UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
Instituto de Biociências
Programa de Pós-Graduação em Ecologia

ecologia
UFRGS

Tese de Doutorado

MODELOS DE DISTRIBUIÇÃO DE ESPÉCIES INVASORAS: TENDÊNCIAS E APLICAÇÕES

Fabiana Gonçalves Barbosa

Porto Alegre, abril de 2011

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Tese de Doutorado

MODELOS DE DISTRIBUIÇÃO DE ESPÉCIES INVASORAS: TENDÊNCIAS E APLICAÇÕES

Fabiana Gonçalves Barbosa

Orientador: Prof. Dr. Adriano Sanches Melo

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Doutor em Ciências com ênfase em Ecologia.

Comissão Examinadora

Prof. Dr. Fernando Gertum Becker (UFRGS)
Prof. Dr. João Carlos Nabout (UEG)
Prof. Dr. Valério De Patta Pillar (UFRGS)

Porto Alegre, abril de 2011

AGRADECIMENTOS

Em primeiro lugar, agradeço aos meus pais, Henrique e Jane, pelo carinho e pelos sacrifícios que fizeram ao longo da vida para garantir a mim uma boa formação educacional. Agradeço também a minha irmã Fernanda, meu afilhado Leonardo e minha madrinha Janir por todo carinho e apoio.

Ao meu orientador Adriano Sanches Melo pelo apoio incondicional para desenvolver esta tese. Agradeço-o também por me apresentar modelos de distribuição de espécies e pelas diversas oportunidades para aprimorar o meu conhecimento. Muito obrigada Adriano!

Aos colegas de laboratório Fabi Schneck, Luiz Hepp, Márlon Vasconcelos, Pâmela Flach e Solana Boschilia pela companhia e convivência. Em especial, agradeço a Fabi Schneck pelas ajudas inestimáveis com o programa R.

Ao Miguel Bastos Araújo pela co-orientação durante estágio sanduíche junto a Cátedra Rui Nabeiro na Universidade de Évora – Portugal. Agradeço também ao pessoal da Cátedra, pelos auxílios referentes à minha pesquisa e estadia e pela companhia durante os seis meses que passei em Évora. Em especial, a Dora Neto pelo suporte com Sistemas de Informação Geográfica (SIG).

Aos co-autores dos artigos, Adriano S. Melo, Anthony Palmer, Fabi Schneck, Miguel B. Araújo e Valério D. Pillar. Em especial, agradeço a Anthony Palmer e Valério D. Pillar pela

concessão dos registros de ocorrência de *Eragrotis plana*, fundamentais para o desenvolvimento do segundo artigo.

Ao Programa de Pós-graduação em Ecologia (UFRGS) e a Cátedra Rui Nabeiro da Universidade de Évora – Portugal, por toda a estrutura.

Aos colegas, funcionários e professores do Pós-graduação em Ecologia. Em especial a Silvana Barzotto, secretária do PPG, por estar sempre tão disposta a ajudar.

Aos colegas de Laboratório de Ecologia de Insetos (UFG) e do Programa de Pós-graduação em Ecologia e Evolução (UFG). Em especial, agradeço a Dani Almeida e Priscila Lemes de Azevedo Silva.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela concessão da bolsa de doutorado e bolsa de doutorado sanduíche.

A todas as pessoas que de forma direta ou indireta contribuíram para a realização deste trabalho.

RESUMO

Modelos de distribuição de espécies, também conhecidos como modelos bioclimáticos ou modelos de nicho ecológico, têm sido aplicados em inúmeras questões ecológicas, incluindo espécies invasoras. Essa tese identificou as principais tendências e lacunas de estudos sobre o uso de modelos de distribuição de espécies para predizer a distribuição potencial de espécies invasoras (primeiro artigo). Adicionalmente, aplicou-se modelos de distribuição de espécies para predizer a distribuição potencial de *Eragrostis plana* Nees na América do Sul e verificar se ocorreu mudança de seu nicho bioclimático durante o processo de invasão (segundo artigo). Finalmente, avaliou-se a resposta em relação às áreas de ocorrência de cinco gramíneas Africanas invasoras nas Américas frente às mudanças climáticas (terceiro artigo). O primeiro artigo realiza uma análise cienciométrica sobre o uso de modelos de distribuição de espécies para predizer a distribuição potencial de espécies invasoras. O segundo artigo utiliza o Algoritmo GARP como técnica de modelagem e foram criados dois modelos para predizer a distribuição potencial de *E. plana*: um utilizando dados da região nativa da espécie (África do Sul) e outro com dados da região nativa e invadida (regiões da Argentina, Brasil e Uruguai). Posteriormente, cada modelo foi projetado na América do Sul para identificar regiões favoráveis ao estabelecimento de *E. plana* e verificar se os registros de ocorrência da espécie encontram-se dentro das regiões preditas com alta probabilidade pelos modelos. Além disso, a hipótese de que espécies podem alterar o seu nicho climático durante o processo de invasão foi avaliada para *E. plana* através de análises estatísticas multivariadas. O terceiro artigo aplica distintas técnicas de modelagem disponíveis no ambiente computacional BIOMOD, seguidas de conjunto de previsões para predizer a distribuição potencial das cinco gramíneas invasoras Africanas nas Américas frente às mudanças climáticas globais.

Palavras-chave: cienciometria, conjunto de previsões, GARP, gramíneas Africanas invasoras, invasão biológica, mudança de nicho ambiental, mudanças climáticas globais.

ABSTRACT

Species distribution models, also known as bioclimatic models or ecological niche models, have been applied in numerous ecological issues, including invasive species. This thesis indentified the main trends and gaps in studies on the use of species distribution models to predict the potential distribution of invasive species (first paper). Additionally, it includes species distribution modelling to predict the potential distribution of *Eragrostis plana* Nees in South America and assess the potential shift of its bioclimatic niche in the process of invasion (second paper). Finally, it includes as assessment of the response in terms of areas of occurrence of five invasive African grasses in the Americas under climate changes (third paper). The first paper provides a scientometric analysis on the use of species-distribution models to predict the potential distribution of invasive species. The second paper uses the algorithm GARP as modelling method and created two models to predict the potential distribution of *E. plana*: the first one used data from the native region (South Africa) and the second one data from both the native and invaded (Argentina, Brazil, and Uruguay). Subsequently, each model was projected in South America to identify regions favorable to the establishment of *E. plana* and assess whether the occurrence records are found within regions predicted by the models with high probability. Moreover, the hypothesis that species can shift their bioclimatic niche during the invasion process was evaluated for *E. plana* using multivariate statistical analysis. The third paper applies distinct modelling methods available in the BIOMOD package, followed by ensembles forecasting to predict the potential distribution of five invasive African grasses in Americas under climate changes.

Keywords: biological invasion, ensemble forecasting, environmental niche shift, GARP, global climate change, invasive African grasses, scientometric.

SUMÁRIO

2. CAPÍTULOS

LISTA DE FIGURAS

INTRODUÇÃO GERAL

CAPÍTULOS

Artigo I

Artigo II

Artigo III

LISTA DE TABELAS

INTRODUÇÃO GERAL

CAPÍTULOS

Artigo I

Artigo III

LISTA DE APÊNDICES

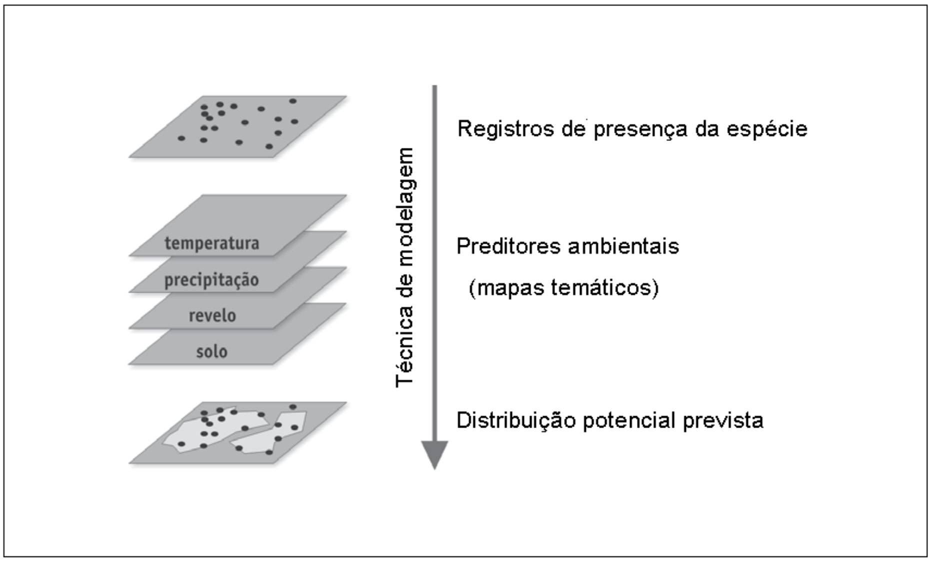
CAPÍTULOS

Artigo III

1. INTRODUÇÃO GERAL

1.1. Modelos de Distribuição de Espécies

Nas duas últimas décadas a aplicação de modelos de distribuição de espécies, também conhecidos como modelos bioclimáticos e modelos de nicho ecológico (ver Elith & Leathwick 2009 para outras denominações), cresceu consideravelmente (Guisan & Thuiller 2005). Tais modelos são criados a partir de técnica de modelagem que relaciona registros de ocorrência da espécie com um conjunto de preditores ambientais para encontrar ambientes adequados, onde uma população possa se manter viável (Guisan & Zimmermann 2000, Anderson et al. 2003). Os resultados produzem previsões probabilísticas de onde a espécie poderá ou não estar presente e a área projetada representa a distribuição potencial da espécie estudada baseada nos preditores ambientais utilizados na modelagem (Guisan & Thuiller 2005, Araújo & Guisan 2006) (Figura 1).



•

Figura 1. Esquema ilustrando o processo de criação de um modelo de distribuição de espécie (adaptada de Scachetti-Pereira & de Siqueira 2007).

1.1.1. Registros de Ocorrência da Espécie e Preditores Ambientais

Os registros de ocorrência da espécie, ou seja, registros de presença e ausência, são representados na forma de coordenadas geográficas (latitude e longitude) e utilizados para alimentar, calibrar e validar os modelos de distribuição de espécies (Guisan & Zimmermann 2000, Guisan & Thuiller 2005). Os registros de presença da espécie são obtidos dos acervos de coleções de herbários e museus (Elith & Leathwick 2007) e de coletas de espécimes e/ou observações de campo (Soberón & Peterson 2004). Além disso, a disponibilidade de bases de dados de biodiversidade, via internet (ver Tabela 1 para algumas bases de dados disponíveis), têm contribuído para o fácil acesso aos registros de presença das espécies (Canhos et al. 2004, Graham et al. 2004, Soberón & Peterson 2004). Por outro lado, os registros de ausência são raros e quando disponíveis devem ser usados com certo cuidado (Gu & Swihart 2004). Esse cuidado é necessário porque no momento de coleta/amostragem a espécie pode não ter sido detectada embora esteja presente no habitat. Ainda a espécie pode estar ausente no local, mas por razões históricas (por exemplo, barreiras geográficas), interações bióticas (por exemplo, competição e predação) ou humanas, embora o habitat seja adequado (Hirzel et al. 2002, Gu & Swihart 2004).

