software was used to delimit a 1 km-radius buffer for the geographic coordinates of each sampling site or the centroid of each group of sampling sites. The mean of pixel values was obtained within each buffer for each vectorial/raster layer used.

Environmental variables

Climate variables were obtained considering monthly averaged data from 1970 to 2000 (Fick & Hijmans 2017). Canopy cover refers to the density of soil cover by the crowns of trees higher than 5 m in the sampling area in the year 2000 (Hansen et al. 2013). The normalized difference vegetation index (NDVI) is an indicator of photosynthetically active biomass on each site and can show changes in canopy cover due to climate seasonality (Alcaraz-Segura et al. 2009). A possible limitation of using this variable is the impossibility of determining whether the canopy cover variation occurred due to leaf deciduousness or due to deforestation. The NDVI values computed for each article refer to the RREL-NDVI (Relative Range of NDVI), which maintains the biological significance of NDVI variation between the dry and rainy seasons but is standardized using the average between these seasons (Alcaraz-Segura et al. 2006; 2009). High RREL-NDVI values indicate a higher degree of change in the canopy between seasons, while low RREL-NDVI values indicate a low change in the canopy between seasons. We used the geographic coordinates where each study was conducted to obtain the NDVI value for that specific location. We used NASA's Application for Extracting and Exploring Analysis Ready Samples (AppEEARS 2023) to obtain a sample for each geographic coordinate over a 20-year timespan (2002-2022). The months of December, January, February and June, July, August were used to represent seasonal variation. We only kept pixels tagged as 'high quality', with low aerosol quantity. Additionally, pixels with NDVI values less than 0.2 were discarded since they are unlikely to reflect vegetation.

Anthropogenic variables

Accessibility refers to travel time (in minutes) by land (roads) or water (navigable rivers or ocean) to the nearest city with more than 50,000 inhabitants (Nelson 2008). It is derived from a distance algorithm that calculates the cost of travelling between two areas on a raster – the "cost" measured in time. The accessibility map developed by Nelson (2008) is available from the *Forest Resources and Carbon Emissions* website (IFORCE 2021).

Population density refers to the estimate of human habitation (number of persons per km^2) based on national censuses and population records for the year 2010 (CIESIN 2020a). The Global Human Influence Index (HII) measures human influence on terrestrial ecosystems. It was developed using raster files of human settlements (population density, built-up area), accessibility (roads, railroads, navigable rivers, access to the ocean), land-use change (land use and cover), and energy infrastructure (night lights). HII values vary between 0 and 64, with values close to zero indicating low human influence, and values close to 64 indicating high human influence (CIESIN 2020b). The data used refer to the year 2005.

GDP *per capita* (gross domestic product) represents the mean *per capita* production per year in a specific administrative unit (base year 2015) in billions of US dollars, *i.e.*, it is a measure of economic performance (Bregar et al. 2008; Kummu et al. 2020). The parity of purchasing power (GDP-PPP) is calculated from the dollar purchasing power of each country and takes into consideration the cost of living and inflation rate (Bregar et al. 2008; Kummu et al. 2020). The human development index (HDI) measures basic human development calculated from health, education, and income data based on the year 2015. This index varies between 0 and 1, with values ≥ 0.8 in regions with high development, 0.8 to 0.5 with moderate development, and ≤ 0.5 with low human development (PNUD 2012).

The measure of night lights refers to the year 2013 and represents lights in cities and other areas with constant artificial illumination. Short-lived events such as fires are not considered (NOAA - *National Centers for Environmental Information* 2020). The data are derived from an aggregation of pixels – a number varying from 1 (dark spot) to 63 (light spot) is attributed to each pixel (Addison & Stewart 2015). This variable is positively correlated with the degree of urbanization, which is estimated from population density and GDP (Mellander et al. 2013).

The raster and vector files were obtained from the global databases *WorldClim* (bio1, bio4, bio5, bio6, bio12, bio13, bio14, bio15) (Fick & Hijmans 2017), *Global Forest Watch* (forest cover) (Hansen et al. 2013), *Earth Resources Observation and Science* - EROS (NDVI), *Forest Observation* (accessibility) (Nelson 2008), *Center for International Earth Science Information Network* (population density, human influence index) (CIESINa, CIESINb), NOAA - *National Centers for Environmental Information* (night lights) (NOAA 2020), and *Dryad* (PIB, PIB PPC, IDH) (Kummu et al. 2020).

Data analyses

We built a generalized linear model (GLM) using the proportion of invasive non-native plants in relation to the total number of species recorded at each site to verify which anthropogenic, climatic, and environmental variables influenced the richness of invasive non-native woody plants, and the degree of their impact. Before building the model, collinearity was checked by excluding explanatory variables with variance inflation factor (VIF) >4 (Zuur et al. 2009). As a result, five variables were excluded: mean annual temperature, minimum temperature of the coldest month, rainfall of the wettest month, rainfall of the driest month, and night lights. Therefore, twelve explanatory variables were used in the full model (Table 1). The full model underwent a backward simplification process in which we eliminated non-significant variables progressively, one at a time, until a final model containing only significant variables was achieved. This stepwise approach allowed for a more focused and interpretable model, as it removed variables that did not contribute significantly to the predictive power of the model. By iteratively assessing the statistical significance of each variable and discarding those with negligible impact, the resulting simplified GLM captured the essential relationships between the dependent and independent variables, providing a clearer understanding of the underlying dynamics influencing the outcome of interest. We assumed a binomial distribution once the response variable varied between 0 and 1, *i.e.,* it represents the proportion of non-native species in relation to the total number of species recorded at each site. As the sampling area varied in each study, we used the sampling area as an offset term in the models (log transformed to correspond to the scale of the response variable). The model was validated using residual diagnostics through a simulation-based approach. We used Nagelkerke's R^2 (Nagelkerke 1991) to verify the goodness of fit of the final model. An analysis of dominance was conducted to verify the relative importance of variables in the final model (Azen & Traxel 2009). The analyses were conducted in R software (R Development Core Team 2014) using the packages "*car*" (Fox & Weisberg 2019) to verify variable collinearity, "*DHARMa*" (Hartig 2021) for model validation, "*visreg*" (Breheny & Burchett 2017) to view the relation between explanatory variables in the response variable, and "*dominanceanalysis*" (Navarrete & Soares 2020) for analysis of dominance.

Table 1. Climatic, environmental, and anthropogenic variables obtained for each sampling area in each study. Variables in bold were used to build the models after the variance inflation factor (VIF) was calculated. Resolution: measure of pixel size (Unit: kilometers).

Variables	**Variable type**	**Resolution**	**Unit**

Climatic			
bio1: Mean annual temperature	Raster	0.9	°C
bio4: Temperature seasonality	Raster	0.9	SD annual temp. x 100
bio5: Maximum temperature of the hottest month	Raster	0.9	°C
bio6: Minimum temperature of the coldest month	Raster	0.9	°C
bio12: Annual precipitation	Raster	0.9	Millimeters
bio13: Rainfall of the wettest month	Raster	0.9	Millimeters
bio14: Rainfall of the driest month	Raster	0.9	Millimeters
bio15: Rainfall seasonality	Raster	0.9	Coefficient of variation
Environmental			
Canopy cover	Raster	0.03	Percentage (%)
RREL– NDVI	Raster	0.25	Index (-1 to 1)
Anthropogenic			
Accessibility	Raster	0.9	Minutes
Population density	Raster	0.9	People/km²
Human development index – HDI	Raster	10	Index (0-1)
Human influence index – HII	Raster	0.9	Index (0-64)
***Per capita* GDP**	Raster	10	Billion US$/2011
GDP (PPC)	Raster	10	Billion US$/2011
Night lights	Raster	0.9	Index (1-63)

Results

We found 1,116 articles published between 1988 and 2019, of which 97 (Fig. 1, Supplementary Table 1) were selected for our analyses. Therefore, the total number of sites considered for this study was 121 (Fig. 1, Supplementary Table 1).

Among the 1,019 articles discarded, 140 focused on other biological groups (109 on animals, 18 on bryophytes, five on lichens, four on fungi, three on algae, and one on cyanobacteria); 313 articles focused on vascular plants but did not contain floristic data; 348 articles on floristic surveys did not provide complete species lists, but only the list of species with higher importance values, or did not indicate the size of the sampling area; 113 articles were reviews (used other floristic studies or databases to compile species lists); and 123 floristic survey articles focused on non-forest vegetation types.

Thirty-two (26.6%) of the 121 sites contained at least one invasive non-native woody plant species. A list of 23 invasive non-native woody plant species was compiled from the articles reviewed (17 trees and six shrubs) (Supplementary Table 2).

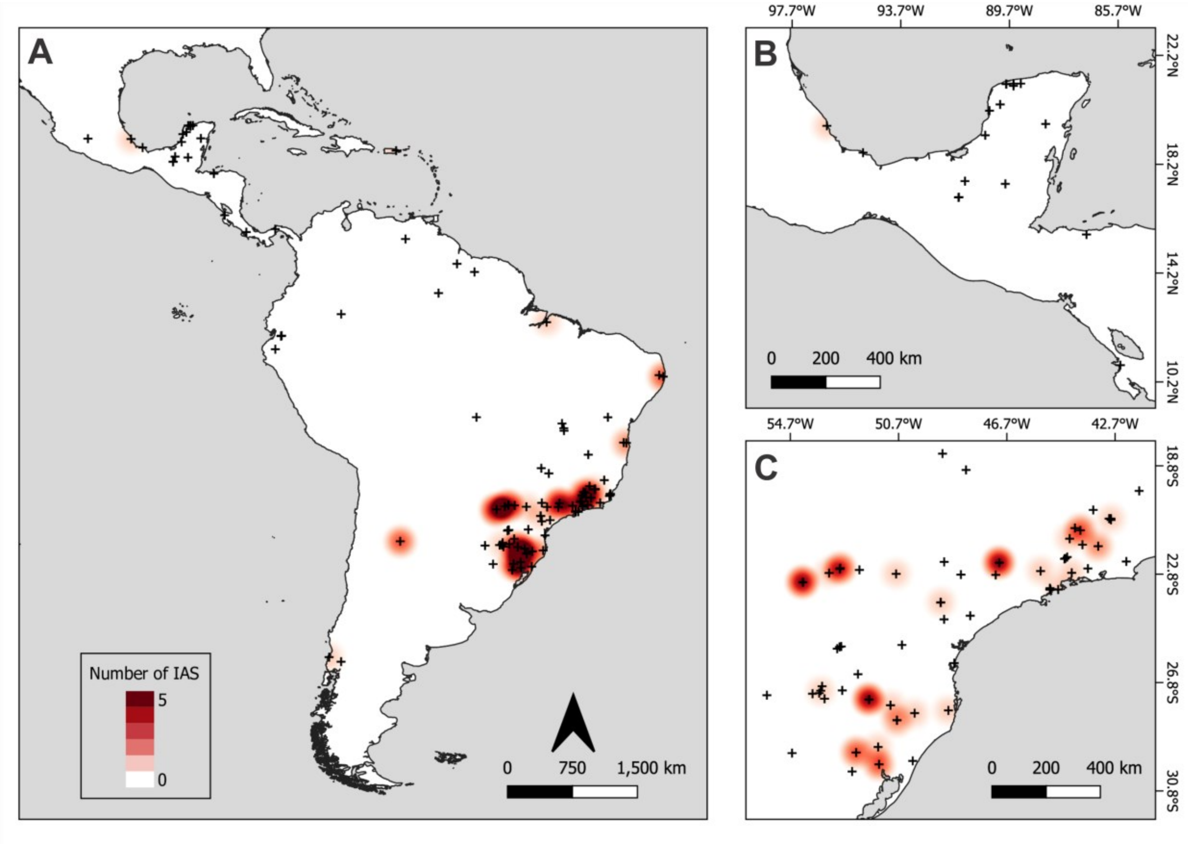

Figure 1. Heatmap representing the Neotropical region, with the location of the 114 sites considered in our study. Darker regions indicate recording of a greater number of invasive non-native woody plants. Figures B and C are an enlargement of the image (A) to better visualize Central America and southern South America, respectively.

Which anthropogenic, climatic, and environmental factors best explain the richness of invasive non-native woody plants in different types of neotropical forests?

The final model that explained the proportion of invasive non-native woody plants in relation to the total number of species contained four variables: accessibility, canopy cover, GDP *per capita*, and temperature seasonality (Table 2). The model residues were adequate. The final model explained 49% of data variation ($R^2_{Nagelkerke} = 0.49$).

Table 2. Result of the relation between explanatory variables of the model selected and their influence on the response variable. General contributions were calculated using Nagelkerke's pseudo R². Significant *p* values are in bold.

Explanatory variable	**Estimate**	**Std. Error**	**z**	***p***	**General contribution**
Temperature seasonality	$7.914e^{-3}$	$1.465e^{-3}$	5.40	< **0.001**	0.20
Canopy cover	$-3.506e^{-2}$	$5.513e^{-3}$	-6.36	< **0.001**	0.09
Per capita GDP	$9.665e^{-10}$	$1.782e^{-10}$	5.42	< **0.001**	0.04
Accessibility	$-6.256e^{-3}$	$2.111e^{-3}$	-2.96	**0.003**	0.16

The results of the dominance analysis showed that temperature seasonality and accessibility were the variables with higher general dominance in the final model, explaining 20% and 16% of data variation, respectively (Table 2). The variables canopy cover and GDP *per capita* explained 9% and 4% of data variation respectively (Table 2).

The proportion of invasive non-native species increased with higher temperature seasonality (temperature variation throughout the year) and GDP *per capita* (Figs. 2A and 2C, respectively; Tab. 2). On the other hand, the proportion of invasive non-native species decreased with increasing canopy cover and decreasing accessibility (distance to urban areas with more than 50,000 inhabitants) (Figs. 2B and 2D, respectively).

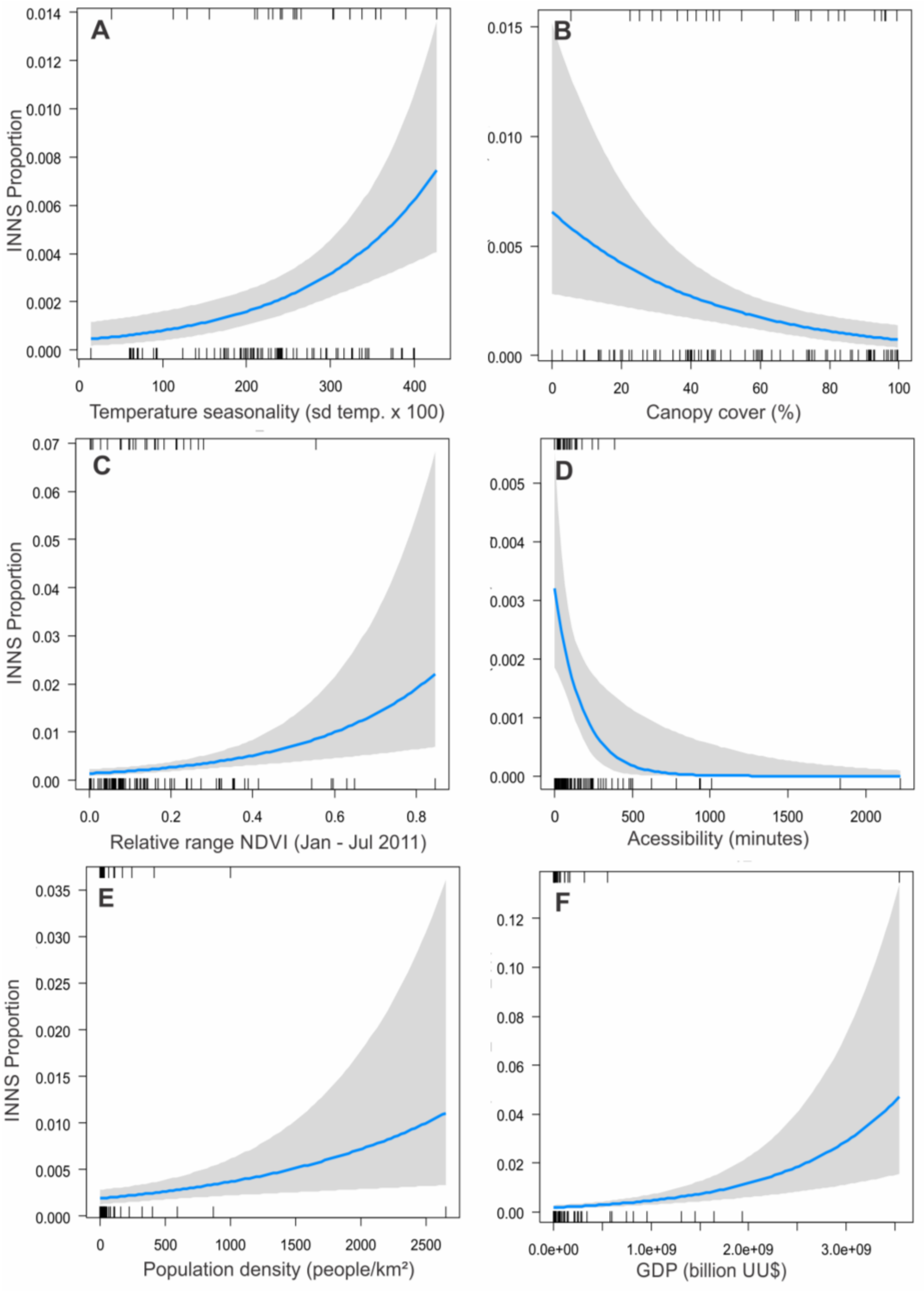

Figure 2. Proportion of invasive non-native species (INNS) in relation to temperature seasonality, canopy cover, relative range NDVI, accessibility, population density, and GDP in neotropical forests. The blue line represents the linear adjustment of the selected model, the shaded areas represent the 95% confidence interval of the adjustment. Ticks at the bottom of each figure represent the frequency of studies in which the proportion of non-native species

(INNS) was = 0; ticks on the superior part of each figure represent the frequency of studies in which the proportion of non-native species (INNS) was ≠ 0.