Os preditores ambientais consistem de mapas temáticos, onde cada mapa possui um conjunto de células contínuas no espaço geográfico com valores de um determinado preditor ambiental. Os preditores mais frequentemente utilizados são oriundos de dados refinados através de técnicas de interpolação, por exemplo, dados climáticos (New et al. 2002, IPCC 2001, Hijmans et al. 2005), e de dados de imagens de satélites (Bradley & Fleishman 2008, Andrew & Ustin 2009), por exemplo cobertura e uso do solo, topográficos, índices de cobertura vegetal e tipos de vegetação e dados de salinidade e temperatura dos oceanos.

Tabela 1. Bases de dados de biodiversidade disponíveis via internet.

Base de dados	Organismos	Site
Global Biodiversity Information Facility (GBIF)	animais, microorganismos e plantas	http://www.gbif.org
InfoNatura	aves, mamíferos e anfíbios da América do Sul	http://www.natureserve.org/infonatura
Instituto Hórus	animais e plantas invasoras do Brasil	http://www.institutohorus.org.br
FishBase	Peixes	http://www.fishbase.org
Herpnet	anfíbios e répteis	http://www.herpnet.org
South African National Biodiversity Institute (SANBI)	animais e plantas da África do Sul	http://www.sanbi.org
SpeciesLink	animais, microorganismos e plantas	http://splink.cria.org.br

Continuação da Tabela 1.

Global Invasive Species Database (GISD)	animais, microorganismos e plantas invasores	http://www.issg.org/database/welcome
Tropicos	plantas	http://www.tropicos.org

Existe um consenso de que, em escalas mais amplas (global ou continental), preditores climáticos, tais como precipitação e temperatura, são mais apropriados para criar modelos de distribuição de espécies. Por outro lado, em escalas menores (regional ou local) outros preditores tornam-se importantes, tais como cobertura e uso do solo (Luoto et al. 2007, Tingley & Herman 2009, Titeux et al. 2009). Assim como os bancos de dados de biodiversidade, as bases de dados ambientais disponíveis são também diversas (Canhos et al. 2004, Sillero & Tarroso 2010) (ver Tabela 2 para algumas bases de dados disponíveis).

Tabela 2. Bases de dados ambientais disponíveis via internet.

Bases de dados	Tipo de dado	Site
Intergovernmental Panel on Climate Change (IPCC)	climáticos	http://www.ipcc.ch
Climatic Research Unit (CRU)	climáticos	http://www.cru.uea.ac.uk
PRISM	climáticos	http://www.prism.oregonstate.edu
Worldclim	climáticos	http://www.worldclim.org

Continuação da Tabela 2.

Hydro1K Elevation Derivative Database	topográficos	http://eros.usgs.gov
Global Land Cover	cobertura da terra	http://edc2.usgs.gov/glcc/glcc.php
Ocean Biogeographic Information System (OBIS)	dados ambientais aquáticos	http://www.iobis.org
Global Land Use Data	uso da terra	http://www.sage.wisc.edu/iamdata

Diante desta vasta disponibilidade de dados, estudos têm sido desenvolvidos para comparar o desempenho de diversos preditores ambientais para prever a distribuição potencial de espécies (Parra et al. 2004, Seoane et al. 2004, Luoto & Heikkinen 2008, Peterson & Nakazawa 2008) ou conjunto de preditores ambientais (Guisan & Hofer 2003, Pearson et al. 2004, Bomhard et al. 2005). Entretanto, dentro de um grande conjunto inicial de preditores ambientais pode existir preditores correlacionados ou preditores com baixo poder preditivo e, portanto, é necessário realizar uma pré-seleção de preditores ambientais usando, por exemplo, Análise de Componentes Principais (PCA) ou Árvore de Regressão, para reduzir a dimensionalidade do conjunto inicial, o que por sua vez proporciona coerência na explanação dos resultados dos modelos (Segurado et al. 2006).

1.1.2. Técnicas de Modelagem e Conjunto de Previsões

Atualmente, existem diversas técnicas de modelagem que podem ser usadas para relacionar os registros de ocorrência da espécie com um conjunto de preditores ambientais (Guisan & Thuiller 2005, Heikkinen et al. 2006) (ver Tabela 3 para algumas técnicas disponíveis). Além disso, existem programas e ambientes computacionais para modelagem que disponibilizam somente uma técnica de modelagem, tais como MAXENT (Phillips et al. 2006) e DesktopGarp (Stockwell & Noble 1992), e ambientes com várias técnicas de modelagem, tais como BIOMOD (Thuiller et al. 2009), ModEco (Guo & Liu 2010) e OpenModeller (Sutton et al. 2007) (ver Tabela 4 para alguns programas e ambientes computacionais disponíveis).

Tabela 3. Algumas técnicas de modelagem disponíveis, classe da técnica segundo a abordagem empregada e exemplos de estudos que aplicaram a técnica.

Técnica de modelagem	Classe	Estudos
Modelo Aditivo Generalizado (GAM)	Regressão	Granadeiro et al. 2004, Trivedi et al. 2008
Modelo Linear Generalizado (GLM)		Guisan & Hofer 2003, Brotons et al. 2007
Curvas de Regressão Adaptativas Multivariadas (MARS)		Leathwick et al. 2005, Mateo et al. 2010
Algoritmo Genético para Produção de Conjunto de Regras (GARP)	Aprendizagem de Máquina	Peterson et al. 2003, Sanchez-Flores 2007
Florestas Aleatórias (RF)		Benito-Garzón et al. 2007, Calleja et al. 2009
Máxima Entropia (MAXENT)		Giovanelli et al. 2008, Phillips & Dudik 2008
Redes Neurais Artificiais (ANN)		Hilbert & Ostendorf 2001, Dedecker et al. 2004
Máquinas de Vetores de Suporte (SVM)		Guo et al. 2005, Drake et al. 2006

Continuação da Tabela 3.

AquaMaps BIOCLIM Surface Range Envelope (SRE)	Envelope Ambiental	Ready et al. 2010 Beaumont et al. 2005, 2007 Beaumont & Hughes 2002
DOMAIN Mahalanobis	Distância Ambiental	Carpenter et al. 1993 Farber & Kadmon 2003, Rotenberry et al. 2006
Análise Discriminante Multivariada (MDA) Árvore de Classificação (CTA)	Classificação	Manel et al. 1999 Vayssiéres et al. 2000, Thuiller et al. 2003
Análise Fatorial de Nicho Ecológico (ENFA)	Ordenação	Cassinello et al. 2006, Acevedo et al. 2007

Tabela 4. Ambiente computacional ou programa, técnicas de modelagem e site do ambiente computacional ou programa.

Ambiente computacional ou programa	Técnica de modelagem	Site
Diva-Gis	BIOCLIM e DOMAIN	http://www.diva-gis.org
BIOMOD	GLM, GAM, CTA, ANN, MDA, MARS, GBM, RF e SRE	http://r-forge.r-project.org/projects/biomod
OpenModeller	AquaMaps, ANN, BIOCLIM, Climate Space Model, Envelope Score, Algoritmos de Distância Ambiental, GARP, SVM, Maxent	http://www.openmodeller.souceforge.net
MAXENT	Maxent	http://www.cs.princeton.edu/~schapire/maxent
BIOMAPPER	ENFA	http://www.unil.ch/biomapper
ModEco	BIOCLIM, DOMAIN, GLM, CTA, ANN, Maxent, SVM, naïve Bayes e rough sets	http://gis.ucmerced.edu/ModEco
DesktopGarp	GARP	http://www.nhm.ku.edu/desktopgarp

Em geral, as técnicas de modelagem são classificadas em dois grupos baseados nos tipos de dados utilizados: i) técnicas que empregam somente registros de presença, por exemplo, BIOCLIM e DOMAIN, e ii) técnicas que empregam registros de presença e ausência, por exemplo, GLM e GAM. Entretanto, algumas técnicas de modelagem utilizam registros de presença e pontos escolhidos aleatoriamente na região de estudo, conhecidos como pseudo-ausências, para construir os modelos, embora estas técnicas ainda sejam classificadas como técnicas que empregam somente registros de presença porque não há emprego real de registros de ausência na criação do modelo (por exemplo, GARP e MAXENT (Tsoar et al. 2007).

Desta forma, estudos têm comparado o desempenho de diferentes técnicas de modelagem para tentar encontrar técnicas estatisticamente mais robustas (Segurado & Araújo 2004, Elith et al. 2006, Leathwick et al. 2006, Tsoar et al. 2007) e estudos que comparam e discutem os resultados dos mapas de distribuição potencial de determinada espécie(s) criados por diferentes técnicas de modelagem (Nabout et al. 2009, Colombo & Joly 2010, Wang et al. 2010). No entanto, é difícil chegar num consenso sobre a técnica de modelagem mais robusta. Assim, para reduzir as incertezas das previsões, Araújo & New (2007) sugerem combinar as previsões dos modelos individuais criados por cada uma das técnicas de modelagem de forma a produzir um conjunto de previsões.

Existem várias métricas que podem ser utilizadas para sintetizar um conjunto de previsões (Araújo & New 2007). No caso de estudos envolvendo modelos de distribuição de espécies, os métodos de consenso são os mais aplicados (Marmion et al. 2009). Os métodos de consenso vão de simples funções aritméticas, tais como média e mediana (Araújo & New

2007, Marmion et al. 2009), a métodos que possuem um algoritmo pré-seletivo, tais como média ponderada e Análise de Componentes Principais (Thuiller 2004, Marmion et al. 2009). Marmion et al. (2009) compararam o desempenho de cinco métodos de consenso mais aplicados em estudos de modelos de distribuição de espécies e constataram que os métodos de consenso média ponderada e média foram estatisticamente mais robustos que os outros métodos e modelos individuais que constituem o consenso. Além disso, o emprego de conjunto de previsões tem demonstrado previsões robustas em estudos de modelos de distribuição de espécies (Coetzee et al. 2009, Roura-Pascual et al. 2009, Diniz-Filho et al. 2010, Marini et al. 2010, Ogawa-Onishi et al. 2010, Stohlgren et al. 2010).

1.1.3. Aplicações dos Modelos de Distribuição de Espécies

Os modelos de distribuição de espécies têm sido aplicados em inúmeras questões ecológicas (ver Guisan & Thuiller 2005). Por exemplo, modelos têm sido aplicados para: i) auxiliar na determinação de áreas prioritárias para conservação (Chen & Peterson 2002, Ortega-Huerta & Peterson 2004, Garcia 2006, Marini et al. 2009), ii) conservação de espécies endêmicas, raras e ameaçadas (Guisan et al. 2006, de Siqueira et al. 2009, Carvalho et al. 2010, Lomba et al. 2010), iii) prever a distribuição potencial de espécies invasoras (Peterson et al. 2003, Giovanelli et al. 2008, Thuiller et al. 2005, Stohlgren et al. 2010) e iv) compreender o impacto das mudanças climáticas globais na distribuição de espécies (Bakkenes et al. 2002, de Siqueira & Peterson 2003, Araújo et al. 2006, Ogawa-Onishi et al. 2010).