Discussion

Climatic (Temperature seasonality), environmental (Forest cover), and anthropogenic (Accessibility, Gross Domestic Product *per capita* - GDP) factors explained the proportion of richness of invasive non-native woody plants in neotropical forests with different deciduousness levels. Richness of invasive non-native plants increased with higher temperature seasonality, accessibility, and Gross Domestic Product *per capita* (GDP), and decreased with the increase of canopy cover. Temperature seasonality and accessibility had the most significant effect on data variation.

Which anthropogenic, climatic, and environmental factors best explain the richness of invasive non-native woody plants in different types of neotropical forests?

There is a higher proportion of invasive non-native woody plants in areas with higher temperature variations throughout the year (higher seasonality). Higher temperature seasonality is common in subtropical regions, where the mean annual temperature may vary between 20° and 35 °C (Meteoblue 2021). In these regions, deciduousness in seasonal forests is due to cold winters (monthly mean ≤ 15 °C) determining partial foliage loss by some tree species. Higher temperature seasonality contributes to providing competitive advantages to invasive plants over native species (Castro et al. 2021). For example, in subtropical climates in the Neotropical region, some invasive non-native grasses and herbs such as *Arundo donax* L. and *Tradescantia zebrina* Bosse grow faster or increase seed germination rates when temperatures start to drop, in early autumn, at the time when native species reduce metabolic processes (Decruyenaere & Holt 2005; Castro et al. 2021). Therefore, conditions provoked by lower temperatures, such as lower rates of competition for resources and herbivore pressure (Mari & Galassin 2010; Castro et al. 2021), are potential explanations for the higher proportion of invasive non-native species in areas with higher temperature seasonality. Additionally, partial foliage loss by some species during cold winters in subtropical decidual forests leads to the formation of clearings that facilitate the arrival and establishment of invasive non-native plants (Spear et al. 2013; Dechoum et al. 2015).

The richness of invasive non-native woody plants was higher in areas of greater accessibility (*i.e.*, closer to cities) and in areas with elevated *per capita* Gross Domestic Product. This result shows the importance of anthropogenic influence on the increase of invasive plant richness, corroborating research that showed how invasive plant richness was higher in more densely populated areas, along roads, or in areas with higher GDP (*e.g.* Spear et al. 2013; Dimitrakopoulos et al. 2017; Essl et al. 2019; Galardo & Vilà 2019; Mungi et al. 2021). Areas closer to cities or roads are also more prone to the arrival of propagules (Veldmam & Putz 2010; 2011; Padmanaba & Sheil 2014; Davis et al. 2016; Galardo & Vilà 2019). Several studies have shown that the likelihood of occurrence of invasive non-native species increases with the proximity to propagule sources. For example, widely commercialized species used for ornamental purposes in residential areas may be dispersed to adjacent areas by animals as in the case of *Ligustrum sinensis* and *Heptapleurum arboricola*, (Davis et al. 2016; Padayachee et al. 2017; Marciniak et al. 2020), or by wind, such as *Quercus rubra* (Woziwoda et al. 2018).

Proximity to roads is also an efficient dispersal pathway to surrounding natural tropical areas, as large amounts of propagules can be transported long distances adhered to tyres or through the flux of air generated by vehicles (Veldmam & Putz 2010; Padmanaba & Sheil 2014). Road margins also function as habitats for invasive non-native plants as disturbance favours the establishment of many species (Joly et al. 2011). The absence of trees or shrubs along roads due to disturbance caused by frequent road maintenance generates conditions of lower competition and higher resource availability compared with natural areas (Joly et al. 2011; Speziale et al. 2018; Woziwoda et al. 2018; Khaniya & Sherestha 2020).

Canopy cover also influenced non-native invasive plant richness. The higher the cover, the lower the richness, which corroborates other research on tropical forests in Asia (Khaniya and Shrestha, 2020; Mungi et al., 2021) and Central America (Lopez et al., 2012). This environmental variable might also be related to accessibility/road opening, considering that proximity to roads plays a fundamental role in the opening of areas for exploitation of forest resources, hunting, mining, and deforestation in tropical regions in South America and Asia (Laurence et al., 2002; Wilkie et al., 2000). Moreover, openings in the forest canopy can facilitate the entry of non-native invasive species propagules once the physical barrier posed by the canopy is broken (Joshi et al., 2015). Such clearings are important even for shade-tolerant species which, despite surviving in low light conditions in the forest interior, grow better at higher light rates (Martin et al., 2010; Schuster et al., 2020).

Limitations

The review of floristic surveys conducted for this study highlighted the low inclusion of invasive non-native species in floristic surveys (26.6%). Non-native trees widely acknowledged as invasive in neotropical forests, such as *Pittosporum undulatum, Spathodea campanulata*, and *Syzygium jambos* were not reported in the studies reviewed, suggesting that floristic and phytosociological surveys as well as regional and state flora catalogues choose to omit invasive non-native species from compiled species lists, as pointed out by Moro et al. (2012). We highlight the relevance of including invasive non-native species in floristic survey lists for review studies such as this one and to provide managers with information on their presence in natural areas. Mapping invasive species improves distribution data and helps subsidize management in protected areas and other areas of relevance for biodiversity conservation (Moro et al. 2012).

Conclusions

Due to a higher temperature seasonality, subtropical forests are more susceptible to the establishment of invasive non-native woody plants than tropical forests in the neotropics especially due to an elevated temperature seasonality. Deciduousness in these forests may also favour the arrival of invasive plant propagules due to the decrease in the physical barrier represented by the canopy and to the increase in the incidence of light. Forests with higher accessibility are also more susceptible to invasion by invasive non-native plants because of the roads that facilitate invasive plant dispersion and a possible higher propagule arrival from species under cultivation in the surroundings. Neotropical forests are currently in a critical state of threat from anthropogenic impacts such as habitat loss, forest fragmentation, and climate change. Considering the synergic effects of anthropogenic pressure on the presence/increase of invasive plant richness, an increase in the richness of invasive non-native species is inevitable unless management policies are implemented both at the national and regional/international scales.

Acknowledgements

We thank Fundação de Amparo à Pesquisa de Santa Catarina (FAPESC) for a Doctorate scholarship paid to AAC. PF received financial support from CNPq (Research Productivity Scholarship - Bolsa de Produtividade em Pesquisa – # 310502/2019-5 and PROTAX 22/2020 – # 441445/2020-9) and from FAPESC (Supplement to External Call for Proposals FAPESC

13/2020 – 2021TR389). MSD received financial support from CNPq (Research Productivity Scholarship - Bolsa de Produtividade em Pesquisa – # 302880/2022-4).

Author contributions

AAC, MSD, PF, RBS delineated the study; AAC, RBS and GMS reviewed the articles and derived the variables used in the study; AAC and RBS conducted the analyses; AAC, RBS, PF and MSD wrote the text.

In our study, we conducted a systematic review using secondary data from floristic surveys in Neotropical countries. We thoroughly searched relevant literature published by scientists from the Neotropical region and efforts were made to consider work published in the local languages. In addition to utilizing the data obtained from the articles themselves, we provided, in the supplementary material of this manuscript, the information of all the articles used in the statistical analyses (author names, article titles and year, country and geographic information). We believe that by disseminating the information from these articles, we contribute to the promotion of studies conducted locally, in the Neotropical region. In addition, we will prepare a summary for policy makers with the key messages of the study to increase awareness about the threats posed by plant invasions on Neotropical forests.

Data Availability Statement

Data will be available on the Dryad Digital Repository.

References

Abreu RCR, Rodrigues, PJFP. 2010. Exotic tree *Artocarpus heterophyllus* Lam. (Moraceae) invades the Brazilian Atlantic Rainforest. Rodriguésia 61: 677–688.

Addison DM, Stewart B. 2015. Nighttime lights revisited: the use of nighttime lights data as a proxy for economic variables. World Bank Policy Research Working Paper 7496.

Alcaraz-Segura D, Paruelo JM, Cabello J. 2006. Identification of current ecosystem functional types in the Iberian Peninsula. Global Ecology & Biogeography 15: 200–212.

Alcaraz-Segura D, Cabello J, Paruelo JM, Delibes M. 2009. Use of descriptors of ecosystem functioning for monitoring a national park network: a remote sensing approach. Environmental Management 43: 38–48.

AppEEARS - Application for Extracting and Exploring Analysis Ready Samples. 2023. https://appeears.earthdatacloud.nasa.gov. 10 Nov. 2023.

Azen R, Traxel N. 2009. Using Dominance Analysis to Determine Predictor Importance in Logistic Regression. Journal of Educational and Behavioral Statistics 34(3): 319-347.

Breheny P, Burchett W. 2017. Visualization of Regression Models using visreg. The R Journal 9: 56-71.

Bregar L, Rovan J, Pavsic M. 2008. Vality of GDP per capita for international development comparisons. Economic and Business Review 10(3): 181-195.

Brooks M. 2007. Effects of land management practices on plant invasions in wildland areas. In: Nentwig, W. (ed.), Biological invasions. Springer. p. 147 – 162.

CABI – Invasive species compendium. 2020. Invasive Species Compendium. https://www.cabi.org/isc. 10 May 2020.

Carvalho G, Barros AC, Moutinho P, Nepstad D. 2001. Sensitive development could protect Amazonia instead of destroying it. Nature 409: 131.

Castro WA, Luz RC, Peres CK. 2021. Seasonality and forest edge as drivers of *Tradescantia zebrina* Hort. ex Bosse invasion in the Atlantic Forest. Brazilian Journal of Biology 82.

Chong KY, Corlett RT, Nuñez MA, Chiu JH, Courchamp F, Dawson W, Kuebbing S, Liebhold AM, Souza S, Andersen KM, Fei S, Lee BPY, Lum S, Luskin MS, Ngo KM, Wardle DA. 2021. Are Terrestrial Biological Invasions Different in the Tropics? Annual Review of Ecology, Evolution, and Systematics 52: 291-314.

CIESIN - Center for International Earth Science Information Network (CIESIN), Columbia University and Wildlife Conservation Society. 2020a. Gridded Population of the World, Versão 4 (GPWv4): Population Density, NASA Socioeconomic Data and Applications Center (SEDAC). https://doi.org/10.7927/H49C6VHW. 5 Jun. 2020.

CIESIN - Center for International Earth Science Information Network (CIESIN), Columbia University and Wildlife Conservation Society. 2020b. The Last of the Wild Data set. http://www.sedac.ciesin.columbia.edu/wildareas. 5 Jun. 2020.

CONABIO - Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México. 2020. Sistema de Información sobre Espécies Invasoras. https://www.biodiversidad.gob.mx/especies/Invasoras. 03 Mar. 2020.

Curtis JR, Robinson WD, Rompré G, Austin SH. 2022. Urbanization is associated with unique community simplification among birds in a neotropical landscape. Landscape Ecology: 1-23.

Davis AJ, Singh KK, Thill JC, Meentemeyer RK. 2016. Accounting for residential propagule pressure improves prediction of urban plant invasion. Ecosphere 7(3): e01232.

Dechoum MS, Castellani TT, Zalba SM, Rejmánek M, Peroni N, Tamashiro JY. 2015. Community structure, succession and invasibility in a seasonal deciduous Forest in southern Brazil. Biological Invasions 17(6): 1697-1712.

Decruyenaere JG, Holt JS. 2005. Ramet demography of a clonal invader, *Arundo donax* (Poaceae), in Southern California. Plant and Soil 277(1-2): 41-52.

Denslow JS, DeWalt SJ. 2008. Exotic plant invasions in tropical forests: patterns and hypotheses. In: W.P. Carson, S.A. Schnitzer (eds.), Tropical Forest Community Ecology. Hoboken: Wiley-Blackwell. p. 409–26.

Dimitrakopoulos PG, Koukoulas S, Galanidis A, Delipetrou P, Gounaridis D, Touloumi K, Arianoutsou M. 2017. Factors shaping alien plant species richness spatial patterns across Natura 2000 Special Areas of Conservation of Greece. Science of the Total Environment 601: 461-468.

Döbert TF, Webber BL, Sugau JB, Dickinson KJ, Didham RK. 2018. Logging, exotic plant invasions, and native plant reassembly in a lowland tropical rain forest. Biotropica 50(2): 254-265.

Essl F, Dawson W, Kreft H, Pergl J, Pyšek P, Van Kleunen M, Winter M. 2019. Drivers of the relative richness of naturalized and invasive plant species on Earth. AoB Plants 11(5): plz051.

Faria BL, Staal A, Silva CA, Martin PA, Panday PK, Dantas VL. 2021. Climate change and deforestation increase the vulnerability of Amazonian forests to post-fire grass invasion. Global Ecology and Biogeography 30(12): 2368-2381.

Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37(12): 4302-4315.

Fine PVA. 2002. The invasibility of tropical forests by exotic plants. Journal of Tropical Ecology 18: 687–705.

Fine PVA, Daly DC, Villa Muñoz G, Mesones I, Cameron KM. 2005. The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the western Amazon. Evolution 59: 1464–1478.

Fox J, Weisberg S. 2019. Using car functions in other functions. R package version 0.4.1. http://ftp.zut.edu.pl/dsk0/CRAN/web/packages/car/vignettes/embedding.pdf

Gallardo B, Vilà L. 2019. La influencia humana, clave para entender la Biogeografía de especies invasoras en el Antropoceno. Cuadernos de investigación geográfica/Geographical Research Letters 45: 61-86.

Gandolfi S, Joly CA, Rodrigues RR. 2007. Permeability-impermeability: canopy trees as biodiversity filters. Scientia Agricola 64: 433-438.

Gandolfi S, Joly CA, Leitão-Filho HDF. 2009. "Gaps of deciduousness": cyclical gaps in tropical forests. Scientia Agricola 66: 280-284.

GISD - Global invasive species database. 2020. http://www.issg.org/database. 05 Apr. 2020.

Gomes VHF, Vieira ICG, Salomão RP. 2019. Amazonian tree species threatened by deforestation and climate change. Nature Climate Change 9: 547–553.

Green PT, Lake PS, O'Dowd DJ. 2004. Resistance of island rainforest to invasion by alien plants: influence of microhabitat and herbivory on seedling performance. Biological Invasions 6(1): 1–9.

Hansen MJ, Clevenger AP. 2005. The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. Biological Conservation 125(2): 249–259.

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG. 2013. High Resolution Global Maps of 21st-Century Forest Cover Change. Science 342: 850–53. http://earthenginepartners.appspot.com/science-2013-global-forest.

Hartig F. 2021. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.1. https://CRAN.Rproject.org/package=DHARMa

I3N - Base de dados de espécies exóticas invasoras do Brasil. 2020. Instituto Hórus de Desenvolvimento e Conservação Ambiental, Florianópolis, Santa Catarina. http://bd.institutohorus.org.br/. 10 Feb. 2020.

IFORCE - Forest Resources and carbon emissions. 2021. Travel time to major cities: A global map of Accessibility. https://forobs.jrc.ec.europa.eu/products/gam/. 13 Apr. 2020.

Joly M, Bertrand P, Gbangou RY, White MC, Dubé J, Lavoie C. 2011. Paving the way for invasive species: Road type and the spread of common ragweed (*Ambrosia artemisiifolia*). Environmental Management 48(3): 514–522.

Joshi AA, Mudappa D, Shankar TR. 2015. Invasive alien species in relation to edges and forest structure in tropical rainforest fragments of the Western Ghats. Tropical Ecology 56: 233–44.

Khaniya L, Shrestha BB. 2020. Forest regrowth reduces richness and abundance of invasive alien plant species in community managed *Shorea robusta* forests of central Nepal. Journal of Ecology and Environment 44(1): 1-8.

Kummu M, Taka M, Guillaume JHA. 2020. Gridded global datasets for Gross Domestic Product and Human Development Index over 1990-2015, Dryad, Dataset. https://doi.org/10.5061/dryad.dk1j0. 12 May. 2020.

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurence SG, Sampaio E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation biology 16(3): 605-618.

Lemke A, Kowarik I, Von der Lippe M. 2019. How traffic facilitates population expansion of invasive species along roads: the case of common ragweed in Germany. Journal of applied Ecology 56(2): 413-422.

Lopez OR. 2012. Introduced alien plant species in the Neotropics: the Panama case. The Open Ecology Journal 5(1): 84-89.

Malhi Y, Aragão LEOC, Galbraith D, Huntingford C, Fisher R, Zelazowski P, Sitche S, McSweeney C, Meir P. 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. Proceedings of the National Academy of Sciences 106: 20610–20615.

Marciniak B, De Sa Dechoum M, Castellani TT. 2020. The danger of non-native gardens: risk of invasion by *Schefflera arboricola* associated with seed dispersal by birds. Biological Invasions 22(3): 997-1010.

Mari EK, Galassin ME. 2010. Factores ambientales o herbivoría controlan la emergencia de plántulas en un bosque fluvial del río Paraná. Interciencia 35(8): 605-612.

Marini L, Battisti A, Bona E, Federici G, Martini F, Pautasso M, Hulme PE. 2012. Alien and native plant life-forms respond differently to human and climate pressures. Global ecology and biogeography 21(5): 534-544.

Martin PH, Canham CD, Marks PL. 2009. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Frontiers Ecological Environment 7: 142–149.

Martin P, Canham C, Kobe R. 2010. Divergence from the growth-survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. Journal of Ecology 98: 778–789.

Mellander C, Stolarick K, Matheson Z, Lobo J. 2013. Night-Time Light Data: A Good Proxy Measure for Economic Activity? The Royal Institute of technology Centre of Excellence for Science and Innovation Studies (CESIS), Electronic Working Paper Series Paper: 315.

Meteoblue. 2021. Subtropical zone. https://content.meteoblue.com/en/meteoscool/general-climate-zones/subtropical-zone. 07 Mar. 2021.

Moro MF, Souza VC, Oliveira-Filho ATD, Queiroz LPD, Fraga CND, Rodal MJN, Araújo FS; Martins FR. 2012. Alienígenas na sala: o que fazer com espécies exóticas em trabalhos de taxonomia, florística e fitossociologia? Acta Botanica Brasílica 26: 991-999.

Mungi NA, Qureshi Q, Jhala YV. 2021. Role of species richness and human impacts in resisting invasive species in tropical forests. Journal of Ecology 109(9): 3308-3321.

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403(6772): 853-858.

Nagelkerke NJ. 1991. A note on a general definition of the coefficient of determination. Biometrika 78(3): 691-692.

Navarrete CB, Soares FC. 2020. Dominance analysis: Dominance Analysis. R package version 2.0.0. https://CRAN.R-project.org/package=dominanceanalysis

Nelson A. 2008. Estimated travel time to the nearest city of 50,000 or more people in year 2000. Global Environment Monitoring Unit - Joint Research Centre of the European Commission, Ispra Italy. https://forobs.jrc.ec.europa.eu/products/gam/. 13 Apr. 2020.

NOAA – National centers for environmental information. 2020. Night time Lights time series. https://ngdc.noaa.gov/eog/dmsp/downloadV4composites.html. 15 Apr. 2020.

Ohlemüller R, Walker S, Bastow Wilson J. 2006. Local vs regional factors as determinants of the invasibility of indigenous forest fragments by alien plant species. Oikos 112(3): 493-501.

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR. 2001. Terrestrial ecoregions of the world: A new map of life on Earth. BioScience 51: 933-938.

Padayachee AL, Irlich UM, Faulkner KT, Gaertner M, Procheş Ş, Wilson JR, Rouget M. 2017. How do invasive species travel to and through urban environments? Biological invasions 19(12): 3557-3570.

Padmanaba M, Sheil D. 2014. Spread of the invasive alien species *Piper aduncum* via logging roads in Borneo. Tropical Conservation Science 7(1): 35-44.

Pennington RT, Lavin M. 2016. The contrasting nature of woody plant species in different neotropical forest biomes reflects differences in ecological stability. New Phytologist 210(1): 25-37.

PNUD - Programa das Nações Unidas para o Desenvolvimento. 2012. Desenvolvimento Humano e IDH. http://www.pnud.org.br/IDH/DH.aspx. 10 Mar. 2020.

QGIS Development Team. 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Development Core Team. 2014. R: A language and environment for statistical computing - R Foundation for Statistical Computing. R Project for Statistical Computing. http://www.R-project.org.

Rejmánek M. 1996 Species richness and resistance to invasions. In: Orians G, Dirzo R, Cushman JH (eds.) Biodiversity and Ecosystem Processes in Tropical Forests. Berlin/Heidelberg: Springer-Verlag. p. 153–72.

Rowland L, Da Costa ACL, Galbraith DR, Oliveira RS, Binks OJ, Oliveira AA, Meir P. 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. Nature 528: 119–122.

Schuster MJ, Wragg PD, Williams LJ, Butler EE, Stefanski A, Reich PB. 2020. Phenology matters: extended spring and autumn canopy cover increases biotic resistance of forests to invasion by common buckthorn (Rhamnus cathartica). Forest Ecology and Management 464: 118067.

Shi J, Luo YQ, Zhou F, He P. 2010. The relationship between invasive alien species and main climatic zones. Biodiversity and Conservation 19: 2485-2500.

Spear D, Foxcroft LC, Bezuidenhout H, McGeoch MA. 2013. Human population density explains alien species richness in protected areas. Biological Conservation 159: 137-147.

Speziale KL, di Virgilio A, Lescano MN, Pirk G, Franzese J. 2018. Synergy between roads and disturbance favour *Bromus tectorum* L. invasion. PeerJ 6: e5529.

Taylor K, Brummer T, Taper ML, Wing A, Rew LJ. 2012. Human-mediated long-distance dispersal: An empirical evaluation of seed dispersal by vehicles. Diversity and Distributions 18: 942–951.

Teo DHL, Tan HTW, Corlett RT,Wong CM, Lum SKY. 2003. Continental rain forest fragments in Singapore resist invasion by exotic plants. Journal of Biogeography 30: 305–10.

The Plant List. 2020. http://www.theplantlist.org/. 17 Apr. 2020.

Veldman JW, Putz FE. 2010. Long-distance dispersal of invasive grasses by logging vehicles in a tropical dry forest. Biotropica 42(6): 697-703.

Veldman JW, Putz FE. 2011. Grass-dominated vegetation, not species-diverse natural savanna, replaces degraded tropical forests on the southern edge of the Amazon Basin. Biological Conservation 144(5): 1419-1429.

Vicente J, Alves P, Randin C, Guisan A, Honrado J. 2010. What drives invasibility? A multi-model inference test and spatial modelling of alien plant species richness patterns in northern Portugal. Ecography 33(6): 1081-1092.

Vilà M, Pino J, Font X. 2007. Regional assessment of plant invasions across different habitat types. Journal of Vegetation Science 18(1): 35–42.

Von der Lippe M, Bullock JM, Kowarik I, Knopp T, Wichmann M. 2013. Human-mediated dispersal of seeds by the airflow of vehicles. PLoS One 8(1): 1–10.

Wassenaar T, Gerber P, Verburg PH, Rosales M, Ibrahim M, Steinfeld H. 2007. Projecting land use changes in the Neotropics: The geography of pasture expansion into forest. Global Environmental Change 17: 86-104.

WFO – World Flora Online. 2019. http://www.worldfloraonline.org. 12 Jun. 2019.

Wilkie D, Shaw E, Rotberg F, Morelli G, Auzel P. 2000. Roads, development, and conservation in the Congo Basin. Conservation Biology 14(6): 1614-1622.

Woziwoda, B., Krzyżanowska, A., Dyderski, M.K., Jagodziński, A.M., Stefańska-Krzaczek, E. (2018). Propagule pressure, presence of roads, and microsite variability influence dispersal of introduced *Quercus rubra* in temperate Pinus sylvestris forest. Forest Ecology and Management 428: 35-45.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R (v. 574). Springer: New York.

SUPPLEMENTARY MATERIAL

S1 Table. List of the 121 sites considered for the statistical analyses. Articles repeated in the list had more than one sampled sites that were more than 5km apart.

Author	Title	Year	Country	Sampled area	lat	long
de Abreu et al	Changes in plant community of seasonally semideciduous sorest after invasion by *Schizolobium parahyba* at southeastern Brazil	2014	Brazil	0.15	-22.7889	-50.788889
Abreu et al	Tree species diversity of coastal lowland semideciduous forest fragments in northern Rio de Janeiro, Brazil	2014	Brazil	0.4	-21.5548	-41.20425
Abreu et al	Tree species diversity of coastal lowland semideciduous forest fragments in northern Rio de Janeiro, Brazil	2014	Brazil	0.2	-21.3358	-41.138417
Abreu et al	Tree species diversity of coastal lowland semideciduous forest fragments in northern Rio de Janeiro, Brazil	2014	Brazil	0.2	-21.3216	-41.119806
Abreu et al	Tree species diversity of coastal lowland semideciduous forest fragments in northern Rio de Janeiro, Brazil	2014	Brazil	0.2	-21.3255	-41.1
Abreu et al	Tree species diversity of coastal lowland semideciduous forest fragments in northern Rio de Janeiro, Brazil	2014	Brazil	0.2	-21.2969	-41.090333
Abreu et al	Tree species diversity of coastal lowland semideciduous forest fragments in northern Rio de Janeiro, Brazil	2014	Brazil	0.2	-21.4152	-41.077472
Andrzejewski et al	Floristic differentiation of a Deciduous Seasonal Forest	2019	Brazil	0.62	-29.403	-54.635

Author	Title	Year	Country	Sampled area	lat	long
	Tree Stratum, Jaguari, RS, Brazil					
Ariotti et al	Estrutura do componente arbóreo e arborescente de um fragmento urbano no município de Sério, Rio Grande do Sul, Brasil	2016	Brazil	0.4	-29.3823	-52.267039
Bongers et al	Structure and floristic composition of the lowland rain-forest of Los-Tuxtlas, Mexico	1988	Mexico	1	18.62626	-95.08688
Bordenave et al	Quantitative botanical diversity descriptors to set conservation priorities in Bakhuis Mountains rainforest, Suriname	2011	Suriname	0.55	4.28	-56.780674
Bordin et al	Community structure and tree diversity in a subtropical forest in southern Brazil	2019	Brazil	1.2	-27.0889	-52.779806
Boubli et al	Structure and floristic composition of one of the last forest fragments containing the critically endangered northern Muriqui (*Brachyteles hipoxanthus*, primates)	2011	Brazil	3	-19.7234	-41.806691
Braga and Jardim	Florística, estrutura e formas de vida do estrato inferior de uma floresta ombrófila densa aluvial, Pará, Brasil	2019	Brazil	0.16	-1.5082	-48.4614
Camargo et al	Avaliação do impacto do fogo no estrato de regeneração em um trecho de floresta estacional semidecidual em Viçosa	2010	Brazil	0.025	-20.7551	-42.861657

Author	Title	Year	Country	Sampled area	lat	long
Campos and Martins	Natural regeneration stratum as an indicator of restoration in area of environmental compensation for mining limestone, municipality of Barroso, MG, Brazil	2015	Brazil	0.016	-21.1803	-43.977719
Campos and Souza	Potencial for natural forest regeneration from seed bank in an upper Parana river floodplain, Brazil	2003	Brazil	0.996	-22.7563	-53.2647
Cardoso-Leite	Analysis of floristic composition and structure as an aid to monitoring protected areas of dense rain forest in southeastern Brazil	2013	Brazil	0.8	-24.3333	-48.05
Carvalho et al	Tree species distribution in canopy gaps and mature forest in an area of cloud forest of the Ibitipoca Range, south-eastern Brazil	2000	Brazil	5	-21.7119	-43.903269
Cenci et al	Composition of the tree flora in the botanical garden on Bento Gonçalves, Rio Grande do Sul, Brazil	2013	Brazil	2.5	-29.1772	-51.454444
Chain-Guadarrama et al	Determinants of rain-forest floristic variation on an altitudinal gradient in southern Costa Rica	2012	Costa Rica	9.25	8.8789	-83.119725
Coelho et al	Tree succession across a seasonally dry tropical forest and forest-savanna ecotone in northern Minas Gerais, Brazil	2017	Brazil	0.48	-16.7785	-43.6447
Colmanetti et al	Phytosociology and structural characterization of woody regeneration from a reforestation with native species in	2016	Brazil	0.45	-22.3745	-46.975282

Author	Title	Year	Country	Sampled area	lat	long
	Southeastern Brazil					
Condé and Tonini	Phytosociology of a dense ombrophilous forest in the northern Amazon, Roraima, Brazil	2013	Brazil	9	1.8417	-60.933333
Costa Filho et al	Floristic and phytosociological description of a riparian forest and the relationship with the edaphic environment in Caiua Ecological Station - Parana - Brazil	2006	Brazil	2.25	-22.6062	-52.870313
Couto-Santos et al	The role of temporal scale in linear edge effects on a submontane Atlantic forest arboreal community	2015	Brazil	0.3	-12.4753	-41.387222
Cysneiros et al	Diversity, community structure and conservation status of an Atlantic Forest fragment in Rio de Janeiro State, Brazil	2015	Brazil	0.4	-22.5911	-43.70311
Rocha et al	Effect of selective logging on floristic and structural composition in a forest fragment from Amazon Biome	2017	Brazil	1.25	-12.4696	-56.55458
Dallabrida et al	Tree component demography in an upper montane mixed ombrophilous forest under chronic anthropogenic disturbances	2017	Brazil	1	-27.929	-50.105017
Souza et al	Regenerative potential of an ecotonal forest in the upper Uruguay region, Santa Catarina state	2018	Brazil	0.6	-28.1914	-50.759445

Author	**Title**	**Year**	**Country**	**Sampled area**	**lat**	**long**
Denslow et al	Patterns in a species-rich tropical understory plant community	2019	Costa Rica	4.5	10.4348	-84.0342
Dezzeo et al	Estructura y composición floristica de bosques secos y sabanas em los Llanos orientales del Orinoco, Venezuela	2008	Venezuela	0.1	8.08	-64.741113
Duivenvoorden	Vascular plant species counts in the rain forests of the middle caqueta area, Colombian Amazonia	1994	Colombia	1	-0.58087	-72.171187
Duran-Fernandez et al	Structure of the high evergreen tropical forest of Naha, Chiapas, Mexico	2018	Mexico	1	16.9912	-91.558335
Duran-Fernandez et al	Floristic inventory of the lacandon community of Naha, Chiapas, Mexico	2016	Mexico	1	16.9815	-91.57617
Dzib-Castillo et al	Structure and composition of two tree communities of tropical deciduous and subdeciduous forests in Campeche, Mexico	2014	Mexico	1.35	19.2668	-90.58981
Faxina et al	Flora of inland Atlantic riparian forests in southwestern Brazil	2015	Brazil	1.12	-23.0973	-54.23168
Fonseca and Carvalho	Floristic and phytosociological aspects of the tree community in an urban atlantic forest fragment (Juiz de Fora, state of Minas Gerais, Brazil)	2012	Brazil	1	-21.7667	-43.320531
Franco et al	Estrato de regeneração natural de um trecho de floresta estacional semidecidual, Viçosa, Minas Gerais	2014	Brazil	0.06	-20.75	-42.85