1.1.3.1. Modelos de Distribuição de Espécies Invasoras e Mudança de Nicho

No contexto de espécies invasoras, os modelos de distribuição de espécies podem ser criados com os registros de ocorrência e preditores ambientais da região nativa da espécie. Posteriormente, o modelo criado é projetado fora de sua região nativa para identificar regiões que apresentem características ambientais adequadas ao estabelecimento dessa espécie (Peterson & Vieglais 2001, Peterson 2003) (Figura 2), assumindo que o nicho se conserva no espaço e tempo (Pearman et al. 2008). Modelos de distribuição de espécies também podem ser criados usando registros de ocorrência e preditores ambientais da região invadida pela espécie, assumindo que a espécie está em equilíbrio com o meio ambiente (Wilson et al. 2007). Posteriormente, o modelo criado é projetado fora de sua região invadida para identificar regiões que apresentem características ambientais adequadas ao estabelecimento dessa espécie (Figura 3). Sendo assim, modelos têm sido criados tanto com dados da região nativa da espécie (Peterson et al. 2003, Fonseca et al. 2006, Ficetola et al. 2007, Giovanelli et al. 2008), como com dados da região invadida pela espécie (Mau-Crimmins et al. 2006, Estrada-Peña et al. 2007, Oliveira et al. 2010).

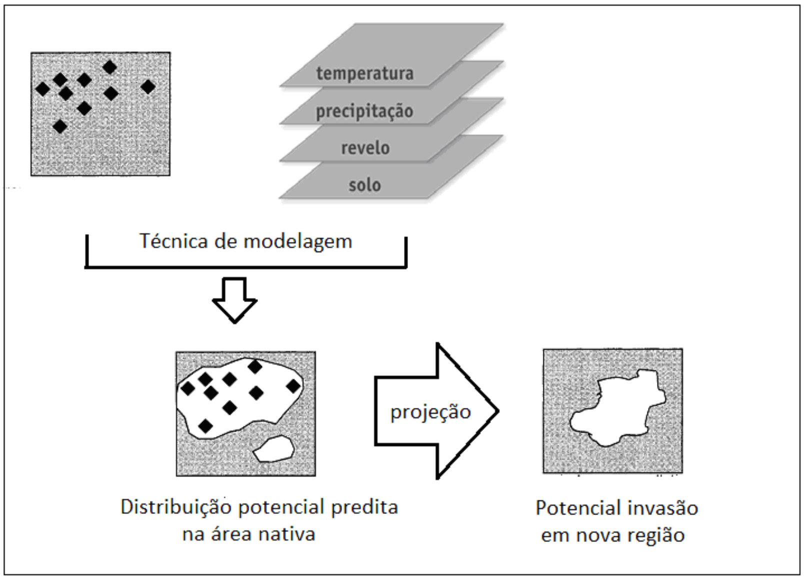


Figura 2. Esquema ilustrando o processo de criação de um modelo de distribuição de espécies usando dados da região nativa da espécie e posterior projeção em uma nova região indicando áreas potenciais para o seu estabelecimento

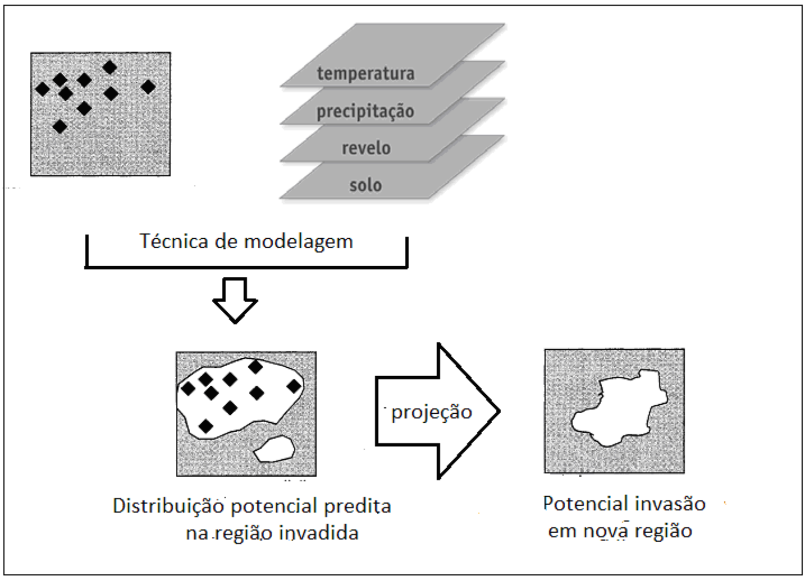


Figura 3. Esquema ilustrando o processo de criação de um modelo de distribuição de espécies usando dados da região invadida pela espécie e posterior projeção em uma nova região indicando áreas potenciais para o seu estabelecimento

Entretanto, caso o processo de invasão não esteja totalmente completo, os modelos criados com dados da área invadida pela espécie provavelmente não serão robustos para predizer sua distribuição potencial (Broennimann & Guisan 2008). Além disso, alguns modelos criados com registros de ocorrência e mapas temáticos da área nativa da espécie quando projetados fora de sua região nativa para identificar regiões que apresentem características ambientais adequadas ao estabelecimento da espécie foram capazes de predizer somente a região de introdução, mas não a região total invadida pela espécie (Broennimann et al. 2007, Estrada-Peña et al. 2007). Isto leva à hipótese de que espécies podem alterar o seu nicho ambiental durante o processo de invasão. Broennimann et al. (2007), por exemplo, usando dados da área nativa (Europa) de uma gramínea invasora (*Centaurea maculosa* Lam.) na América do Norte, mostraram que o modelo criado foi capaz de predizer corretamente a região de introdução nos Estados Unidos, mas não a região total de invasão. Neste sentido, estudos têm sugerido como alternativa o uso de dados de ambas as regiões nativa e invadida para criar os modelos de distribuição de espécies invasoras (Mau-Crimmins et al. 2006, Broennimann & Guisan 2008, Beaumont et al. 2009a) (Figura 4), pois podem ser mais representativos para identificar regiões onde a espécie pode se dispersar (Mau-Crimmins et al. 2006). Além disso, análises adicionais têm sido empregadas, tais como medidas de sobreposição de nicho e/ou análises estatísticas multivariadas, para avaliar a hipótese de que espécies podem alterar o seu nicho ambiental durante o processo de invasão (Broennimann et al. 2007, Beaumont et al. 2009a, Mata et al. 2010).

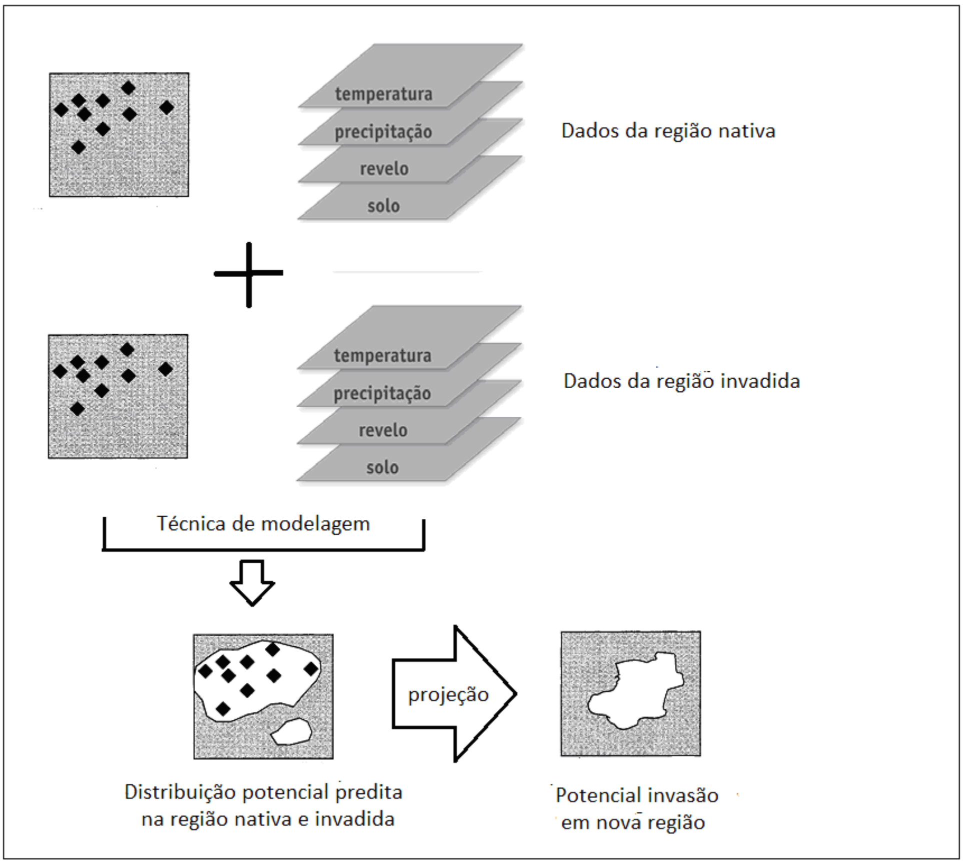


Figura 4. Esquema ilustrando o processo de criação de um modelo de distribuição de espécies usando dados da região nativa e invadida pela espécie e posterior projeção em uma nova região indicando áreas potenciais para o seu estabelecimento

1.1.3.2. Modelos de Distribuição de Espécies Invasoras frente às Mudanças Climáticas Globais

No contexto de mudanças climáticas globais, os modelos de distribuição de espécies são criados com registros de ocorrência de espécies e preditores climáticos atuais. Posteriormente, o modelo criado é projetado no mesmo espaço geográfico ou em um novo espaço sob cenário de clima futuro para predizer a distribuição potencial futura da espécie (Pearson & Dawson 2003, Thuiller 2004). Neste sentido, modelos de distribuição de espécies têm sido aplicados para predizer o impacto das mudanças climáticas sobre a distribuição potencial de espécies invasoras, tais como plantas (Beaumont et al. 2009b, Bradley 2009, Parker-Allie et al. 2009), insetos (Roura-Pascual et al. 2004) e anfíbios e répteis (Rödder et al. 2008, Rödder et al. 2009). Os modelos criados têm demonstrado que a distribuição potencial de determinadas espécies invasoras pode diminuir (Bradley 2009, Bradley et al. 2009) ou aumentar (Kriticos et al. 2003, Bradley et al. 2010) frente às mudanças climáticas.

1.1.4. Uso dos Mapas de Modelos de Distribuição de Espécies Invasoras em Ações de Prevenção e Restauração

Invasões biológicas e mudanças climáticas representam sérias ameaças à biodiversidade mundial (Sala et al. 2000, Thomas et al. 2004). A distribuição potencial de espécies invasoras predita por modelos de distribuição de espécies podem servir de base para medidas pró-ativas. Por exemplo, os casos preditos de invasão/dispersão potencial após estabelecimento da espécie dentro da região invadida e expansão potencial da espécie invasora frente às mudanças climáticas podem ser usados como base para medidas de prevenções atuais e futuras (Arriaga et al. 2004, Lee et al. 2008, Bradley et al. 2010), uma vez que medidas de controle e erradicação são muitas vezes ineficazes e com custos elevados (Simberloff 2003, Hulme 2006). Por outro lado, a contração da distribuição potencial de espécies invasoras frente às mudanças climáticas pode criar oportunidades de restauração (Bradley & Wilcove 2009, Bradley et al. 2009).