Author	Title	Year	Country	Sampled area	lat	long
Freitas et al	Floristic, diversity and spatial distribuition of tree species in a dry forest in southern Brazil	2017	Brazil	1.4	-27.4261	-51.788333
Gastauer and Neto	Community dynamics in a species-rich patch of old-growth forest in a global changing scenario	2013	Brazil	1	-20.7956	-42.847223
Georgin et al	Floristic and phytosociological aspects of a deciduous forest in the region of the Upper Uruguay - RS	2015	Brazil	0.15	-27.3979	-53.434211
Gomes et al	Diferenças florísticas e estruturais entre duas cotas altiduninais da floresta ombrófila densa submontana atlântica, do Parque Estadual da Serra do Mar, município de Ubatuba/SP, Brasil	2011	Brazil	2	-23.3704	-45.0822
Gonzaga et al	Floristic and structural diagnosis of the tree component of a forest at Serra de Sao Jose, Tiradentes, Minas Gerais State, Southeast Brazil	2008	Brazil	0.9	-21.0973	-44.179909
Gonzalez et al	Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico	2002	Mexico	0.05	21.15	-89.81669
Gonzalez et al	Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico	2002	Mexico	0.06	21.1501	-89.816496

Author	Title	Year	Country	Sampled area	lat	long
Gonzalez et al	Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico	2002	Mexico	0.05	21.0833	-89.550004
Gonzalez et al	Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico	2002	Mexico	0.07	21.1667	-89.550004
Gonzalez et al	Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico	2002	Mexico	0.08	21.16666	-89.283335
Gonzalez-Valdivia et al	Indicadores ecológicos de hábitat y biodiversidad en un paisaje neotropical: perspectiva multitaxonómica	2011	Mexico	1.2	17.5806	-91.335687
Grasel et al	Fitossociologia do componente arborescente-arbóreo de uma floresta estacional no Vale do Rio Uruguai, sul do Brasil	2017	Brazil	1.02	-27.1011	-53.575556
Grau et al	Floristic and structural patterns along a chronosequence of secondary forest succession in Argentinean subtropical montane forests	1997	Argentina	6	-26.7732	-65.35124
Hans et al	Tropical rain forest types and soil factors in a watershed area in Guyana	1993	French Guiana	12.6	5.216667	-58.8
Hermuche and	Relação entre NDVI e florística em fragmentos de	2011	Brazil	1	-13.1899	-46.682138

Author	Title	Year	Country	Sampled area	lat	long
Felfilli	floresta estacional decidual no Vale do Paranã, Goiás					
Hermuche and Felfilli	Relação entre NDVI e florística em fragmentos de floresta estacional decidual no Vale do Paranã, Goiás	2011	Brazil	1	-13.7336	-46.476361
Hermuche and Felfilli	Relação entre NDVI e florística em fragmentos de floresta estacional decidual no Vale do Paranã, Goiás	2011	Brazil	1	-14.0156	-46.449643
Homeier et al	Tree Diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest	2010	Equador	0.68	-3.9666	-79.0667
Jadan et al	Forest communities in high Andean secondary forests (Azuay, Ecuador)	2017	Equador	0.4	-3.11461	-79.122238
Jadan et al	Forest communities in high Andean secondary forests (Azuay, Ecuador)	2017	Equador	0.35	-3.10205	-79.103427
Jadan et al	Forest communities in high Andean secondary forests (Azuay, Ecuador)	2017	Equador	0.25	-3.06658	-79.043773
Jorge et al	Diameter structure and spatial arrangement of the most abundant species in a seasonal semideciduous forest fragment in Botucatu, Southeastern Brazil	2015	Brazil	1.85	-22.8152	-48.394427
Kalacska et al	Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest	2004	Costa.Rica	1	10.8147	-85.615

Author	**Title**	**Year**	**Country**	**Sampled area**	**lat**	**long**
Kappelle et al	Altitudinal zonation os montane *Quercus* forests along two transects in Chirripó National Park, Costa Rica	1995	Costa Rica	1.2	9.4653	-83.6032
Kelly et al.	Floristics and biogeography of a rain forest in the Venezuelan Andes	1994	Venezuela	0.864	8.5833	-71.1167
Kukkonen e Hohnwald	Comparing floristic composition in treefall gaps of certified, conventionally managed and natural forests of northern Honduras	2009	Honduras	0.46	15.6188	-86.862241
Laska	Structure of understory shrub assemblages in adjacent secondary and old growth tropical wet forests, Costa Rica	1997	Costa Rica	0.08	10.4305	-84.007
Ledo et al	Forest biodiversity assessment in Peruvian Andean Montane cloud forest	2012	Peru	1.68	-4.62767	-79.770562
Lieberman et al	Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica	1996	Costa Rica	23.4	10.1291	-84.0988
Lima et al	Short-term impact of a hydroeletric power plant's reservoir on the tree component in a ecotonal area in Santa Catarina	2017	Brazil	4.82	-27.6358	-50.993951
Longhi et al	Caracterização fitossociológica do estrato arbóreo em um remanescente de floresta estacional semidecidual, em Montenegro, RS	2008	Brazil	1.83	-29.8184	-51.420663
Lopes et al	Physiognomic-structural characterization of dry- and	2008	Brazil	2	-7.61675	-35.466682

Author	Title	Year	Country	Sampled area	lat	long
	humid-forest fragments (Atlantic Coastal Forest) in Pernambuco State, NE Brazil					
Marangon et al	Phytosociological structure and sucession classification of the arboreous component in fragment of seasonal semideciduous forest in Vicosa - Minas Gerais	2007	Brazil	1	-20.75	-42.916667
Marchiori et al	Tree community composition and aboveground biomass in a secondary atlantic forest, Serra do Mar State Park, São Paulo, Brazil	2016	Brazil	1	-23.3161	-45.103248
Martinez-Adriano et al	Floristic survey of flowering plants in a tropical coastal ecosystem in Veracruz, Mexico	2016	Mexico	1.72	19.6145	-96.418381
Martins et al	Colonization of gaps produced by death of bamboo clumps in a semideciduous mesophytic forest in south-eastern Brazil	2004	Brazil	0.2	-22.8271	-47.107544
Milhomen et al	Estrutura do estrato arbóreo e regenerativo de um fragmento de floresta estacional semidecidual em Itumbiara, GO	2013	Brazil	1	-18.3483	-49.073889
Munguia-Rosas et al	Continuous forest has greater taxonomic, functional and phylogenetic plant diversity than an adjacent naturally fragmented forest	2014	Mexico	0.68	20.1704	-90.43307

Author	Title	Year	Country	Sampled area	lat	long
Negrelle	The Atlantic forest in the Volta Velha Reserve: a tropical rain forest site outside the tropics	2002	Brazil	1	-26.0828	-48.639957
Nesheim et al	Plant composition in the Maya Biosphere Reserve: natural and anthropogenic influences	2010	Guatemala	5	17.4792	-89.850311
Norden et al	Resilience of tropical rain forests: tree community reassembly in secondary forests	2009	Costa Rica	6	104.305	-84.007
Oliveira et al	Effect of flooding regime and understorey bamboos on the physiognomy and tree species composition of a tropical semideciduous forest in southeastern Brazil	1994	Brazil	1.59	-21.4884	-44.376164
Orihuela et al	Markedly divergent tree assemblage responses to tropical forest loss and fragmentation across a strong seasonality gradient	2015	Brazil	6	-27.2116	-53.877996
Orihuela et al	Markedly divergent tree assemblage responses to tropical forest loss and fragmentation across a strong seasonality gradient	2015	Brazil	6	-26.4908	-52.198889
Orihuela et al	Markedly divergent tree assemblage responses to tropical forest loss and fragmentation across a strong seasonality gradient	2015	Brazil	6	-27.8282	-48.857469
Pedreira and Sousa	Tree community of a permanent flooded forest and its adjacent vegetation area in Ouro Preto, Minas Gerais	2011	Brazil	0.42	-20.4273	-43.505019

Author	Title	Year	Country	Sampled area	lat	long
	state, Brazil					
Pereira et al	Caracterização ecológica de espécies arbóreas ocorrentes em ambientes de mata ciliar, como subsídio a recomposição de áreas alteradas nas cabeceiras do Rio Grande, Minas Gerais, Brasil	2010	Brazil	0.4	-22.2334	-44.566679
Pereira et al	Caracterização ecológica de espécies arbóreas ocorrentes em ambientes de mata ciliar, como subsídio a recomposição de áreas alteradas nas cabeceiras do Rio Grande, Minas Gerais, Brasil	2010	Brazil	1.04	-22.2163	-44.533135
Pereira et al	Caracterização ecológica de espécies arbóreas ocorrentes em ambientes de mata ciliar, como subsídio a recomposição de áreas alteradas nas cabeceiras do Rio Grande, Minas Gerais, Brasil	2010	Brazil	0.4	-22.1667	-44.466671
Pinheiro and Monteiro	Florística de uma floresta estacional semidecidual, localizada em ecótono savanico-florestal, no município de Bauru, SP, Brasil	2008	Brazil	0.26	-22.3446	-49.013039
Polisel et al	Structure of the understory community in four stretches of Araucaria forest in the state of São Paulo, Brazil	2014	Brazil	1	-23.8369	-49.14052

Author	Title	Year	Country	Sampled area	lat	long
Polisel et al	Structure of the understory community in four stretches of Araucaria forest in the state of São Paulo, Brazil	2014	Brazil	1	-24.4667	-49.016689
Polisel et al	Structure of the understory community in four stretches of Araucaria forest in the state of São Paulo, Brazil	2014	Brazil	1	-22.6833	-45.45
Polisel et al	Structure of the understory community in four stretches of Araucaria forest in the state of São Paulo, Brazil	2014	Brazil	0.86	-22.75	-44.300002
Ribeiro et al	Mixed rain forest in southeastern Brazil: tree species regeneration and floristic relationships in a remaining stretch of forest near the city of Itabera, Brazil	2013	Brazil	1	-23.8464	-49.144167
Rocha and Amorim	Altitudinal heterogeneity in northern Atlantic Forest: a case study in southeastern Bahia, Brazil	2012	Brazil	0.5	-15.3917	-39.564063
Rocha et al	Functional decay in tree community within tropical fragmented landscapes: Effects of landscape-scale forest cover	2017	Brazil	1	-15.4336	-39.246734
Rodal et al	Natural forest regeneration in abandoned sugarcane fields in northeastern Brazil: floristic changes	2012	Brazil	1.8	-7.78524	-34.993857
Rode et al	Comparação floristica entre uma floresta ombrófila mista e uma vegetação arbórea estabelecida sob um povoamento de *Araucaria angustifolia* de 60 anos	2008	Brazil	25	-25.4118	-50.573931
Romero-Mieres et	Recuperación natural del bosque siempreverde afectado	2014	Chile	0.135	-40.1328	-73.563978

Author	Title	Year	Country	Sampled area	lat	long
al	por tala rasa y quema en la Reserva Costera Valdiviana, Chile					
Ruschel et al	Estrutura e composição florística de dois fragmentos da floresta estacional decidual do Alto-Uruguai, SC	2009	Brazil	1.12	-27.1904	-53.633889
Ruschel et al	Estrutura e composição florística de dois fragmentos da floresta estacional decidual do Alto-Uruguai, SC	2009	Brazil	1.12	-26.9368	-53.524989
Saldana	Relationship between species richness and functional diversity of leaf traits in two evergreen species assemblages in a temperate rainforest	2013	Chile	0.225	-40.6501	-72.183299
Sanchez et al	Changes in tree community composition and structure of Atlantic rain forest on a slope of the Serra do Mar range, southeastern Brazil, from near sea level to 1000 m of altitude	2013	Brazil	1.94	-23.3667	-44.800012
Sansevero et al	Natural regeneration in plantations of native trees in lowland brazilian atlantic forest: community structure, diversity, and dispersal syndromes	2011	Brazil	0.06	-22.3301	-42.280903
Scipioni et al	Distribuição do compartimento arbóreo em gradiente de relevo e solos na encosta Meridional da Serra Geral, RS	2019	Brazil	2	-30.0826	-52.41573
Silva and Araujo	Dinâmica da comunidade arbórea de uma floresta	2009	Brazil	0.5	-18.9507	-48.203935

Author	**Title**	**Year**	**Country**	**Sampled area**	**lat**	**long**
	semidecidual em Uberlândia, MG, Brasil					
Souza and Batista	Restoration of seasonal semideciduous forests in Brazil: influence of age and restoration design on forest structure	2004	Brazil	0.09	-22.5792	-52.853632
Souza and Batista	Restoration of seasonal semideciduous forests in Brazil: influence of age and restoration design on forest structure	2004	Brazil	0.09	-22.6409	-52.144485
Souza et al	Ecological outcomes and livelihood benefits of community-managed agroforests and second growth forests in Southeast Brazil	2017	Brazil	0.6	-28.1906	-50.758438
Souza et al	Floristic and structure of the arboreal community of an ombrophilous dense forest at 800 m above sea level, in Ubatuba/SP, Brazil	2018	Brazil	1	-23.3598	-45.108758
Souza et al	Regenerative potential of an ecotonal forest in the upper Uruguay region, Santa Catarina state	2018	Brazil	0.6	-28.1914	-50.759445
Valdez-Hernandez et al	Recovery and early succession after experimental disturbance in a seasonally dry tropical forest in Mexico	2014	Mexico	0.6	19.68309	-88.366684
Van Breugel et al	Succession of Ephemeral Secondary Forests and Their Limited Role for the Conservation of Floristic Diversity in a Human-Modified Tropical Landscape	2013	Panama	9.8	9.216525	-79.783332
Velazco et al	Floristic and Phytosociology in a semideciduous seasonal	2015	Argentina	0.48	-27.2665	-55.564667

Author	Title	Year	Country	Sampled area	lat	long
	forest - Osununu Private Reserve, Misiones, Argentina					
Viani et al	Caracterização florística e estrutural de remanescentes florestais de Quedas do Iguaçu, Sudoeste do Paraná	2011	Brazil	0.61	-25.55	-52.966.693
Viani et al	Caracterização florística e estrutural de remanescentes florestais de Quedas do Iguaçu, Sudoeste do Paraná	2011	Brazil	0.52	-25.4829	-52.881951
Viani et al	Caracterização florística e estrutural de remanescentes florestais de Quedas do Iguaçu, Sudoeste do Paraná	2011	Brazil	0.5	-25.4678	-52.816524
Weaver	El Toro Wilderness, Luquillo Experimental Forest, Puerto Rico	2011	Puerto Rico	5.6	18.2696	-65.829077
Zacarias-Eslava et al	Composición, estructura y diversidad del cerro El Águila, Michoacán, México	2011	Mexico	0.64	19.65	-101.4
Zamora-Crescencio et al	Floristic composition and structure of the secondary vegetation in northern Campeche, Mexico	2011	Mexico	0.1	20.4	-90.0403
Zanini et al	Atlantic rain forest recovery: successional drivers of floristic and structural patterns of secondary forest in Southern Brazil	2014	Brazil	0.84	-29.6907	-50.17506

Supplementary Table 2. Names of the 23 invasive non-native woody plant species compiled from the articles reviewed.

Family - Species
Anacardiaceae
Mangifera indica L.
Schinus molle L.
Asparagaceae
Dracaena fragrans (L.) Ker Gawl.
Bignoniaceae
Tecoma stans (L.) Juss. Ex Kunth
Euphorbiaceae
Hevea brasiliensis (Willd ex. A. Juss.) Mull. Arg.
Ricinus communis L.
Fabaceae
Leucaena leucocephala (Lam.) de Wit
Schizolobium parahyba (Vell.) S.F. Blake
Ulex europaeus L.
Lauraceae
Cinnamomum verum J. Presl.
Meliaceae
Melia azedarach L.
Moraceae
Artocarpus heterophyllus Lam.
Morus nigra L.
Myrtaceae
Psidium guajava L.
Syzygium jambos (L.) Alston
Syzygium malaccense (L.) Merr. & L.M. Everry
Oleraceae
Ligustrum lucidum W.T. Aiton
Pinaceae
Pinus elliottii Engelm.
Rhamnaceae

Hovenia dulcis Thumb.
Rosaceae
Eriobotrya japonica (Thunb.)Lindl.
Rubus rosifolius Stokes
Rubiaceae
Coffea arabica L.
Solanaceae
Solanum mauritianum Scop.

CAPÍTULO 2

Invasiveness in Schefflera s.l.: do non-native species outperform phylogenetically related native species?

Invasiveness in *Schefflera* s.l.: do non-native species outperform phylogenetically related native species?

Amanda Angélica Carmes[1,5], Rafael Barbizan Sühs[2], Pedro Fiaschi[3], Michele de Sá Dechoum[2,4]

[1] Universidade Federal de Santa Catarina, Programa de Pós-Graduação em Biologia de Fungos, Algas e Plantas, CCB, Campus Universitário Reitor João David Ferreira Lima, Trindade, 88040-900, Florianópolis, Santa Catarina, Brazil.

[2] Universidade Federal de Santa Catarina, Programa de Pós-Graduação em Ecologia, CCB, Campus Universitário Reitor João David Ferreira Lima, Trindade, 88040-900, Florianópolis, Santa Catarina, 88040-900, Brazil

[3]Universidade Federal de Santa Catarina, Departamento de Botânica, CCB, Campus Universitário Reitor João David Ferreira Lima, Trindade, 88040-900, Florianópolis, Santa Catarina, Brazil

[4] Universidade Federal de Santa Catarina, Departamento de Ecologia e Zoologia, CCB, Campus Universitário Reitor João David Ferreira Lima, Trindade, 88040-900, Florianópolis, Santa Catarina, 88040-900, Brazil

[5] Corresponding author: amandacarmes@hotmail.com

ABSTRACT

Can differences in biological attributes related to seed germination and seedling development between phylogenetically close native species and non-native invasive species help explain biological invasion potential in subtropical forests? Can the expression of these attributes vary according to different conditions of light when assessed experimentally? To answer these questions, we collected seeds of four phylogenetically close species, two of which are native to Brazil (*Didymopanax angustissimus* and *Didymopanax calvus*) and two non-native invasive species (*Heptapleurum actinophyllum*, *Heptapleurum arboricola*) on coastal regions of southern Brazil. The seeds were set to germinate under different light conditions (100% and 50%) for a period of 180 days. We compared seed germination, seedling survival and growth between the native and non-native species.

Germination velocity and the proportion of germinated seeds were higher for non-native invasive species than for native species under both conditions of light. The rate of survival of the non-native invasive species was higher at 50% light. The higher germination velocity and proportion of non-native invasive species explain their invasive potential regardless of light intensity. Our results highlight the invasive potential of the species assessed, especially of *H. arboricola*, which may be classified as '*superinvasive'*.

Key words: growth, invasive potential, non-native invasive plants, seed germination, shade tolerance, survival.

Potencial de invasão em *Schefflera* s.l.: as espécies não nativas superam as espécies nativas filogeneticamente relacionadas?

RESUMO

As diferenças nos atributos biológicos relacionados à germinação de sementes e ao desenvolvimento de plântulas entre espécies nativas filogeneticamente próximas e espécies invasoras não nativas podem ajudar a explicar o potencial de invasão biológica em florestas subtropicais? A expressão desses atributos pode variar de acordo com as diferentes condições de luz quando avaliada experimentalmente? Para responder essas perguntas, coletamos sementes de quatro espécies filogeneticamente próximas, duas das quais são nativas do Brasil (*Didymopanax angustissimus* e *Didymopanax calvus*) e duas espécies invasoras não nativas (*Heptapleurum actinophyllum*, *Heptapleurum arboricola*) em regiões costeiras do sul do Brasil. As sementes foram submetidas a diferentes condições de luz (100% e 50%) por um período de 180 dias. Comparamos a germinação das sementes, a sobrevivência e o crescimento das mudas entre as espécies nativas e não nativas. A velocidade de germinação e a proporção de sementes germinadas foram maiores para as espécies invasoras não nativas, comparado às espécies nativas em ambas as condições de luz. A taxa de sobrevivência das espécies invasoras não nativas foi maior com 50% de luz. A maior velocidade de germinação e a maior proporção de espécies invasoras não nativas explicam seu potencial invasivo, independentemente da intensidade da luz. Nossos resultados destacam o potencial de invasão das espécies avaliadas, especialmente da *H. arboricola*, que pode ser classificada como "superinvasora".

Palavras-chave: crescimento, germinação de sementes, plantas invasoras não nativas, potencial de invasão, sobrevivência, tolerância à sombra

INTRODUCTION

Invasion success by introduced plants has been explained by differences in ecological attributes of native and non-native species (Funk et al. 2008, Moodley et al. 2013, Leffler et al. 2014, Duffin et al. 2019). For example, seedlings of invasive species perform better in terms of germination, growth, and survival compared with co-occurring congener native species (Leicht-Young et al. 2007, Stricker and Stiling 2013). However, many comparisons do not take the phylogeny of compared species into account (Porté et al. 2011, Mathakutha et al. 2017, Yu and He 2021). Phylogenetically close species have similar biological attributes because they share a recent common ancestral (Antúnez et al. 2001, Van Kleunen et al. 2010). In a global meta-analysis, it has been shown that attributes such as fitness, height, growth rate and shoot allocation differed more between phylogenetically close invasive and non-invasive species compared with phylogenetically more distant species (Van Kleunen et al. 2010). Therefore, comparisons between attributes of phylogenetically related species may be more robust to predict invasion success (Van Kleunen et al. 2010, Stricker and Stiling 2013).

Invasion success may also be influenced by local environmental conditions such as water availability, nutrients in the soil, and light availability (Burns et al. 2006, Richards et al. 2006). Low light availability in forests my limit the survival of non-native species (Davis et al. 2000, Fridley et al. 2023). However, shade-tolerant non-native plants may invade forests, using different strategies to persist under different conditions of light (Martin et al. 2009, Rejmánek 2014, Berg et al. 2016, Medvecká et al. 2018). For example, shade-tolerant non-native invasive species may combine low survival with rapid growth under intermediate to high light conditions, and high survival with slow growth in conditions of lower incidence of light (Martin et al. 2010). On the other hand, shade-tolerant native species have attributes that minimize breathing and tissue renovation, preventing rapid growth and competitive dominance in conditions of higher incidence of light (Lusk and Jorgensen 2013, Sendall et al. 2016).

The hypothesis of existence of a special class of invasive woody plants, named ‘superinvasive’, is recent (Fridley et al. 2023). This group of species would require less light (lower whole-plant light compensation point) to balance loss of carbon and individual maintenance (*i.e.*, growth, tissue renovation, response to herbivory) when compared with native species. Therefore, the ‘superinvasive’ plants would grow fast under high light conditions and maintain high survival rates under a closed canopy.

Although the number of experimental studies comparing co-occurring non-native invasive and native plants has increased in recent years, many of the comparisons do not consider the phylogeny of compared species (Porté et al. 2011, Mathakutha et al. 2017, Yu and He 2021). Important attributes shared by phylogenetically close species might be left aside in the determination of invasion success (Yu and He 2021).

Schefflera, for a long time considered the largest genus of Araliaceae, has been segregated in five geographically coherent groups: Pacific, which includes the generic-type, Melanesian, Afro-Malagasy, Asian, and Neotropical clades (Plunkett et al. 2005). All species of the former Asian clade of *Schefflera* s.l. are now treated under *Heptapleurum* (Lowry and Plunkett 2020), while species of Neotropical *Schefflera* are currently arranged in five genera, of which *Didymopanax* accounts for most Brazilian species (Fiaschi et al. 2020). Despite *Heptapleurum* and *Didymopanax* are not sister-groups, they both belong to the Asian-Palmate clade of Araliaceae (Plunkett et al. 2019), which includes all species of the Asian and Neotropical clades of *Schefflera* s.l. Both groups include non-prickly woody plants with palmately-compound leaves and ligulate stipules, and their preferential habitats are tropical and subtropical forests from the sea level to more than 3,000 m a.s.l.

The general objective of our study was to verify how the biological attributes related to seed germination, seedling survival and growth differ between non-native invasive and native species of *Schefflera sensu lato* (Araliaceae), which currently belong, respectively, to *Heptapleurum* and *Didymopanax*, on coastal regions of southern Brazil. The questions posed were: (1) Can differences in biological attributes related to seed germination and seedling development between phylogenetically close native and non-native invasive species help explain biological invasion potential in subtropical forests? (2) Can the expression of these attributes vary according to different conditions of light?

MATERIALS AND METHODS

1. Native and non-native species contemplated in this study

Four tree species in the genus *Schefflera* s.l. occurring in the study area were selected for the study (Figure 1), two of which are non-native and invasive (*Heptapleurum actinophyllum* and *H. arboricola*), and two native species (*Didymopanax angustissimus* and *D. calvus*). Recent studies confirm that *Schefflera* s.l. is a polyphyletic genus represented by five distinct clades (Plunkett et al. 2005, Plunkett et al. 2019). Species earlier acknowledged within the Asian *Schefflera* clade are currently treated as *Heptapleurum*, while *Didymopanax* species are part of the Neotropical clade, which also includes other four genera (Plunkett et al. 2019).

Heptapleurum actinophyllum is a tree species native to the South of New Guinea and Northeast of Australia (Lowry and Plunkett 2020). It is considered invasive in Singapore, the United States, Puerto Rico, Cuba, Brazil, and Australia (CABI 2020, Instituto Hórus 2022). It can be found invading pastures, coastal dunes, degraded areas, and secondary forests (Gucker 2011, CABI 2020). *Heptapleurum arboricola* occurs naturally in humid forests or along rivers in China and Taiwan (Lowry and Plunkett, 2020, Instituto Hórus 2022). It is acknowledged as invasive in the United States, the Reunion Islands, Brazil, Chile, and on several Pacific islands (Instituto Hórus 2022). When outside its native range, it can grow in open areas as well as in forests (Atlas of Living Australia 2020, Instituto Hórus 2022). Both *Heptapleurum* species are frequently used as ornamental plants in tropical and subtropical regions (Chen et al. 2003, Lowry and Plunkett 2020). The seeds are bird-dispersed and germinate easily on several types of substrate, developing as epiphytes until the roots reach the ground (Marciniak et al. 2019).

Didymopanax angustissimus is endemic to Brazil and occurs throughout the Atlantic Forest domain. It grows in direct sunlight (heliophilous), is fast-growing, and a prolific seeder, forming dense seedling banks with high mortality rates (Armelin 2005). *Didymopanax calvus,* also endemic to Brazil, occurs in subtropical and tropical Atlantic forests in the south and southeast (Fiaschi and Plunkett 2018). Both native species have low germination rates, possibly due to physiological or tegumentary dormancy or to the percentage of seeds injured by insect larvae (Franco and Ferreira 2002, Ohashi and Leão 2005, Vilarinho et al. 2019). None of the native species are considered invasive anywhere in the world.

2. Seed collection and preparation

Seeds of the native species were obtained from trees located in protected areas, registered in the Floristic and Forest Survey conducted in the state of Santa Catarina (Vibrans et al. 2013) and available from the CRIA database - *SpeciesLink* (2018). The seeds of the invasive species were collected from plants in urban and peripheral areas. Two populations were selected for each species, and three to four mother trees were selected for each population (Figure 1). A minimum number of three plants per population and six plants per species was selected. The selected plants were at least 10 meters apart in each population. The number of mother trees was low due to the difficulty in finding native individuals at the sites available for collection. Fruits were collected from the crown and from the ground. The seeds of the different plants and populations of the same species were mixed before being sowed. The seeds were processed for the pulp to be removed, disinfected with 70° alcohol, and dried at room temperature. Little developed seeds or seeds with granivory signs were discarded. In the case of native species, the rigid coat of the endocarp involving the seed was scarred in order to break the impermeable tegument (Carvalho 2008). The seeds of non-native invasive species were placed to germinate without prior treatment.

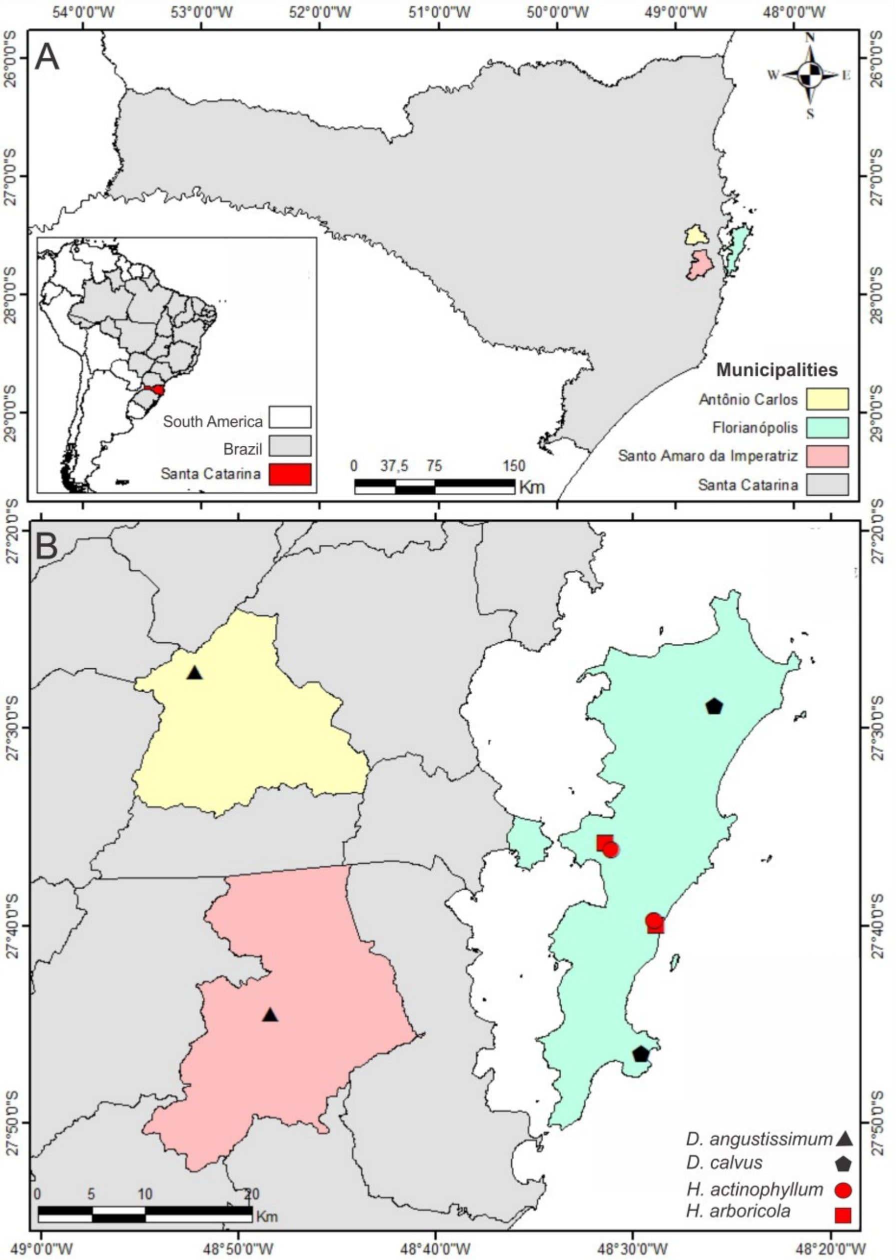

Figure 1. Location map of the *Schefflera* s.l. species selected for the seed germination and seedling growth and survival experiments. A) Location of the state of Santa Catarina and the three municipalities in which the populations were sampled. B) Collection sites, different geographical shapes represent the different species, red shapes represent non-native invasive species, black shapes represent native species.

3. Experimental design

The experiment was set up in the seedling nursery of Corrego Grande Municipal Park, in Florianopolis, Southern Brazil (27°35’53.35’’S; 48°30’39.88’’O). The local climate is Cfa type according to the Köppen-Geiger classification, humid mesothermal with a hot summer and no defined dry season. The seeds were sown in pots, with a volume of two liters (20cm height x 15 cm diameter), using a mixture of sand and fertilized soil (1:1). The pots were placed in the open, in natural conditions of temperature and rainfall, irrigated when the substrate dried, as needed. Two treatments were defined: 100% light intensity (T100) and 50% light intensity (T50). In T100, the seeds were exposed to solar radiation without protection; in T50, 50% shading was used to filter direct sunlight. One seed was sown per pot. A total of 160 seeds of *D. angustissimus* and *H. arboricola* were sown, with 80 seeds per treatment (T50 and T100). In the case of *H. actinophyllum*, 122 seeds were sown, 61 per treatment, and 200 seeds of *D. calvus*, with 100 seeds per treatment. Each pot was considered a replica.