1.2. Organização da Tese

Essa tese investiga as tendências sobre o uso de modelos de distribuição de espécies para predizer a distribuição potencial de espécies invasoras e aplica estes modelos para predizer a distribuição potencial de gramíneas invasoras Africanas nas Américas. Para isso, o presente estudo foi estruturado em três artigos. O primeiro artigo busca identificar as principais tendências e lacunas de estudos sobre o uso de modelos de distribuição de espécies para predizer a distribuição potencial de espécies invasoras através de uma análise cienciométrica. O segundo artigo aplica modelos de distribuição de espécies para predizer a distribuição potencial da gramínea Africana *Eragrostis plana* Nees na América do Sul. Para esse estudo, o algoritmo GARP foi utilizado como técnica de modelagem e foram criados dois modelos: um utilizando dados da região nativa da espécie (África do Sul) e outro com dados da região nativa e invadida (regiões da Argentina, Brasil e Uruguai). Posteriormente, cada modelo foi projetado na América do Sul para identificar regiões favoráveis ao estabelecimento de *E. plana* e verificar se os registros de ocorrência da espécie encontram-se dentro das regiões preditas com alta probabilidade pelos modelos. Além disso, a hipótese de que espécies podem alterar o seu nicho climático durante o processo de invasão foi verificado para *E. plana* através de análises estatísticas multivariadas. O terceiro artigo aplica modelos de distribuição de espécies para predizer o impacto das mudanças climáticas globais sobre a distribuição de cinco gramíneas invasoras Africanas nas Américas. Foram utilizadas diversas técnicas de modelagem disponíveis no ambiente computacional BIOMOD foram utilizadas, seguidas de conjunto de previsões para predizer a distribuição potencial das cinco gramíneas invasoras Africanas nas Américas frente às mudanças climáticas globais.

A primeira seção, Introdução Geral, de uma maneira geral, definiu e abordou modelos de distribuição de espécies, assim como suas aplicações, incluindo espécies invasoras. Da segunda a quarta seção (capítulos) encontram-se os três artigos. Os artigos I e II seguem a formatação de citação e referências bibliográficas do período *Biological Invasions*. O artigo II segue a formatação de citação e referências bibliográficas do período *Global Change Biology*. Finalmente, a última seção, Considerações Finais, agrupa as principais conclusões desses artigos.

1.3. Referências Bibliográficas

Acevedo P., Alzaga V., Cassinello J., Gortázar C. (2007) Habitat suitability modelling reveals a strong niche overlap between two poorly known species, the broom hare and the Pyrenean grey partridge, in the north of Spain. Acta Oecologica, 31:174-184.

Anderson RP., Lew D., Peterson AT. (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecological Modelling, 162:211-232.

Andrew ME. & Ustin SL. (2009) Habitat suitability modelling of an invasive plant with advanced remote sensing data. Diversity and Distributions, 15:627-640.

Araújo BA. & Guisan A. (2006) Five (or so) challenges for species distribution modelling. Journal of Biogeography, 33:1677-1688.

Araújo BA., Thuiller W., Pearson RG. (2006) Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography, 33:1712-1728.

Araújo MB. & New M. (2007) Ensemble forecasting of species distributions. Trends in Ecology & Evolution, 22:42-47.

Arriaga L., Castellanos AE., Moreno E., Alarcon J. (2004) Potential ecological distribution of alien invasive species and risk assessment: a case study of buffel grass in arid regions of Mexico. Conservation Biology, 18:1504-1514.

Bakkenes M., Alkemade JRM., Ihle F., Leemansand R., Latour JB. (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Global Change Biology, 8:390-407.

Beaumont LJ. & Hughes L. (2002) Potential changes in the distribution of latitudinally restricted Australian butterfly species in response to climate change. Global Change Biology, 8:951-971.

Beaumont LJ., Hughes L., Poulsen M. (2005) Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. Ecological Modelling, 186:250-269.

Beaumont LJ., Pitman AJ., Poulsen M., Hughes L. (2007) Where will species go? Incorporating new advances in climate modelling into projections of species distributions. Global Change Biology, 13:1368-1385.

Beaumont LJ., Gallagher RV., Thuiller W., Downey PO., Leishman MR., Hughes L. (2009a) Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. Diversity and Distributions, 15:409-420.

Beaumont LJ., Gallagher RV., Downey PO., Thuiller W., Leishman MR., Hughes L. (2009b) Modelling the impact of *Hieracium* spp. on protected areas in Australia under future climates. Ecography, 32:757-764.

Benito-Garzón M., de Dios RS., Ollero HS. (2007) Predictive modelling of tree species distributions on the Iberian Peninsula during the Last Glacial Maximum and Mid-Holocene. Ecography, 30:120-134.

Bomhard B., Richardson DM., Donaldson JS., Hughes GO., Midley GF., Raimondo DC., Recelo AG., Rouget M., Thuiller W. (2005) Potential impacts of future land use and climate change on the Red List status of the Proteaceae in the Cape Floristic Region, South Africa. Global Change Biology, 11:1452-1468.

Bradley BA. & Fleishman E. (2008) Can remote sensing of land cover improve species distribution modelling? Journal of Biogeography, 35:1158-1159.

Bradley B. (2009) Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Global Change Biology, 15:196-208.

Bradley BA. & Wilcove DS. (2009) When invasive plants disappear: transformative restoration possibilities in the western United States resulting from climate change. Restoration Ecology, 17:715-721.

Bradley BA., Oppenheimer M., Wilcove DS. (2009) Climate change and plant invasions: restoration opportunities ahead? Global Change Biology, 15:1511-1521.

Bradley BA., Wilcove DS., Oppenheimer M. (2010) Climate change increases risk of plant invasion in the Eastern United States. Biological Invasions, 12:1855-1872.

Broennimann O., Treier UA., Muller-Scharer H., Thuiller W., Peterson AT., Guisan A. (2007) Evidence of climatic niche shift during biological invasion. Ecology Letters 10:701-709.

Broennimann O. & Guisan A. (2008) Predicting current and future biological invasions: both native and invaded ranges matter. Biology Letters, 4:585-589.

Brotons L., Herrando S., Pla M. (2007) Updating bird species distribution at large spatial scale: applications of habitat modelling to data from long-term monitoring programs. Diversity and Distributions, 13:276-288.

Canhos VP., Souza S., Giovanni R., Canhos AL. (2004) Global biodiversity informatics: setting the scene for a “New World” of ecological modeling. Biodiversity Informatics, 1:1-13.

Calleja JA., Benito-Garzón M., Ollero HS. (2009) A quaternary perspective on the conservation prospects of the Tertiary relict tree *Prunus lusitanica* L. Journal of Biogeography, 36: 487-498.

Carpenter G., Gillison AN., Winter J. (1993) DOMAIN: a flexible modeling procedure for mapping potential distributions of plants and animals. Biodiversity and Conservation, 2:667-680.

Carvalho SB., Brito JC., Crespo EJ., Possingham HP. (2010) From climate change predictions to actions – conserving vulnerable animal groups in hotspots at a regional scale. Global Change Biology, 16:3257-3270.

Cassinello J., Acevedo P., Hortal J. (2006) Prospects for population expansion of the exotic aoudad (Ammotragus lervia; Bovidae) in the Iberian Peninsula: clues from habitat suitability modelling. Diversity and Distributions, 12:666-678.

Chen G. & Peterson AT. (2002) Prioritization of areas in China for the conservation of endangered birds using modeled geographical distributions. Bird Conservation International, 12:197-209.

Coetzee BW., Robertson MP., Erasmus BFN., van Rensburg BJ., Thuiller W. (2009) Ensemble models predict important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. Global Ecology and Biogeography, 18:701-710.

Colombo AF. & Joly CA. (2010) Brazilian Atlantic forest lato sensu: the most ancient Brazilian forest, and a biodiversity hotspot, is highly threatened by climate change. Brazilian Journal of Biology, 70:697-708.

Dedecker AP., Goethals PLM., Gabriels W., de Pauw N. (2004) Optimization of Artificial Neural Network (ANN) model design for prediction of macroinvertebrates in the Zwalm river basin (Flanders, Belgium). Ecological Modelling, 174:161-173.

de Siqueira MF., Durigan G., de Marco Júnior P., Peterson AT. (2009) Something from nothing: using landscape similarity and ecological niche modeling to find rare plant species. Journal for Nature Conservation, 17:25-32.

de Siqueira MF. & Peterson AT. (2003) Consequences of global climate change for geographic distributions of Cerrado tree species. Biota Neotropica, 3:1-14.

Diniz-Filho JAF., Nabout JC., Bini LM., Loyola RD., Rangel TFLB., Nogués-Bravo D., Araújo MB. (2010) Ensemble forecasting and geographic range of *Tropidacris cristata* (Orthoptera: Acridoidea: Romaleidae) under climate change. Insect Conservation and Diversity, 3:213-221.

Drake JM., Randin C., Guisan A. (2006) Modelling ecological niche with support vector machines. Journal of Applied Ecology, 43:424-432.

Elith J., Graham CH., Anderson RP., Dudik M., Ferrier S., Guisan A., Hijmans RJ., Huettmann F., Leathwick JR., Lehmann A., Li J., Lohmann LG., Loiselle BA., Manion, G, Moritz C., Nakamura M., Nakazawa Y., Overton J., Peterson AT., Phillips SJ., Richardson K., Scachetti-Pereira R., Schapire RE., Soberón J., Williams S., Wisz MS., Zimmermann NE. (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29:129-151.

Elith J. & Leathwick J. (2007) Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. Diversity and Distributions, 13:265-275.

Elith J. & Leathwick J. (2009) Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics, 40:677-697.

Estrada-Peña G., Pegram RG., Barré N., Venzal JM. (2007) Using invaded range data to model the climate suitability for *Amblyomma variegatum* (Acari: Ixodidae) in the New World. Experimental and Applied Acarology, 41:203-214.

Farber O. & Kadmon R. (2003) Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. Ecological Modelling, 160:115-130.

Ficetola GF., Thuiller W., Miaud C. (2007) Prediction and validation of the potential global distribution of a problematic alien invasive species - the American bullfrog. Diversity and Distributions, 13: 476-485.

Fonseca RL., Guimarães PR., Morbiolo SR., Scachetti-Pereira R. (2006) Predicting invasive potential of smooth crotalaria (*Crotalaria pallida*) in Brazilian national parks based on African records. Weed Science, 54:458-463.

Garcia A. (2006) Using ecological niche modelling to identify diversity hotspots for the herpetofauna of Pacific lowlands and adjacent interior valleys of Mexico. Biological Conservation, 130:25-46.

Giovanelli JGR., Haddad CFB., Alexandrino J. (2008) Predicting the potential distribution of the alien invasive American bullfrog (Lithobates catesbeianus) in Brazil. Biological Invasions, 10:585-590.

Graham CH., Ferner S., Huettman F., Moritz C., Peterson AT. (2004) New developments in museum-based informatics and applications in biodiversity analysis. Trends in Ecology and Evolution, 19:497-503.

Granadeiro JP., Andrade J., Palmeirim JM. (2004) Modelling the distribution of shorebirds in estuarine areas using generalized additive models. Journal of Sea Research, 52:227-240.

Guisan A. & Zimmermann NE. (2000) Predictive habitat distribution models in ecology. Ecological Modelling, 135:147-186.

Guisan A. & Hofer U. (2003) Predicting reptile distributions at the mesoscale: relation to climate and topography. Journal of Biogeography, 30:1233-1243.