4. Data analysis

4.1. Germination

The accumulated germination curve and index of velocity of germination (IVG) were calculated for each of the species in each of the treatments. The accumulated germination curve describes the time needed for the seeds of a given treatment to germinate throughout the duration of the experiment (Aravind et al. 2019). The index of velocity of germination (IVG) considers the number of seedlings germinated per day during the experiment (Aravind et al. 2019). The final values of the proportion of germinated seeds used to produce the germination curves and the indices of velocity of germination were compared between species and treatments (fixed effects) by means of Generalized Linear Models using the normal distribution. Comparisons between the mean values obtained per species and per treatment were made by contrast analysis. *p* values for multiple comparisons were adjusted using the Holm-Bonferroni method (Holm 1979). Seed germination was evaluated for a period of 180 days. Hypocotyl height and diameter of the seedlings developed from the germinated seeds were measured every 30 days from the date of germination using a graduated ruler and pachymeter, respectively.

4.2. Survival

Survival functions were estimated per species and per treatment using the Kaplan-Meyer method for censored data (Rich et al. 2010). As a result, new data were added to the curve as more seedlings died throughout the duration of the experiment (180 days). The comparison between species survival curves was made using a

Log-rank test (Kaplan and Meier 1958). Seedling survival was evaluated for a period of 180 days after germination.

4.3. Growth

Relative growth rate based on plant height was calculated based on the seedling height values measured weekly for 180 days. After 180 days since germination each live seedling was removed from the plastic bag and the aerial part (shoot: hypocotyl, cotyledons, and leaves) was separated from the subterranean part (roots). The shoot and root were weighed separately for records of fresh mass. Leaves were detached and scanned for measurement using Image software (Rasband 1997) to generate leaf area data. Dry mass was obtained after the seedling parts were oven-dried at 60°C for 48 hours, then weighed. The root/shoot ratio was obtained from the dried material.

The values of total means were compared between species and treatments for each species using Generalized Linear Models (GLM), followed by contrast analysis for comparison of pairs. *p* values for multiple comparisons were adjusted using the Holm-Bonferroni method (Holm 1979).

The analyses were conducted in R software (R Development Core Team 2014), using the "*survival*" and "*survminer*" packages (Therneau and Lumley 2013, Kassambara et al. 2017) for survival analysis, "*germinationmetrics*" (Aravind et al. 2019) to calculate index of velocity of germination, and "*emmeans*" and "*lmeans*" (Lenth and Lenth 2018) for the comparison of pairs.

RESULTS

Germination

The total values of proportion of germinated seeds were higher for the non-native invasive species than for the native species. *H. actinophyllum* germinated 37 of 122 (30%) seeds, while *H. arboricola* germinated 23 of 160 (15%). The native species *D. angustissimus* germinated 14 of 160 (9%) seeds, and *D. calvus*, 5 of 200 (2%) (Tables 1 and 2). The non-native invasive species also performed better in terms of proportion of seeds germinated between treatments, with higher values in both treatments (Table 1). In the paired comparison, germination rates were higher for all species in treatment T50 (Table 2, Table1 –Supplementary material).

Table 1. Number of seeds sown and number and proportion of seeds that germinated of the native species *Didimopanax angustissimus* and *D. calvus*, and the non-native invasive *Heptapleurum actinophyllum* and *H. arboricola*, in two treatments, direct sunlight (T100) and 50% protection from direct sunlight (T50). The values of the proportions of germinated seeds were rounded to the closest integer.

Species	**Seeds sown**		**Germinated seeds**	
	T50	T100	T50	T100
Native species				
D. angustissimus	80	80	10 (9%)	7 (12%)
D. calvus	100	100	3 (3%)	2 (2%)
Non-native invasive species				
H. actinophyllum	61	61	23 (23%)	14 (38%)
H. arboricola	80	80	13 (16%)	10 (12%)

Table 2. Total germination proportion and per treatment at the end of 180 days of the native species *Didimopanax angustissimus* and *D. calvus* and the non-native invasive species *Heptapleurum actinophyllum* and *H. arboricola*, in two treatments, direct sunlight (T100) and 50% protection from direct sunlight (T50). Letters discriminate differences between proportions, verified by comparison in pairs (Table 1 –supplementary material).

Species	**Total mean**	**Standard deviation**	**T50**	**T100**
Native species				
D. angustissimus	0.087	±0.053	0.087^{a}	0.125^{b}
D. calvus	0.025	±0.007	0.030^{c}	0.020^{d}
Non-native invasive species				
H. actinophyllum	0.303	±0.104	0.229^{e}	0.377^{f}
H. arboricola	0.146	±0.029	0.167^{g}	0.125^{h}

Germination curve

Mean time for germination was shorter in treatment T50 for *H. arboricola* and *D. calvus* [24 (±5) and 27 (±0) days], while *H. actinophyllum* and *D. angustissimus* had higher mean values [65 (±37) and 77 (±19) days] (Figure 2). In treatment T100, *D. calvus* and *H. arboricola* had the lowest mean values for germination time [27 (±0) and 43(±39)], while *H. actinophyllum* and *D. angustissimus* had the highest mean values [45 (±17) and 169 (±56) days] (Figure 2).

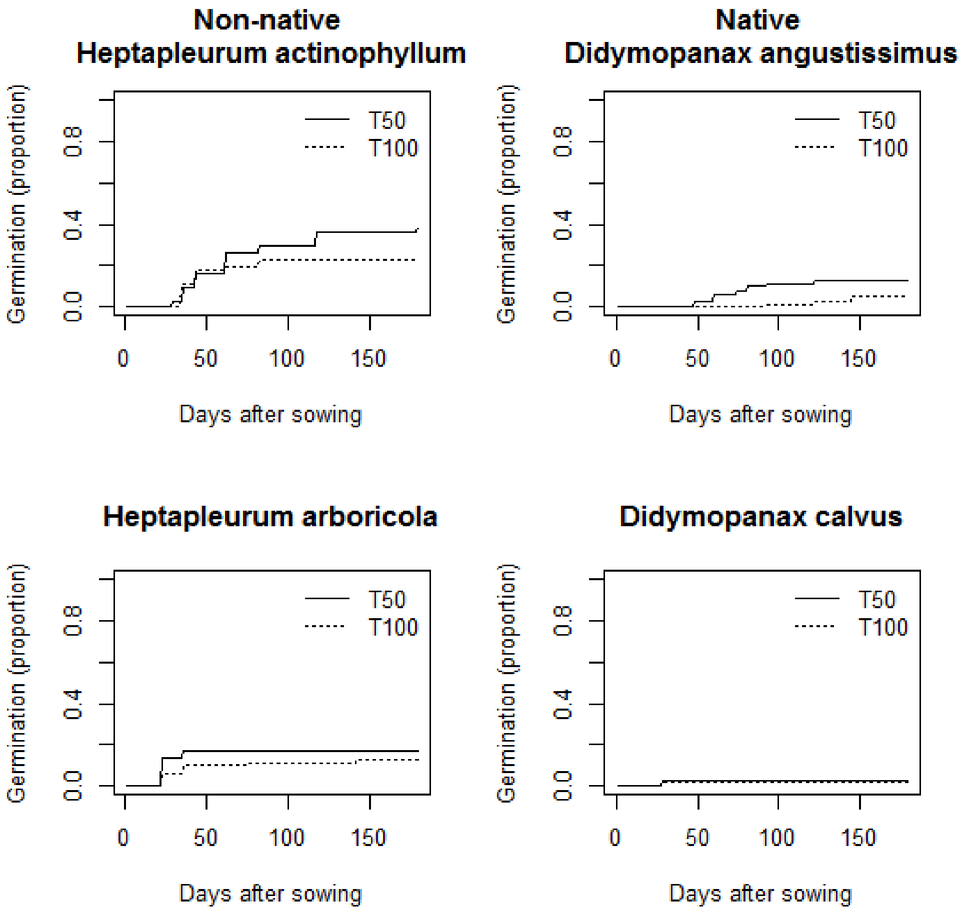

Figure 2. Cumulative germination curves of the non-native invasive species seeds *H. actinophyllum* and *H. arboricola* and the native species *D. angustissimus* and *D. calvus* in two treatments: direct sunlight (T100) and 50% protection from direct sunlight (T50).

Index of velocity of germination

The mean index of velocity of germination was four times higher for the non-native invasive species compared with the native species (Table 3). The four species germinated faster in treatment T50 compared with T100 (Table 3; Table 2– supplementary material).

Table 3. General indices of velocity of germination and per treatment of the native species *D. angustissimus* and *D. calvus* and of the non-native invasive species *H. actinophyllum* and *H. arboricola* in two treatments: direct sunlight (T100) and 50% protection from direct sunlight (T50). Different letters represent differences between the observed values per species in the two treatments (Table 2 -supplementary material).

	Overall mean	**T50**	**T100**
Native species			
D. angustissimus	5.535	9.568^a	1.501^b
D. calvus	4.703	5.644^a	3.762^b
Non-native species			
H. actinophyllum	22.86	25.729^a	20.010^b
H. arboricola	21.639	26.655^a	16.624^b

Survival curve

Survival rates in terms of the proportion of seedlings that survived in treatment T50 (0.82 and 0.70, respectively) were higher for *H. actinophyllum* and *D. angustissimus*, and lower for *Didimopanax calvus* and *H. arboricola* (0.66 and 0.23, respectively). In treatment T100, *H. actinophyllum* had the highest survival rate (0.92), followed by *D. calvus* and *H. arboricola* with 0.50, and *D. angustissimus*, with the lowest rate (0.42). The curves obtained by the *Kaplan-Meier* estimator differed between the four species and between treatments (X^2= 19.5, d*f*= 7, *p-value*= 0.007; Figure 3).

The survival rate of *Heptapleurum actinophyllum* was the highest in both treatments at the end of the experiment; however, in treatment T50, it was lower than in treatment T100. On the other hand, the survival rate of *H. arboricola* was low in both treatments. The native species had better survival rates in T50 compared with treatment T100.

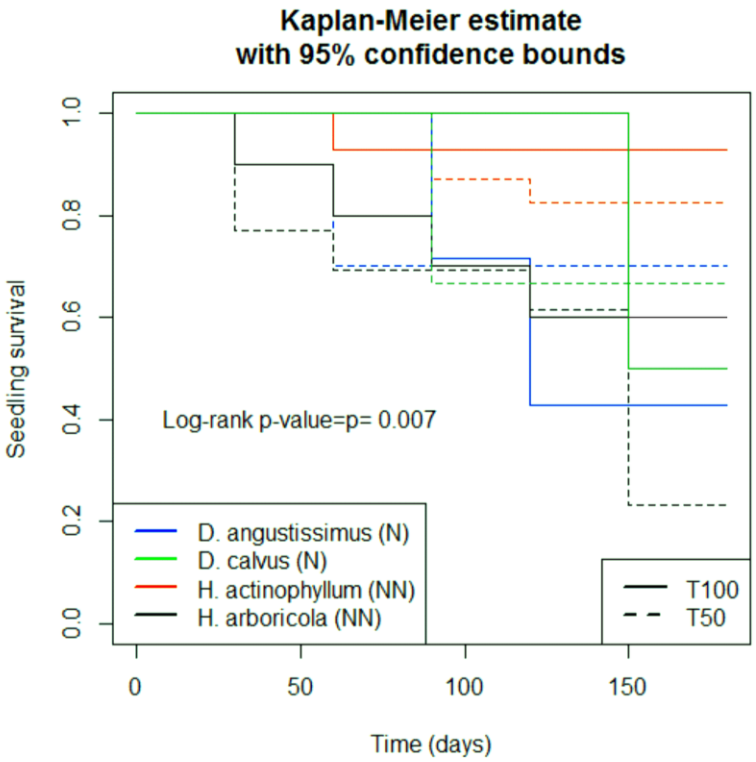

Figure 3. Survival curves of seedlings of the native species *D. angustissimus* and *D. calvus* and of the non-native invasive species *H. actinophyllum* and *H. arboricola* in two treatments: direct sunlight (T100) and 50% protection from direct sunlight (T50). NN: non-native, N: native.

The survival rate of *Didimopanax angustissimus* was high during the first month of the experiment, but after 60 days it declined in both treatments. In the case of *D. calvus*, the survival rate declined after 90 days in treatment T50, and after 150 days in treatment T100. The survival rate of *Heptapleurum actinophyllum* was higher during the initial two months in treatment T100 and during the first three months in T50. The survival rate of *Heptapleurum arboricola* declined in the first month in both treatments, and continued to fall until the 150th day of the experiment.

In treatment T50, the mean life time was 141 and 150 days for the native species *D. angustissimus* and *D. calvus*, respectively. In this treatment, the mean life time was 165 and 120 days for the non-native invasive species *H. actinophyllum* and *H. arboricola*, respectively. In treatment T100, the mean life time was 137, 165, 171, and 135 days for *D. angustissimus*, *D. calvus*, *H. actinophyllum* and *H. arboricola*, respectively (Supplementary material– Table 5).

Growth

Given the low number of germinated seeds of the native species (*D. angustissimum*: 14; *D. calvus*: 5), it was not feasible to compare the results on growth parameters. The results are available from the supplementary material – Table 5. The root/soot ratio was higher for *Heptapleurum arboricola* than for *H. actinophyllum* (estimate=-0.18, SE=0.09, *t* value=-1.97, *p*=0.05). On the other hand, the leaf area means (estimate=-30.85, SE=18.05, *t* value=-1.70, *p*=0.09), total dry mass (estimate=-0.28, SE=0.19, *t* value=-1.49, *p*=0.14), and relative growth rate based on height (estimate=-0.0008, SE=0.005, *t* value=1.40, *p*=0.16) did not differ between species (Figure 4). No difference was found in the means between treatments T100 and T50 per species (Supplementary material – Table 5).

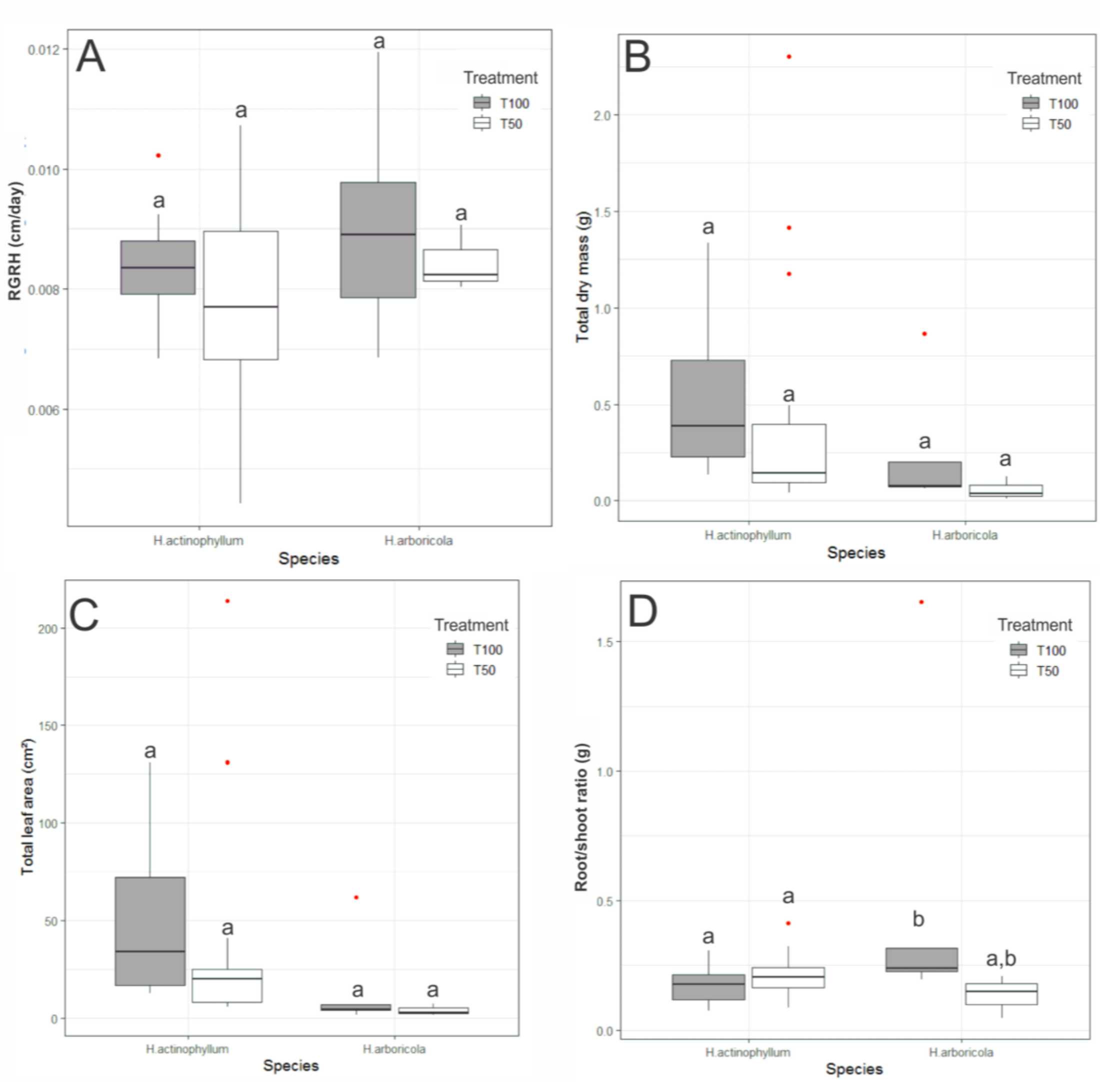

Figure 4. A) RGRH - Relative growth rate based on height; B) Total dry mass; C) Total leaf area; D) Root/shoot ratio. The central line in the box indicates the median, the higher and lower lines, the quartiles 25 and 75%,

vertical lines on top and at the bottom of each boxplot represent maximum and minimum values in the database. *Outliers* were verified using the *"Dharma*" package in R software; only the red dot in graph D represents an outlier for *H. arboricola*; the other dots are data away from the mean, but not considered outliers by the *"Dharma"* package. There is no significant difference between groups that share the same letter.

DISCUSSION

We found differences in the germination and survival parameters between native and non-native species of *Schefflera* s.l. Germination proportion was higher for non-native invasive species, which also germinated faster than native species. Germination proportion and velocity were higher in the 50% light treatment for all species. The non-native species had higher survival rates at 50% light, while survival was higher for *H. actinopyllum* in both conditions. The low germination proportion of the native species prevented the comparison of growth parameter between the native and non-native species. Root/shoot comparisons indicated that *H. arboricola* invested proportionally more in roots than *H. actinophyllum*, especially in the 100% light treatment.

Germination rate was four times higher for the non-native invasive than for native species. This result is in line with other comparative studies between non-native invasive and native species (Dickson et al. 2012, Wainwright et al. 2012, Kardol et al. 2013, Wainwright and Cleland 2013, Gioria and Pysek 2017), and may indicate that germination advantage is a factor that may facilitate invasion by the non-native species in our study (Gioria and Pysek 2017). Early germination may benefit initial establishment of the invasive species because they are able to use available resources before other species, also developing faster in conditions of interspecific competition (Abraham et al. 2009, Grman and Suding 2010).

The germination proportion of the non-native invasive species was higher compared with the native species. Even though the seeds of the native species were scarred and seeds damaged by granivory were discarded, less than 10% of the seeds germinated. The low germination rates may be a consequence of the low viability of seeds from native species, as demonstrated by Armelim (2005) for *D. angustissimus* (15% predictability), which is a limitation in the present study. Additionally, this result corroborates other studies in which low germination rates were observed for *D. angustissimus* (*e.g.* Armelin 2005, Anastácio 2010, Vilarinho et al. 2019), suggesting the possibility of physiological dormancy (Ohashi and Leão 2005). There were differences in germination percentage of the non-native invasive species between treatments, which were higher for both species at 50% light. This indicates higher shade tolerance, in turn enabling the species to invade the forest undergrowth. Invasion by these species may thus be considered a threat to tropical and subtropical forests with closed or seasonally closed canopies (Olson 2001). Records of established populations of *H. actinophyllum* and *H. arboricola* in Brazil include degraded areas as much as undisturbed subtropical humid forest and coastal scrub (*restinga*) remnants (Instituto Hórus 2022).

The non-native invasive species *H. arboricola* and *H. actinophyllum* are widely cultivated in Brazil for ornamental purposes (Lorenzi et al. 2003). Cultivated species undergo a breeding process and differ from wild species in ornamental characteristics and ecological attributes (Chrobock et al. 2011). Thus, human-mediated selection for certain characteristics may contribute to observed differences between invasive exotics and natives, such as traits that enhance germination potential (Chrobock et al. 2011). Some studies comparing individuals from cultivars and wild populations of the same species have shown that seeds from the cultivated group germinate more rapidly and in greater proportion compared to the wild group (Wilson and Mecca 2003, Chrobock et al. 2011). Therefore, targeted selection for plant cultivars, such as rapid and complete germination, may potentially increase the likelihood of becoming invasive (Chrobock et al. 2011).

The results obtained from the evaluation of root/shoot ratio may indicate that *H. arboricola* has higher plasticity to different light conditions, investing more in roots at higher light exposure and more in the shoot when light is low. Changes in the allocation of biomass to roots or shoot is possibly essential for seedling survival in the forest undergrowth. In general, changes in biomass allocation are commonly observed in the behavior of woody non-native invasive species under low light conditions in the forest undergrowth (Leicht-Young et al. 2007, Granata et al. 2020). Fridley et al. (2023) suggest the existence of a particular class of woody invasive species, termed ‘superinvasives’. In comparison with co-occurring native species, the species in this group grow faster under abundant light, persist in the shade and allocate many resources to seed production (Fridley et al. 2023). Considering these criteria, and based on the results of our study, *H. arboricola* may be considered a ‘superinvasive’ species, once it grew faster under 100% light in comparison with the native species, and had more persistent seedlings under conditions of lower light (50%).

Low light availability is a limiting condition to plant growth in forest ecosystems (Chazdon et al. 1996, Pattinson et al. 1998). Therefore, the ability to develop mechanisms to optimize light capture is an important determinant of competitive capacity of plants able to survive under low light (Chazdon et al. 1996, Pattinson et al. 1998). Phenotypical plasticity allows plants to occupy a high diversity of ecological niches, contributing to the success of biological invasions especially in the establishment phase (Matesanz et al. 2010, Godoy et al.

2011). The results obtained from our study highlight the potential of the non-native species evaluated, especially *H. arboricola*, to invade forest borders, clearings, or the forest interior under closed canopies.

CONCLUSIONS

Differences in germination and survival were verified between non-native invasive and native species in the genus *Schefflera* s.l. The higher germination proportion and germination velocity of the non-native invasive species compared with the native species contribute to initial establishment as they benefit from reduced competition. Both non-native invasive species are shade-tolerant, therefore able to germinate in the forest undergrowth. Our results indicate possible plasticity of *H. arboricola* in the allocation of root/shoot biomass under different conditions of light availability. This attribute may contribute to establishment and invasion success in forests. Invasion success by *H. arboricola* in forest ecosystems is likely favored by attributes characteristic of 'superinvasive' species. Both *H. actinophyllum* and *H. arboricola* should be considered a threat to closed canopy forests.

ACKNOWLEDGEMENTS

We thank Fundação de Amparo à Pesquisa e Inovação do Estado de Santa Catarina (FAPESC) for the Doctorate scholarship provided to AAC. PF received financial support from CNPq (Bolsa de Produtividade em Pesquisa # 310502/2019-5, # 309205/2022-0 and PROTAX 22/2020 #441445/2020-9) and FAPESC (Suplemento a Edital Externo FAPESC 13/2020 # 2021TR389). MSD received financial support from CNPq (Bolsa de Produtividade em Pesquisa # 302880/2022-4).

AUTHORS' CONTRIBUTIONS

AAC, PF, and MSD delineated the study; AAC, PF, and MSD located the species populations and collected seeds for the experiment; AAC cared for the seedlings; AAC performed the statistical analyses; AAC, RBS, PF, and MSD wrote the text. All authors contributed to revisions and discussions in the manuscript. All authors gave final approval for publication.

REFERENCES

Abraham, J.K., Corbin, J.D., D'Antonio, C.M. (2009) California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. *Plant Ecology* 201, 445–456. https://doi.org/10.1007/978-90-481-2798-6_7

Anastácio, M.R., Santana, D.G.D., Oliveira, R.C.D., Babata, M.M., Oliveira, C.A.A.D. (2010) Maturação e qualidade física de frutos na germinação dos pirênios de *Schefflera morototoni* (Araliaceae). *Ciência Florestal* 20, 429-437. https://doi.org/10.5902/198050982058

Antúnez, I., Retamosa, E.C., Villar, R. (2001) Relative growth rate in phylogenetically related deciduous and evergreen woody species. *Oecologia* 128, 172–180. http://www.jstor.org/stable/4222993

Aravind, J., Vimala, D., Radharani, J., Jacob, S.R., Srinivasa, K. (Eds.) (2019) *The germinationmetrics package: A brief introduction*. New Delhi, India: ICAR-National Bureau of Plant Genetic Resources.

Armelin, R.S. (2005) As dinâmicas de *Schefflera angustissima* (March.) Frodin (Araliaceae) e de *Andira anthelmia* (Vell.)March. (Fabaceae) na Reserva de Morro Grande, São Paulo. [Doctoral thesis, Universidade de São Paulo]. https://www.teses.usp.br/teses/disponiveis/41/41134/tde-11012006-090156/en.php

Atlas of living Australia. Australian Plant Census: *Schefflera actinoplhylla* (Endl.) Harms. http://bie.ala.org.au/species/http://id.biodiversity.org.au/node/apni/2919723. Accessed 20 June 2017.

Berg, C., Drescher, A., Wagner, V., Essl, F. (2016) Temporal trends in the invasions of Austrian woodlands by alien trees. *Preslia* 88(2), 185-200. http://www.preslia.cz/2016.html#berg

Burns, J.H. (2006) Relatedness and environment affect traits associated with invasive and non-invasive introduced Commelinaceae. *Ecological Applications* 16, 1367–1376. https://doi.org/10.1890/1051-0761

CABI - Invasive species compendium. Rojas-Sandoval, J., Acevedo-Rodrigues, P. *Schefflera actinophylla*. https://www.cabi.org/isc/datasheet/48920. Accessed 20 January 2020.

Carvalho, P. (2008) Aipim-Brabo (*Schefflera angustissimum*). *Embrapa Florestas-* Circular Técnica (INFOTECA-E). https://www.infoteca.cnptia.embrapa.br/bitstream/doc/314966/1/circtec156.pdf

Chazdon, R.L., Pearcy, R.W., Lee, D.W., Fetcher, N. (1996) Photosynthetic responses of tropical forest plants to contrasting light environments. In: Mulkey, S., Chazdon, R.L., Smith, A.P. (Eds.). *Tropical plant ecophysiology* (pp 5-55). Chapman & Hall: New York.

Chen, J., Henny, R.J., McConnell, D.B. (2003) Development of New Foliage Plant Cultivars. In: Janick, J., Whipkey, A. (Eds.), *Trends in new crops and new uses* (pp. 466-472). ASHS press: Alexandria.

Chrobock, T., Kempel, A., Fischer, M., van Kleunen, M. (2011). Introduction bias: Cultivated alien plant species germinate faster and more abundantly than native species in Switzerland. *Basic and Applied Ecology* 12(3), 244-250. https://doi.org/10.1016/j.baae.2011.03.001

CRIA - Centro de Referência e Informação Ambiental. 2018. Specieslink - simple search. http://www.splink.org.br/index. Accessed 02 April 2018.

Davis, M.A., Grime, J.P., Thompson, K. (2000) Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology* 88(3), 528– 534.https://doi.org/10.1046/j.1365-2745.2000.00473.x

Dickson, T., Hopwood, J., Wilsey, B. (2012) Do priority effects benefit invasive plants more than native plants? An experiment with six grassland species. *Biological Invasions* 14, 2617–2624. https://doi.org/10.1007/s10530-012-0257-2

Duffin, K.I., Li, S.P., Meiners, S.J. (2019) Species pools and differential performance generate variation in leaf nutrients between native and exotic species in succession. *Journal of Ecology* 107(2), 595-605. https://doi.org/10.1111/1365-2745.13043

Fiaschi, P., Plunkett, G.M. (2018) Revision of the *Didymopanax* group of Neotropical *Schefflera* (Araliaceae). *Annals of the Missouri Botanical Garden* 103(1), 24-105. https://doi.org/10.3417/2017031

Fiaschi, P., Lowry, P.P., Plunkett, G.M. (2020) Studies in Neotropical Araliaceae. III. Resurrection of the New World genus *Didymopanax* Decne. & Planch., previously included in *Schefflera* (Araliaceae). *Brittonia* 72, 16-22. https://doi.org/10.1007/s12228-019-09604-w

Franco, E.T.H., Ferreira, A.G. (2002) Tratamentos pré-germinativos em sementes de *Didymopanax morototoni* (Aubl.) Dcne. et Planch. *Ciência Florestal* 12(1), 1-10. https://doi.org/10.5902/198050981695

Fridley, J.D., Bellingham, P.J., Closset-Kopp, D., Daehler, C.C., Dechoum, M.S., Martin, P.H., Murphy, H.T., Rojas-Sandoval, J., Tng, D. (2023) A general hypothesis of forest invasions by woody plants based on whole-plant carbon economics. *Journal of Ecology* 111(1), 4-22. https://doi.org/10.1111/1365-2745.14001

Funk, J.L. (2008) Differences in plasticity between invasive and native plants from low resource environment. *Journal of Ecology* 96, 1162–1173. https://doi.org/10.1111/j.1365-2745.2008.01435.x

Gioria, M., Pyšek, P. (2017) Early bird catches the worm: germination as a critical step in plant invasion. *Biological Invasions* 19(4), 1055-1080. https://doi.org/10.1007/s10530-016-1349-1

Godoy, O., Saldaña, A., Fuentes, N., Valladares, F., Gianoli, E. (2011) Forests are not immune to plant invasion: phenotypic plasticity and local adaptation allow *Prunella vulgaris* to colonize a temperate evergreen rainforest. *Biological Invasions* 13, 1615-1625. https://doi.org/10.1007/s10530-010-9919-0

Granata, M.U., Bracco, F., Catoni, R. (2020) Phenotypic plasticity of two invasive alien plant species inside a deciduous forest in a strict nature reserve in Italy. *Journal of Sustainable Forestry* 39(4), 346-364. https://doi.org/10.1080/10549811.2019.1670678

Grman, E., Suding, K.N. (2010) Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. *Restoration Ecology* 18, 664–670. https://doi.org/10.1111/j.1526-100X.2008.00497.x

Gucker, C.L. (2011) *Schefflera actinophylla*. Fire Effects Information System., USA: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. http://www.fs.fed.us/database/feis/. Accessed 14 February 2020.

Holm, S. (1979) A Simple Sequentially Rejective Multiple Test Procedure. *Scandinavian Journal of Statistics* 6 (2), 65-70. https://www.jstor.org/stable/4615733

Instituto Hórus de Desenvolvimento e Conservação Ambiental (2020) I3N – Invasives Information Network Brasil. http://i3n.institutohorus.org.br/www. Accessed 10 january 2020.

Kaplan, E.L., Meier, P. (1958) Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53(282), 457-481.

Kardol, P., Souza, L., Classen, A.T. (2013) Resource availability mediates the importance of priority effects in plant community assembly and ecosystem function. *Oikos* 122, 84–94. https://doi.org/10.1111/j.1600-0706.2012.20546.x

Kassambara, A., Kosinski, M., Biecek, P., Fabian, S. (2017) Package 'survminer'. Drawing Survival Curves using 'ggplot2'(R package version 03 1).

Leffler, A.J., James, J.J., Monaco, T.A., Sheley, R.L. (2014) A new perspective on trait differences between native and invasive exotic plants. *Ecology* 95, 298–305. https://doi.org/10.1890/13-0102.1

Leicht-Young, S.A., Silander, J.A., Latimer, A.M. (2007) Comparative performance of invasive and native *Celastrus* species across environmental gradients. *Oecologia* 154, 273-282. https://doi.org/10.1007/s00442-007-0839-3

Lenth, R., Lenth, M.R. (2018) Package '*lsmeans*'. *The American Statistician* 34(4), 216-221.