Guisan A. & Thuiller W. (2005) Predicting species distribution: offering more than simple habitat models. Ecology Letters, 8:993-1009.

Guisan A., Broennimann O., Engler R., Vust M., Yoccoz NG., Lehmann A., Zimmermann NE. (2006) Using niche-based models to improve the sampling of rare species. Conservation Biology, 20:501-511.

Gu W. & Swihart RK. (2010) Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. Biological Conservation, 116:195-203.

Guo Q., Kelly M., Graham CH. (2005) Support vector machines for predicting distribution of sudden oak death in California. Ecological Modelling, 182:75-90.

Guo Q. & Liu Y. (2010) ModEco: an integrated software package for ecological niche modeling. Ecography, 33:1-6.

Heikkinen RK., Luoto M., Araújo MB., Virkkala R., Thuiller W., Sykes MT. (2006) Methods and uncertainties in bioclimatic envelope modeling under climate change. Progress in Physical Geography, 30:751-777.

Hijmans RJ., Cameron SE., Parra JL., Jones PG., Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25:1965-1978.

Hilbert DW. & Ostendorf B. (2001) The utility of artificial neural networks for modelling the distribution of vegetation past, present and future climates. Ecological Modelling, 146:311-327.

Hirzel AH., Hausser J., Chessel D., Perrin N. (2002) Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology, 83:2027-2036.

Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. Journal of Applied Ecology, 43:835-847.

International Panel on Climate Change (IPCC). (2001) Climate change 2001: synthesis report. Cambridge University Press, London.

Kriticos DJ., Sutherst RW., Brow JR., Adkins SW, Maywald GF. (2003) Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. Indica in Australia. Journal of Applied Ecology, 40:111-124.

Leathwick JR., Rowe D., Richardson J., Elith J., Hastie T. (2005) Using multivariate adaptive regression splines to predict the distributions of New Zealand's freshwater diadromous fish. Freshwater Biology, 50:2034-2052.

Leathwick JR., Elith J., Hastie T. (2006) Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. Ecological Modelling, 199:188-186.

Lee H., Reusser DA., Olden JD., Smith SS., Graham JIM., Burkett V., Dukes JS., Piorkowski RJ., McPhedran J. (2008) Integrated monitoring and information systems for managing aquatic invasive species in a changing climate. Conservation Biology, 22:575-584.

Lomba A., Pellissier L., Randin C., Vicente J., Moreira F., Honrado J., Guisan A. (2010) Overcoming the rare species modelling paradox: A novel hierarchical framework applied to an Iberian endemic plant. Biological Conservation, 143:2647-2657.

Luoto M., Virkkala R., Heikkinen RK. (2007) The role of land cover in bioclimatic models depends on spatial resolution. Global Ecology and Biogeography, 16:34-42.

Luoto M. & Heikkinen RK. (2008) Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. Global Change Biology, 14:483-494.

Manel D., Dias JM., Buckton ST., Ormerod SJ. (1999) Alternative methods for predicting species distribution: an illustration with Himalayan river birds. Journal of Applied Ecology, 36:734-747.

Marini MA., Barbet-Massin M., Lopes LE., Jiguet F. (2009) Major current and future gaps of Brazilian reserves to protect Neotropical savanna birds. Biological Conservation, 142:3039-3050.

Marini MA., Barbet-Massin M., Lopes LE., Jiguet F. (2010) Predicting the occurrence of rare Brazilian birds with species distribution models. Journal of Ornithology, 151:857-866.

Marmion M., Parviainen M., Luoto M., Heikkinen RK., Thuiller W. (2009) Evaluation of consensus methods in predictive species distribution modelling. Diversity and Distributions, 15:59-69.

Mata RA., Tidon R., Côrtes LG., De Marco P., Diniz-Filho JAF. (2010) Invasive and flexible: niche shift in the drosophilid *Zaprionus indianus* (Insecta, Díptera). Biological Invasions, 12:1231-1241.

Mateo RG., Felicisimo AM., Munoz J. (2010) Effects of the number of presences on reliability and stability of MARS species distribution models: the importance of regional niche variation and ecological heterogeneity. Journal of Vegetation Science, 21:908-922.

Mau-Crimmins TM., Schussman HR., Geiger EL. (2006) Can the invaded range of a species be predicted sufficiently using only native-range data? Lehmann lovegrass (*Eragrostis lehmanniana*) in the southwestern United States. Ecological Modelling, 193:736-746.

Nabout JC., de Marco Júnior P., Bini LM., Diniz-Filho JAF. (2009) Distribuição geográfica potencial de espécies americanas do caranguejo “violinista” (*Uca* spp) (Crustácea, Decapoda) com base em modelagem de nicho ecológico. Iheringia – Série Zoologia, 99:92-98.

New M., Lister D., Hulme M., Makin I. (2002) A high-resolution data set of surface climate over global land areas. Climate Research, 21:1-25.

Ogawa-Onishi Y., Berry PM., Tanaka N. (2010) Assessing the potential impacts of climate change and their conservation implications in Japan: A case study of conifers. Biological Conservation, 143:1728-1736.

Ortega-Huerta MA. & Peterson AT. (2004) Modelling spatial patterns of biodiversity for conservation prioritization in North-eastern Mexico. Diversity and Distributions, 10:39-54.

Oliveira MD., Hamilton SK., Calheiros DF., Jacbi CM., Latini RO. (2010) Modeling the potential distribution of the invasive golden mussel *Limnoperna fortunei* in the Upper Paraguay River system using limnological variables. Brazilian Journal of Biology, 70:831-840.

Parra JL., Graham CC., Freile JF. (2004) Evaluating alternative data sets for ecological niche models of birds in the Andes. Ecography, 27:350-360.

Parker_Allie F., Musil CF., Thuiller W. (2009) Effects of climate warming on the distributions of invasive Eurasian annual grasses: a South African perspective. Climatic Change, 94:87-103.

Pearman PB., Guisan A., Broennimann O., Randin CF. (2008) Niche dynamics in space and time. Trends in Ecology and Evolution, 21:149-158.

Pearson R. & Dawson T. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimatic envelope models useful? Global Ecology and Biogeography, 12:361-371.

Pearson RG., Dawson TP., Liu C. (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. Ecography, 27:285-298.

Peterson AT. & Vieglais DA. (2001) Predicting species invasions using ecological niche modelling: new approaches from bioinformatics attack a pressing problem. Bioscience, 51:362-371.

Peterson AT. (2003) Predicting the geographic of species' invasions via ecological niche modeling. The Quarterly Review of Biology, 78:419-433.

Peterson AT., Papes M., Kluza DA. (2003) Predicting the potential invasive distributions of four alien plant species in North America. Weed Science, 51:863-868.

Peterson AT. & Nakazawa Y. (2008) Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. Global Ecology and Biogeography, 17:135-144.

Phillips SJ., Anderson RP., Schapire RE. (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling, 190:231-259.

Phillips SJ. & Dudik M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography, 31:161-175.

Ready J., Kaschner K., South AB., Eastwood PD., Rees T., Rius J., Agbayani E., Kullander S., Froese R. (2010) Predicting the distributions of marine organisms at the global scale. Ecological Modelling, 221:467-478.

Rödder D., Solé M., Bohme W. (2008) Predicting the potential distributions of two alien invasive Housegeckos (Gekkonidae: *Hemidactylus frenatus, Hemidactylus mabouia*). North-Western Journal of Zoology, 4:236-246.

Rödder D. & Weinsheimer F. (2009) Will future anthropogenic climate change increase the potential distribution of the alien invasive Cuban treefrog (Anura: Hylidae)? Journal of Natural History, 43:1207-1217.

Rotenberry JT., Preston KL., Knick ST. (2006) GIS-based niche modeling for mapping species habitat. Ecology, 87:1458-1464.

Roura-Pascual N., Suarez AV., Gómez C., Pons P., Touyama Y., Wild AL., Peterson AT. (2004) Geographical potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change. Proceedings of the Royal Society B: Biological Sciences, 271:2527-2535.

Roura-Pascual N., Brotons L., Peterson AT., Thuiller W. (2009) Consensual predictions of potential distributional areas for invasive species: a case study of Argentine ants in the Iberian Peninsula. Biological Invasions, 11:1017-1031.

Sala OE., Chapin FS., Armesto JJ., Berlow R., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke LF., Jackson RB., Kinzig A., Leemans R., Lodge D., Mooney HÁ., Oesterheld M., Poff NL., Sykes MT., Walker BH., Walker M., Wall DH. (2000) Global biodiversity scenarios for the year 2100. Science, 287:1770-1774.

Sanchez-Flores E. (2007) GARP modeling of natural and human factors affecting the potential distribution of the invasives *Schismus arabicus* and *Brassica tournefortil* in ‘El Pinacate y Gran Desierto de Altar’ Biosphere Reserve. Ecological Modelling, 204:457-474.

Scachetti-Pereira R. & de Siqueira MF. (2007) Algoritmo genético para produção de conjunto de regras (GARP). Megadiversidade, 3:47-55.

Segurado P. & Araújo MB. (2004) An evaluation of methods for modelling species distributions. Journal of Biogeography, 31:1555-1568.

Segurado P., Araújo MB., Kunin WE. (2006) Consequences of spatial autocorrelation for niche-based models. Journal of Applied Ecology, 43:433-444.

Seoane J., Bustamante J., Díaz-Delgado R. (2004) Competing roles for landscape, vegetation, topography and climate in predictive models of bird distribution. Ecological Modelling, 171:209-222.

Sillero N. & Tarroso P. (2010) Free GIS for herpetologists: free data sources on Internet and comparison analysis of proprietary and free/open source software. Acta Herpetologica, 5:63-85.

Simberloff, D. (2003) Eradication – preventing invasions at the outset. Weed Science, 51: 247-253.

Soberón J. & Peterson AT. (2004) Biodiversity informatics: managing and applying primary biodiversity data. Philosophical Transactions of the Royal Society of London B, 359:689-698.

Stockwell DRB. & Noble IR. (1992) Induction of sets of rules from animal distribution data: a robust and informative method of analysis. Mathematics and Computers in Simulation, 33:385-390.

Stohlgren TJ., Ma P., Kumar S., Rocca M., Morisette JT., Jarnevich CS., Benson N. (2010) Ensemble habitat mapping of invasive plant species. Risk Analysis, 30:224-235.

Sutton T., Giovani R., Siqueira MF. (2007) Introducing OpenModeller. OSGeo Journal, 1:1-6.

Thomas CD., Cameron A., Green RE., Bakkenes M., Beaumont LJ., Collingahm YC., Erasmus BFN., de Siqueira MF., Grainger A., Hannah L., Hughes L., Huntley B., van Jaarsveld AS., Midley GF., Miles L., Ortega-Huerta MA., Peterson AT., Phillips OL., Williams SE. (2004) Extinction risk form climate change. Nature, 427:145-148.

Tingley R. & Herman TB. (2009) Land-cover data improve bioclimatic models for anurans and turtles at a regional scale. Journal of Biogeography, 36:1656-1672.

Titeux N., Maes D., Marmion M., Luoto M., Heikkinen RK. (2009) Inclusion of soil data improves the performance of bioclimatic envelope models for insect distributions in temperate Europe. Journal of Biogeography, 36:1459-1473.