Lorenzi, H., Souza, H.M., Torres, M.A.V., Bacher, L.B. (2003) *Árvores exóticas no Brasil: madeiras, ornamentais e aromáticas*. Instituto Plantarum: Nova Odessa.

Lowry, P.P., Plunkett, G.M. (2020) Resurrection of the genus *Heptapleurum* for the Asian clade of species previously included in *Schefflera* (Araliaceae). *Novon* 28(3), 143-170. https://doi.org/10.3417/2020612

Lusk, C.H., Jorgensen, M.A. (2013) The whole-plant compensation point as a measure of juvenile tree light requirements. *Functional Ecology* 27(6), 1286–1294. https://doi.org/10.1111/1365-2435.12129

Marciniak, B., Dechoum, M.S., Castellani, T.T. (2019) The danger of non-native gardens: risk of invasion by *Schefflera arboricola* associated with seed dispersal by birds. *Biological Invasions* 22(3), 997-1010. https://doi.org/10.1007/s10530-019-02139-x

Matesanz, S., Gianoli, E., Valladares, F. (2010) Global change and the evolution of phenotypic plasticity in plants. *Annual NY Academic Science* 1206, 35–55. https://doi.org/10.1111/j.1749-6632.2010.05704.x

Mathakutha, R., Steyn, C., le Roux, P.C., Blom, I.J., Chown, S.L., Daru, B.H., Ripley, B.S., Loun, A., Greve, M. (2019) Invasive species differ in key functional traits from native and non-invasive alien plant species. *Journal of Vegetation Science* 30(5), 994-1006. https://doi.org/10.1111/jvs.12772

Martin, P.H., Canham, C.D., Marks, P.L. (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Frontiers in Ecology Environmental* 7, 142–149. https://doi.org/10.1890/070096

Martin, P., Canham, C., Kobe, R. (2010) Divergence from the growth-survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. *Journal of Ecology* 98, 778–789. https://doi.org/10.1111/j.1365-2745.2010.01666.x

Medvecká, J., Jarolímek, I., Hegedüšová, K., Škodová, I., Bazalová, D., Botková, K., Šibíková, M. (2018) Forest habitat invasions–Who with whom, where and why. *Forest Ecology and Management* 409, 468-478. https://doi.org/10.1016/j.foreco.2017.08.038

Moodley, D., Geerts, S., Richardson, D.M., Wilson, J.R.U. (2013) Different Traits Determine Introduction, Naturalization and Invasion Success In Woody Plants: Proteaceae as a Test Case. *PLoS one* 8, 1–8. https://doi.org/10.1371/journal.pone.0075078

Ohashi, S.T., Leão, N.V.M. (2005) Morototó *Schefflera morototoni* (Aubl.) Maguire,

Steyern. & Frodin. *Informativo Técnico Rede de Sementes da Amazônia*, n. 12, https://www.inpa.gov.br/sementes/iT/12_Morototo.pdf

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R. (2001) Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience* 51, 933-938. https://doi.org/10.1641/0006-3568

Pattison, R.R., Goldstein, G., Ares, A. (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* 117(4), 449–459. https://doi.org/10.1007/s004420050680

Plunkett, G.M., Lowry II, P.P. (2012). Phylogeny and diversification in the Melanesian *Schefflera* clade (Araliaceae) based on evidence from nuclear rDNA spacers. *Systematic Botany* 37, 279–291. https://doi.org/10.1600/036364412x616837

Plunkett, G.M., Lowry II, P.P., Frodin DG, Wen J (2005) Phylogeny and geography of *Schefflera*: Pervasive polyphyly in the largest genus of Araliaceae. *Annual Missouri Botanical Garden* 92, 202–224. https://www.jstor.org/stable/3298514

Plunkett, G.M., Lowry II, P.P., Fiaschi, P., Frodin, D.G., Nicolas, A.N. (2019) Phylogeny, biogeography, and morphological evolution among and within the Neotropical and Asian clades of *Schefflera* (Araliaceae). *Taxon* 68, 1278–1313. https://doi.org/10.1002/tax.12177

Porté, A.J., Lamarque, L.J., Lortie, C.J., Michalet, R., Delzon, S. (2011) Invasive *Acer negundo* outperforms native species in non-limiting resource environments due to its higher phenotypic plasticity. *BMC Ecology* 11, 1-13. https://doi.org/10.1186/1472-6785-11-28

R Development Core Team (2014) R: A language and environment for statistical computing - R Foundation for Statistical Computing. *R Project for Statistical Computing*. http://www.R-project.org.

Accessed 24 June 2021.

Rasband, W.S. (2020) ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA.https://imagej.nih.gov/ij/. Accessed 31 March 2020.

Rejmánek, M. (2014) Invasive trees and shrubs: where do they come from and what we should expect in the future? *Biological Invasions* 16(3), 483-498. https://doi.org/10.1007/s10530-013-0603-z

Rich, J.T., Neely, J.G., Paniello, R.C., Voelker, C.C., Nussenbaum, B., Wang, E.W. (2010) A practical guide to understanding Kaplan-Meier curves. *Otolaryngology—Head and Neck Surgery* 143(3), 331-336. https://doi.org/10.1016/j.otohns.2010.05.007

Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J., Pigliucci, M. (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9, 981–993. https://doi.org/10.1111/j.1461-0248.2006.00950.x

Sendall, K.M., Lusk, C.H., Reich, P.B. (2016) Trade-offs in juvenile growth potential vs. Shade tolerance among subtropical rain forest trees on soils of contrasting fertility. *Functional Ecology* 30(6), 845–855. https://doi.org/10.1111/1365-2435.12573

Stricker, K., Stiling, P. (2013) Seedlings of the introduced invasive shrub *Eugenia uniflora* (Myrtaceae) outperform those of its native and introduced non-invasive congeners in Florida. *Biological invasions* 15, 1973-1987. https://doi.org/10.1007/s10530-013-0425-z

Therneau, T., Lumley, T. (2013) R survival package. *R Core Team*.

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

Vibrans, A.C., Sevegnani, L., Gasper, A.L., Lingner, D.V. (2013) *Inventário Florístico Florestal de Santa Catarina: Floresta Ombrófila Densa* (v. 4). Edifurb: Blumenau.

Vilarinho, M.K., Sales, V.H., Nascimento, J., Caldeira, D., Souza, W. (2019) Quebra de dormência em sementes de *Schefflera morototoni* (Aubl.) Maguire et al. *Enciclopédia Biosfera* 16(29). https://doi.org/10.18677/EnciBio_2019A115

Wainwright, C.E., Cleland, E.E. (2013) Exotic species display greater germination plasticity and higher germination rates than native species across multiple cues. *Biological Invasions* 15(10), 2253-2264. https://doi.org/10.1007/s10530-013-0449-4

Wainwright, C.E., Wolkovich, E.M., Cleland, E.E. (2012) Seasonal priority effects: implications for invasion and restoration in a semi-arid system. *Journal of Applied Ecology* 49, 234–241. https://doi.org/10.1111/j.1365-2664.2011.02088.x

Wilson, S.B., Mecca, L.K. (2003) Seed production and germination of eight cultivars and the wild type of *Ruellia tweediana*: A potentially invasive ornamental. *Journal of Environmental Horticulture* 21, 137–143. https://doi.org/10.24266/0738-2898-21.3.137

Yu, H.W., He, W.M. (2021) Congeneric invasive versus native plants utilize similar inorganic nitrogen forms but have disparate use efficiencies. *Journal of Plant Ecology* 14(2), 180-190. https://doi.org/10.1093/jpe/rtaa085

SUPPLEMENTARY MATERIAL

Table 1. Results of the comparison by pairs of germination proportions between treatments, per species. Abbreviations: T50 – treatment in which shading was used to maintain 50% light incidence; T100 –treatment in which seedlings were directly exposed to full light. *p* numbers in bold indicate significant values.

Treatment: comparisons between species	**Estimate**	**SE**	**ratio**	***p* value**
Treatment T100				
*H. actinophyllus (*T100)-*D. angustissimus* (T100)	0.16	0.004	32.73	**<.0001**
H. actinophyllus (T100)-*D. calvus* (T100)	0.18	0.004	37.64	**<.0001**
H.arboricola (T100)-*D. angustissimus* (T100)	-0.07	0.004	-15.50	**<.0001**
H.arboricola (T100)-*D.calvus* (T100)	0.09	0.004	20.40	**<.0001**
H. actinophyllus (T100)-*H.arboricola* (T100)	0.08	0.004	17.24	**<.0001**
D. angustissimus (T100)-*D.calvus* (T100)	0.02	0.004	4.91	**<.0001**
Treatment T50				
H. actinophyllus (T50)-*D. angustissimus* (T50)	0.15	0.004	32.73	**<.0001**
H. actinophyllus (T50)-*D. calvus* (T50)	0.18	0.004	37.64	**<.0001**
H.arboricola (T50)-*D. angustissimus* (T50)	-0.07	0.004	-15.50	**<.0001**
H.arboricola (T50)-*D.calvus* (T50)	0.09	0.04	20.40	**<.0001**
H. actinophyllus (T50)-*H.arboricola* (T50)	0.08	0.004	17.24	**<.0001**
D. angustissimus (T50)-*D.calvus* (T50)	0.02	0.004	4.91	**<.0001**
Comparison treatments T100 X T50				
H. actinophyllus (T50)-*H. actinophyllus* (T100)	-0.04	0.003	-13.33	**<.0001**
H. arboricola (T50)-*H. arboricola* (T100)	-0.04	0.003	-13.33	**<.0001**
D. angustissimus (T50)-*D. angustissimus* (T100)	-0.04	0.003	-13.33	**<.0001**
D. calvus (T50)-*D. calvus* (T100)	-0.04	0.003	-13.33	**<.0001**

Table 2. Results of the comparison by pairs between indices of germination velocity (IVG) between treatments, per species. *p* numbers in bold indicate significant values.

Treatment: comparisons between species	**Estimate**	**SE**	***t* ratio**	***p* value**
Treatment T100				

*H. actinophyllus (*T100) – *D. angustissimus* (T100)	16.96	0.36	46.93	**<.0001**
H. actinophyllus (T100) - *D. calvus* (T100)	18.87	0.60	31.42	**<.0001**
H.arboricola (T100) - *D. angustissimus* (T100)	-15.37	0.48	-32.00	**<.0001**
H.arboricola (T100) - *D.calvus* (T100)	17.28	0.67	25.49	**<.0001**
H. actinophyllus (T100) – *H.arboricola* (T100)	1.58	0.39	3.98	**0.0009**
D. angustissimus (T100) - *D.calvus* (T100)	1.91	0.65	2.92	**0.010**
Treatment T50				
H. actinophyllus (T50) – *D. angustissimus* (T50)	16.96	0.36	46.93	**<.0001**
H. actinophyllus (T50) - *D. calvus* (T50)	18.87	0.60	31.42	**<.0001**
H.arboricola (T50) - *D. angustissimus* (T50)	-15.37	0.48	-32.00	**<.0001**
H.arboricola (T50) - *D.calvus* (T50)	17.28	0.67	25.49	**<.0001**
H. actinophyllus (T50) – *H.arboricola* (T50)	1.58	0.39	3.98	**0.0009**
D. angustissimus (T50) - *D.calvus* (T50)	1.91	0.65	2.92	**0.010**
Comparisons T100 X T50				
H. actinophyllus (T50) – *D. actinophyllus* (T100)	-6.57	0.28	-23.25	**<.0001**
H. arboricola (T50) – *H. arboricola* (T100)	-6.57	0.28	-23.22	**<.0001**
D. angustissimus (T50) - *D. angustissimus* (T100)	-6.57	0.28	-23;22	**<.0001**
D. calvus (T50) – *D. calvus* (T100)	-6.57	0.28	-23.22	**<.0001**

Table 3. Mean total life time (days) and standard deviation per species and per treatment; and percentage of seedlings that survived until the end of the experiment (180 days).

Species	**Mean total life time**	**Mean life time T50**	**Mean life time T100**
Native			
D. angustissimus	139.41(±54.0)	141 (±63.3)	137 (±41.9)
D. calvus	156.00 (±39.1)	150 (±51.9)	165 (±21.2)
Non-native			
H. actinophyllum	167.83(±31.9)	165 (±32.4)	171 (±32)
H. arboricola	126.52(±57.8)	120 (±60)	135 (±57)

Table 4. Comparisons between growth parameters means conducted by pairs between species by contrast. Abbreviations: RGRH–relative growth rate based on height. *p* numbers in bold indicate significant differences between the total means of the species compared.

Comparisons between species	**RGRH (*p* value)**	**Leaf area (*p* value)**	**Dry mass (*p* value)**	**Root/shoot ratio: (*p* value)**
Non-native x non-native				
H. actinophyllum - H. arboricola	0.16	0.09	0.14	**0.05**

Table 5. Means and total standard deviation per species, and means and standard deviation per treatment and per species. *p* values represent the comparison between treatments for each species. Abbreviations: RGRH–relative growth rate based on height; SD–standard deviation; T50 – treatment in which shading was used to maintain 50% light incidence; T100 –treatment in which seedlings were directly exposed to full light.

	Mean/SD total		**Mean/SD between treatments**				***p* value between treatments**
	Mean	**SD**	**T50**	**SD**	**T100**	**SD**	
RGRH (cm/day)							
Non-native							
H. actinophyllum	0.008	0.001	0.007	0.001	0.008	0.001	0.34
H. arboricola	0.008	0.001	0.008	0.001	0.009	0.005	0.59
LEAF AREA (cm²)							
Non-native							
H. actinophyllum	42.36	49.60	38.78	56.40	47.60	39.15	0.64
H. arboricola	11.51	20.59	4.07	3.10	15.97	25.89	0.36
DRY MASS (g)							
Non-native							
H. actinophyllum	0.46	0.51	0.41	0.58	0.53	0.39	0.57
H. arboricola	0.18	0.28	0.05	0.061	0.25	0.034	0.29
ROOT/SHOOT RATIO							

Non-native							
H. actinophyllum	0.19	0.07	0.21	0.08	0.17	0.06	0.20
H. arboricola	0.37	0.52	0.13	0.08	0.52	0.63	0.22

CONSIDERAÇÕES FINAIS

Florestas neotropicais encontram-se em um estado crítico de ameaça em virtude dos impactos antrópicos. No capítulo 1 verificamos que as florestas neotropicais subtropicais são mais susceptíveis ao estabelecimento de plantas lenhosas exóticas invasoras, comparado a florestas tropicais. A deciduidade foliar que ocorre nestas florestas, devido à diminuição de temperatura, promove a diminuição da barreira física do dossel e aumento de luminosidade, favorecendo a chegada e o estabelecimento de propágulos de plantas invasoras. Também verificamos que as florestas com maior acessibilidade são mais susceptíveis à invasão por espécies lenhosas exóticas invasoras, devido à maior disponibilidade de propágulos de espécies cultivadas nas regiões do entorno.

No capítulo 2 verificamos que as espécies exóticas invasoras mostraram maior proporção e velocidade de germinação quando comparadas às nativas, característica que contribui para o estabelecimento inicial, uma vez que espécies que germinam antecipadamente se beneficiam da competição reduzida. Verificamos também uma maior proporção de germinação de espécies invasoras sob 50% de luz, resultado que pode indicar que ambas as espécies invasoras possuem tolerância à sombra, conseguindo germinar mesmo sob condições mais escuras do subosque florestal. Sugerimos também que a espécie exótica invasora *Heptapleurum arboricola* possui atributos de uma 'superinvasora' em potencial (crescimento superior sob luz e persistência de plântulas sob sombra). Somado a isto, a maior plasticidade na alocação de biomassa raiz:parte aérea em condições de diferentes luminosidades contribui para o sucesso no estabelecimento e invasão de florestas.

Em síntese, os resultados obtidos neste estudo mostram que florestas de dossel fechado não limitam a ocorrência de espécies exóticas invasoras, como é o caso das espécies de *Schefflera* s.l. aqui estudadas. Somado a isto, a crescente pressão antrópica à qual as florestas neotropicais estão sujeitas contribuem para o aumento da riqueza das espécies exóticas invasoras, aumentando ainda mais a susceptibilidade destes ecossistemas à invasão por plantas.