Thuiller W., Vayreda J., Pino J., Sabate S., Lavorel S., Gracia C. (2003) Large-scale environmental correlates of forest tree distributions in Catalonia (NE Spain). Global Ecology and Biogeography, 12:313-325.

Thuiller W. (2004) Patterns and uncertainties of species' range shifts under climate change. Global Change Biology, 10:2020-2027.

Thuiller W., Richardson DM., Pysek P., Midley GF., Hughes GO., Rouget M. (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. 2005. Global Change Biology, 11:2234-2250.

Thuiller W., Lafourcade B., Engler R., Araújo MB. (2009) BIOMOD – a platform for ensemble forescating of species distributions. Ecography, 32:369-373.

Trivedi MR., Berry PM., Morecroft MD., Dawson TP. (2008) Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. Global Change Biology, 14:1089-1103.

Tsoar A., Steinitz O., Rotem D., Kadmon R. (2007) A comparative evaluation of presence only methods for modelling species distribution. Diversity and Distributions, 13:397-405.

Vayssiéres MP., Plant RE., Allen-Diaz BH. (2000) Classification trees: an alternative non-parametric approach for predicting species distributions. Journal of Vegetation Science, 11:679-694.

Wang XY., Huang XL., Jiang LY., Qiao GX. (2010) Predicting potential distribution of *chestnut phylloxerid* (Hemiptera: Phylloxeridae) based on GARP and Maxent ecological niche models. Journal of Applied Entomology, 134:45-54.

Wilson JRU., Richardson DM., Rouget M., Proches S., Amis MA., Henderson L. Thuiller W. (2007) Residence time and potential range: crucial considerations in modelling plant invasions. Diversity and Distributions, 13:11-22.

2. CAPÍTULOS

I Predicting biological invasions using species-distribution models: a scientometric analysis

II Predicting the current distribution and potential spread of the exotic grass *Eragrostis plana* Nees in South America and identifying a bioclimatic niche shift during invasion

III Impact of climate changes on the distributions of invasive African grasses in the Americas: predicted scenarios from ensemble forecast

ARTIGO I

Predicting biological invasions using species-distribution models: a scientometric analysis

Predicting biological invasions using species-distribution models: a scientometric analysis[1,2]

Abstract

We conducted a scientometric analysis to determine the main trends and gaps of studies about the use of ecological niche models (ENMs) to predict the distribution of invasive species. We used the database of the Thomson Institute for Scientific Information (ISI). We found 190 papers published between 1991 and 2010 in 82 journals. The number of papers was low in the 1990s, but began to increase after 2003. One-third of the papers were published by researchers from the United States of America, and consequently, the USA were also the most studied region. The majority of studies were carried out in terrestrial environments, while only a few investigated aquatic systems, probably because important aquatic predictor variables are scarce or unavailable for most regions in the world. Species-occurrence records were mainly composed of presence-only records, and almost 70% of the studies were carried out with plants and insects. Twenty-three different distribution modeling methods were used. The Genetic Algorithm for Rule-set Production (GARP) was used most often. Our scientometric analysis showed a growing interest in the use of ENMs to predict the distribution of invasive species, especially in the last decade, which is probably related to the increase in species introductions worldwide. Among some important gaps that need to be filled, the relatively small number of studies conducted in developing countries and in aquatic environments deserves careful attention.

---

[1] Com colaboração de Fabiana Schneck & Adriano Sanches Melo

Keywords: biodiversity, biological invasion, scientific production, trends

---

[2] Capítulo aceito para publicação no periódico Brazilian Journal Biology em 25 de janeiro de 2012

Introduction

The intensification of global trade is continuously increasing the number of exotic species (also known as non-native species or non-indigenous species) introduced intentionally or accidentally to a new area (Westphal et al., 2008). The majority of the species do not succeed in establishing in the areas where they were introduced (Mack et al., 2000), but once established, they may spread and cause ecological and/or economic problems (Pimentel et al., 2005), becoming invasive species (Mack et al., 2000).

Biological invasions are causing dramatic changes in global biodiversity, often leading to a decline and/or extinction of native species (Mack et al., 2000; Pimentel et al., 2005). The development and use of preventive measures to deal with invasive species are thus a priority in biodiversity conservation (Hulme, 2006). Preventive measures are more cost-effective than control and/or eradication measures (Leung et al., 2002). In this context, Ecological Niche Models (ENMs), also known as Bioclimatic Models, Climate Envelopes, Habitat Models, Species Distribution Models, Range Maps, and Resource Selection Functions (Elith and Leathwich, 2009), have been applied to predict the potential distribution of exotic species (Jiménez-Valverde et al., 2011). ENMs are fitted to data from a species' native area and are then used to identify suitable areas for the establishment of the invasive species in a new region (Peterson and Vieglais, 2001). Models can also be built using data from the native and invaded areas to predict the potential distribution of invasive species (Broennimann and Guisan, 2008). The models are constructed using a variety of modeling methods and combine species-occurrence records (geographical coordinates of the occurrence records) with a set of predictor variables (e.g., climate, land use type, and salinity). Models are used to predict suitable habitats in which species are able to maintain a population in order to persist through time (see Guisan and Thuiller, 2005 and Mateo et al., 2011 for reviews). Modeling methods are classified into two groups based on the type of occurrence-records input used to create the models: i) methods that use presence-only records (e.g., BIOCLIM and DOMAIN), and ii) methods that use presence and absence records (e.g., logistic regression and generalized additive model (GAM)) (Tsoar et al., 2007). Some methods use pseudo-absence data (see Engler et al., 2004 to a definition of pseudo-absence data and ways to generate these data) for model construction (e.g., Genetic Algorithm for Rule-set Production (GARP) and Maximum Entropy (MAXENT)), but these are still classified as methods that use presence-only records because there is no real use of absence records in the construction of the model (Tsoar et al., 2007).

Scientometric studies use quantitative analyses to identify irregularities, patterns, or trends that may exist in publications of a given field of scientific research (e.g. Melo et al., 2006). For instance, in the case of biological invasions, two scientometric studies found a growing academic interest in invasion ecology in recent decades (Pysek et al., 2006; Qiu and Chen, 2009). In the area of ENMs, Cayuela et al. (2009) used publications from the period 1995-2007 to perform a scientometric study on the applications of ENMs to support conservation planning in tropical areas.

We conducted a scientometric study focused on the use of ecological niche models to predict the distribution of invasive species. We analyzed papers published in peer-reviewed scientific journals from 1991 to 2010. Our main questions were: i) Is the number of papers on the use of ENMs to predict the distribution of invasive species increasing? ii) Is there a temporal trend in the quality or visibility (Scarano et al., 2009) of the journals, measured by their impact factor, in which these papers were published? iii) Which countries are the major publishers of papers using ENMs to predict the distribution of invasive species? iv) What are the main characteristics of the studies on this subject (predictor variables, methods, organisms, and regions studied)? v) What are the main gaps in the studies on this subject?

Material and Methods

We used the database of the Thomson Institute for Scientific Information (ISI; www.isiknowledge.com) to search for papers. The analysis was based on papers published between 1991 and 2010 that contained in the title, abstract, or keywords the following combination of words: “invasion* and ecological niche model* or bioclimatic model* or ecological niche model* or climate envelope* or habitat model* or species distribution model* or resource selection function* or range map*”. We collected the data from the Thomson ISI in April 2011.

We analyzed each paper according to (i) year of publication, (ii) journal of publication and impact factor of each journal, (iii) number of citations, (iv) first author’s country, (v) region covered by the study, (vi) type of species-occurrence records (presence-only, or presence and absence), (vii) biological groups (algae, amphibians, birds, fish, fungi, insects, mammals, other invertebrates, plants, and reptiles), (viii) type of predictor variables (aquatic, climatic, human, land cover, land use, soil properties, topographic, and vegetation), (ix) spatial scale of the study (global, continental, national, regional, and local), (x) environment covered by the study (aquatic or terrestrial), and (xi) methods used to generate the models in each study. We also obtained the journal impact factors from the Journal Citation Reports (JCR) published in the year of publication of each paper (JCR 1990-2009). We used the scheme presented by Pearson and Dawson (2003) to assign the environmental predictors to different spatial scales of study.

We used a regression tree to identify possible trends over time in the number of papers on the use of ENMs to predict the distribution of invasive species. This method partitions the predictor variable in segments that are composed by similar values of the response variable. Each segment is then partitioned again and the partition process continues until the number of observations is considered small (De'Ath and Fabricius, 2000; see Melo et al., 2006 for a similar use of this method). We used the relative contribution (x1000) of papers in relation to the total number of papers published in a given year in all journals in the ISI database. We conducted the analysis using the package *rpart* (Therneau and Atkinson, 2010) in the *R* environment (R Development Core Team, 2010).

To test if the impact factor of the journals in which the papers were published increased through the years, we standardized the journal impact factor in a given year to the maximum impact factor for a journal in the field of ecology in the same year. We initially conducted a linear regression. However, because of the triangular arrangement of the data in the scatter diagram, we conducted a permutation test to evaluate whether this pattern could be generated by chance (Bardsley et al., 1999). The test evaluated simultaneously whether the mean and the variation of the impact factors increased in recent years. We used the software Ecosim (Gotelli and Entsminger, 2001), module “Macroecology” to conduct the analysis.

Results

A total of 190 papers related to the use of ENMs to predict the distribution of invasive species were published between 1991 and 2010. From 1991 to 1999, few papers were published, and in several years no paper appeared on this subject. The regression tree analysis partitioned the predictor variable (i.e, year of publication) in two segments, before and after 2003.5. The segment from 1991 to 2003 corresponds to the period with a low and relatively constant proportion of papers on EMS to predict the distribution of invasive species. The second segment (2004 to 2010) reflects the period with a trend of increase in the percentage of papers published (Figure 1).

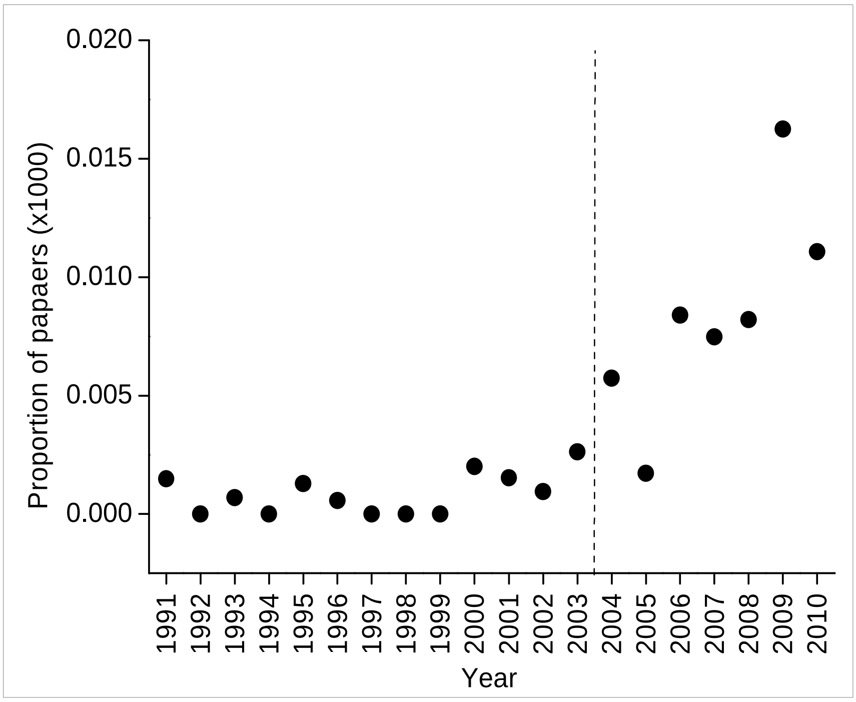


Figure 1. Proportion of papers (x1000) on the use of ecological niche models to predict the distribution invasive species in relation to the total number of papers published from 1991 to 2010, indexed by the Institute for Scientific Information (ISI). The dashed line indicates the year (2003.5) in which the regression tree partitioned the data in two segments.

The studies were published in 82 journals, although 55 of them contained only one paper and 10 contained only two papers. The 16 journals that published more than two papers on the distribution of invasive species using ENMs accounted for 60% (114 papers) of the total number of papers (Figure 2a). The journal Diversity and Distributions published 21 papers, followed by Biological Invasions (17 papers) and Weed Research (9 papers). The mean and the variation of the impact factors of the journals that published papers which used ENMs to predict the distribution of invasive species increased through the years (test for triangular arrangement of data, $P = 0.040$; Figure 2b).

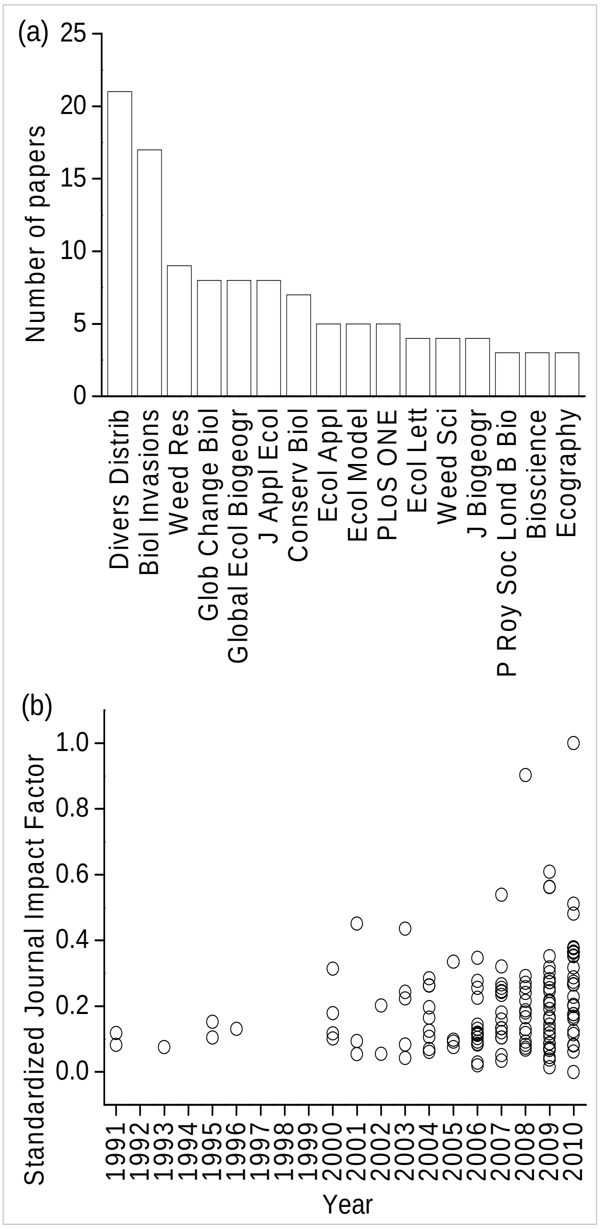


Figure 2. Journals that published more than two papers on ecological niche models to predict the distribution invasive species indexed by the ISI from 1991 to 2010 (a) and temporal variation in the standardized impact factor (journal impact factor in a given year divided by the maximum impact factor for a journal in the field of ecology in the same year; JCR 1990-2009) of the journals (b).

Many papers received only 1-5 citations (62 of 190 papers), while 13 papers were never cited (Figure 3a). The most cited article was by Peterson and Vieglais (2001), which received 242 citations. Other heavily cited papers were by Peterson (2003), by Thuiller et al. (2005) and by Broennimann et al. (2007), which received 222, 158 and 112 citations, respectively. The papers by Kearney and Porter (2009), Broennimann et al. (2007), and Peterson (2003) figured among the most cited after we standardized the number of citations by the year of publication (i.e., divided the number of citations by the number of years since their publication) (Figure 3b).

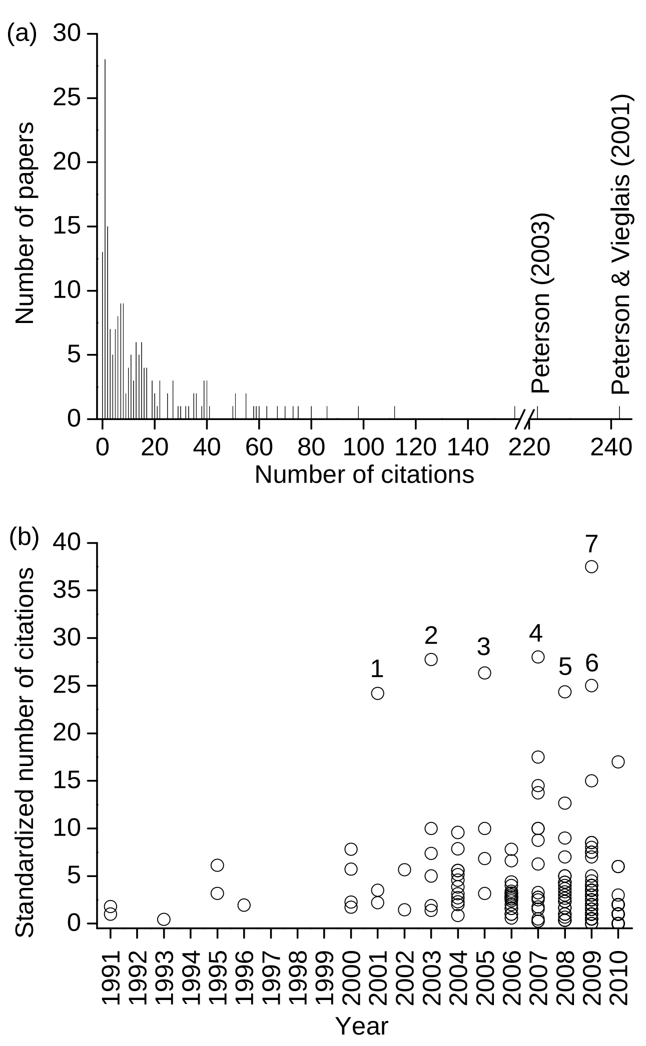


Figure 3. Number of papers in relation to the number of citations received (a) and temporal variation in the standardized (number of citations divided by the number of years since the paper was published) number of citations received by each paper (b). Numbers in (b) are: 1=Peterson and Vieglais (2001); 2=Peterson (2003); 3=Thuiller et al. (2005); 4=Broennimann et al. (2007); 5=Pearman et al. (2008); 6=Elith and Leathwick (2009); 7=Kearney and Porter (2009)

Researchers from 23 countries published papers on ENMs to predict the distribution of invasive species (Figure 4a). Sixty-four papers were published by researchers from the United States of America, followed by Australia (21 papers), New Zealand (14 papers), Canada, Spain, and South Africa (11 papers, each). Following the same trend, the region most studied was the United States of America (36 papers). Global studies (32 papers) and North America (20 papers) were the second and third most studied regions, respectively (Figure 4b).

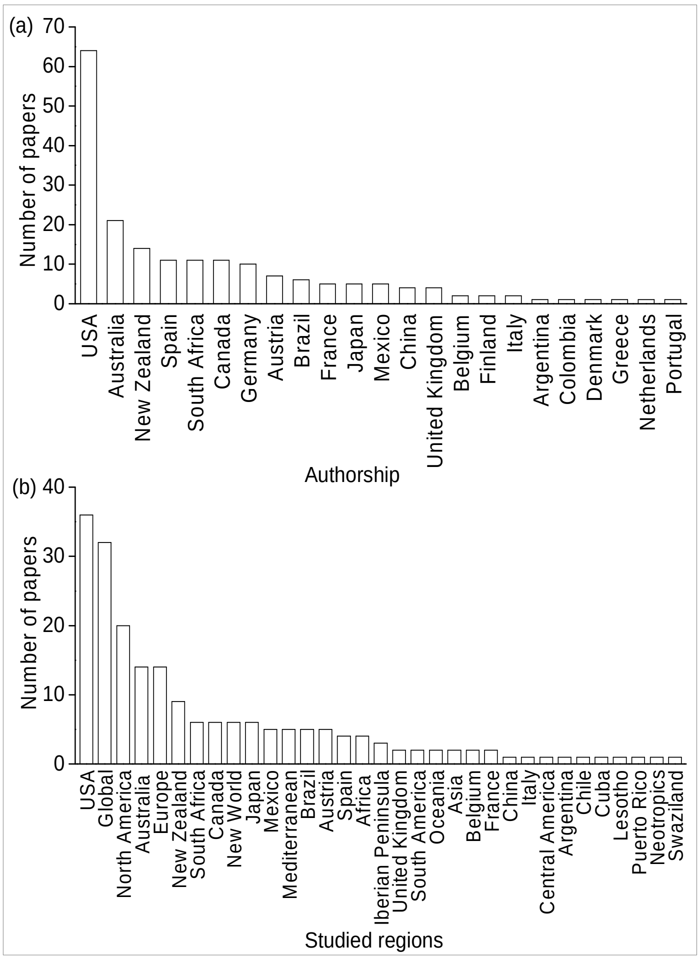


Figure 4. Nationality of the first author (a) and the regions most studied (b) in ecological niche models to predict the distribution of invasive species

Species-occurrence records (n = 178 papers) were composed mainly of presence-only records (85.40%), while records on presence and absence were used in only 14.60% of the articles. Almost half of the studies were carried out with plants (85 of 181 papers). Insects were the second most investigated biological group (29 papers), followed by other invertebrates (15 papers), amphibians (11 papers), fish and reptiles (10 papers, each), birds (8 papers), fungi (6 papers), mammals (5 papers), and algae (2 papers).

We identified eight types of predictor variables used to construct the ENMs to predict the distribution of invasive species. Climatic variables – such as temperature and precipitation - were used in 55.18% of the articles, followed by topographic variables (22.22%). Land cover (4.44%), land use and vegetation (4.07%, each), aquatic - such as salinity and dissolved oxygen - (3.70%), soil properties (2.96%), and human - such as human populations and footprints - (2.22%) were the other types of variables used. The climatic variables were most often used in the global and regional scales (above 50%), while in the national to local scales other environmental predictors were used (Table 1). Additionally, 81.66% of the studies (147 of 180) were carried out in terrestrial environments, while only 18.34% of the studies investigated aquatic systems. Most studies in freshwater environments used only terrestrial predictor variables (16 of 32 papers) rather than using aquatic variables (12 papers) or both types of variables (4 papers). In contrast, studies in marine or estuarine environments used only aquatic variables or both types of variables (4 papers) to generate ecological niche models of invasive species.

Table 1. Percentage of each predictor used in ENMs to predict the distribution of invasive species within different spatial scales

	Spatial scale				
Type of predictor	Global	Continental	National	Regional	Local
Aquatic	2.78	4.23	3.03	5.66	14.28
Climatic	80.56	61.98	57.57	50.94	20.00
Human	2.78	1.40	-	1.88	8.57
Land cover	-	5.63	3.03	5.66	8.57
Land use	-	1.40	6.06	9.43	2.85
Soil properties	-	-	4.54	-	5.71
Topographic	13.88	22.54	24.24	20.77	31.45
Vegetation	-	2.82	1.53	11.32	8.57

Twenty-three different methods were used in 180 papers of the 190 papers we analyzed (Figure 5). The Genetic Algorithm for Rule-set Production (GARP) method was the most used, appearing in 59 papers, followed by the CLIMEX (33 papers), the Maximum Entropy (MAXENT) (30 papers), and the logistic regression (LR; 23 papers) methods.

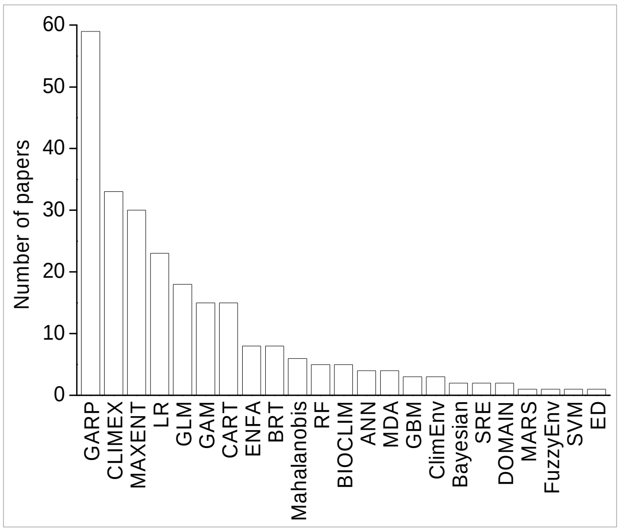


Figure 5. Number of studies carried out with different methods used to generate ecological niche models to predict the distribution invasive species. GARP = genetic algorithm for rule-set production; MAXENT = maximum entropy; LR = logistic regression; GAM = generalized additive models; GLM = generalized linear models; CART = classification and regression tree models; ANN = artificial neural networks; ENFA = ecological niche factor analysis; BRT = boosted regression trees; GBM = generalized boosted models; RF = random forest; MDA = mixture discriminant analysis; ClimEnv = climatic envelope; SRE = surface range envelope; MARS = multivariate adaptive regression splines; FuzzyEnv = fuzzy envelope; SVM = support vector machines; ED = environmental distance

Discussion

Our results showed an increase in the number of publications on ENMs over time, which is probably related to the increasing interest in invasive species in recent decades (Pysek et al., 2006). In parallel to the increasing interest in biological invasions, the application of ENMs in different areas of ecology has been widely used (Guisan and Thuiller, 2005), contributing to the growth of studies on ENMs to predict the distribution of invasive species in the last decade.

Although most of the papers were published in only a few journals, the majority of these journals have high impact factors and are among the main journals in the subject categories of Ecology and Biodiversity Conservation. Further, the growing interest of ENMs to predict the distribution of invasive species is also apparent in the increases of journals' impact factors, including journals with high impact factors in more recent years.

Citation frequency is also a criterion to quantify the impact and quality of a paper, although controversial (see Leimu and Koricheva, 2005 and Padial et al., 2010 for discussions). According to Garfield (2006), most published papers are never cited or cited only a few times. However, our results do not support clearly this suggested pattern since 60% of the papers were cited more than 5 times. Among the most cited articles, the one by Peterson and Vieglais (2001) explores the applicability of new bioinformatic tools (GARP) to predict species invasions, and was published in the beginning of the last decade when interest in ENMs to predict the distribution of invasive species began to increase. The other papers that were highly cited are a review (Peterson, 2003) and articles that tested new approaches and new tools to predict invasions (Thuiller et al., 2005; Broennimann et al., 2007). For instance, Peterson and Vieglais (2001) and Peterson (2003) created ENMs using data of the native region of the species, and thus assumed niche conservation across space and time. On the other hand, Broennimann et al. (2007) demonstrated through ENMs and additional analyses that a species may alter its niche during the invasion process. This means that some models created with data of the native region of the species may not predict the total region of invasion. Therefore greater attention is needed in interpretation of model predictions. The paper by Thuiller et al. (2005) is a broad study that builds multispecies projections to examine global risks of species invasions, in contrast to previous studies that focused on creating models for one specific species.

The United States of America was the country that showed the largest number of first authors and concentrated most of the studies. The position of the United States of America reflects its high investment in infrastructure and research (Fazey et al., 2005), providing basic data for the development of studies on ENMs to predict high-risk areas for invasions. This may allow researchers and governments to focus on prevention rather than eradication or control strategies. Similarly, in a recent bibliometric study, Qiu and Chen (2009) showed that research on biological invasions is mostly conducted in developed countries, following the general pattern noted by Pysek et al. (2008). Also interesting is the strong contribution of Australia and New Zealand, which figured out among the countries with the largest number of authorships and studies. This is likely due to the problems caused by invasive species (specially vertebrates and plants) to the remarkable and endemic biota of the pacific islands, including Australia and New Zealand. For instance, invasive vertebrates contributed to the extinction of many mammals and birds in both countries (Kingsford et al., 2009). The low representation of developing countries in studies on this subject may have several explanations, such as fewer resources for scientific studies and scarcity of data on exotic species (see Nuñez and Pauchard, 2010 for more explanations).

Species-occurrence records serve as the primary data for ENMs (Mateo et al., 2011), and the large number of studies composed by presence-only records may be attributed to the fact that presence records are easier to obtain and more reliable, since they typically derive from herbarium specimens, museum collections, and field observations by experts (Mateo et al., 2011). In contrast, absence records are rarely available, since species absence is more difficult to confirm, and often a recorded absence is actually nothing more than an undetected presence (Elith and Leathwick, 2009). Additionally, recent advances in biodiversity informatics and the development of extensive databases on biodiversity available via the Internet (Mateo et al., 2011) have facilitated the acquisition of presence-only records to generate ENMs. The implications in using presence-only records or presence and absence to create ENMs was discussed by Mateo et al. (2011).

Plants and insects were the biological groups most often used for predict the distribution of invasive species. Invasive insects and plants can cause severe economic problems in cropland production systems, urban environments, or natural environments (Pimentel et al., 2005) and, according to Pysek et al. (2008), it is the impact of the invasive species that determines whether or not it is studied. For instance, Pimentel et al. (2005) estimated that about 30% of the US$ 120 billion annually spent for invasive species in USA is directed to invasive plants. Despite the larger amount of studies on invasive plants than on invasive animals (Pysek et al., 2008; Qiu and Chen, 2009; our results), invasive insects have a prominent place in the list of invasive exotic fauna worldwide (Kenis et al., 2009), and this will probably lead to increasing interest in ENMs to predict the distribution of invasive species during the coming years.

We found that climatic variables are the type of predictor most used. The applicability of predictor variables is influenced by the spatial scale in the modelling process: at global, continental and national scales the climate appears to be the dominant factor determining species distributions, while at regional to local scales topography and land use become more important (Pearson and Dawson, 2003). This pattern is probably related to the fact that small spatial scales are associated with fine data resolutions, while large scales are associated with coarse data resolutions (see Pearson and Dawson, 2003 and Mateo et al., 2011 for more explanations). Our results showed that the spatial scale was also the determining factor in the choice of environmental predictors used to create the ENMs.

Most of the studies on ENMs to predict the distribution of invasive species were developed in terrestrial environments, whereas studies in aquatic environments are few. For many years, the attention of governments and scientists was focused on terrestrial invasive species (Pysek et al., 2008). Therefore, the large number of studies on ENMs conducted in the terrestrial environments is due to greater availability of information on these organisms (e.g., species occurrence records). Additionally, Puth and Post (2005) conducted a scientometric study on the invasion process using publications of the periods 1995-2005 and found more studies in terrestrial environments than aquatic environments at all stages of the invasion process. Ecological niche models in aquatic environments are limited because the most important predictor variables to determine the presence of a species (e.g., water temperature, salinity, and dissolved oxygen) are scarce or unavailable for most regions in the world (Ready et al., 2010). In freshwater environments, the aquatic variables are usually restricted to few sampling points (e.g., water monitoring stations), hindering the creation of ENMs (McNyset, 2005; Oliveira et al., 2010). Therefore, many studies in freshwater environments have used terrestrial predictor variables to generate ENMs (McNyset, 2005). However, it is worth noting that the use of terrestrial predictor variables can produce robust models (eg., Hopkins, 2009; Kumar et al., 2009). In marine environments, the ENMs have been generated using marine predictor variables, because of the availability of several global databases (e.g., Integrating Multiple Demands on Coastal Zones with Emphasis on Aquatic Ecosystems and Fisheries – Incofish; NOAA World Ocean Database). Moreover, in aquatic environments, species-occurrence records are scarce, and so far, only a fraction of aquatic invaders are known (Ready et al., 2010).

GARP, CLIMEX, MAXENT, and logistic regression were the methods most used to predict the distribution of invasive species (see Elith et al., 2006 to explanations on advantages and problems of each method). compared with other In this case, wide availability may be an important factor, because the three methods most used are software packages of easy accessibility and use, when methods that require specialized knowledge. Moreover, GARP, CLIMEX, and MAXENT are methods that use presence-only records as the primary data to create ENMs, and therefore their use is favored by the greater availability of presence records than of absence records. Comparative analyses of the statistical performance of GARP and MAXENT are available (Kumar et al., 2009; Colombo and Joly, 2010; Oliveira et al., 2010; Terribile et al., 2010). The CLIMEX method has been mainly applied to evaluate the invasion potential of exotic organisms (Kriticos et al., 2003). The logistic regression is also frequently used in ecological niche models, although it belongs to the group of presence-absence methods (Guisan and Thuiller, 2005).

Our scientometric analysis showed a growing interest and popularity in the use of ENMs to predict the distribution of invasive species, especially in the last decade. However, some important gaps need to be filled, such as the relatively small numbers of studies conducted in developing countries and in aquatic environments. The lack of studies on these two issues cannot be scientifically justified, since many developing countries harbor the highest biodiversity in the world (Nuñez and Pauchard, 2010), and invading species are a major concern in biodiversity conservation. Detailed data on invasive species distribution are usually not available in developing countries or its availability is limited and little disclosure (Rodríguez, 2001), forming a gap in the construction of predictive models for invasive species in these regions. However, it is worth noting that the few papers on ENMs to predict the distribution of invasive species carried out in developing countries found in the present study does not necessarily represent a total lack of studies, but may be related to the fact that such studies are only available in other small or regional databases. Moreover, aquatic environments are more vulnerable to invasive species than terrestrial environments (Ready et al., 2010). Ecological niche models can be used for strengthening the development and use of preventive measures to deal with invasive species. Therefore, basic information, records of occurrence of invasive species and predictor variables, are urgently needed to that researchers can devote more effort to studies of ENMs to predict the distribution of invasive species, both in developing countries and in all types of ecosystems.

References

BARDSLEY, WE., JORGENSEN, MA., ALPERT, P. and BEN-GAI, T., 1999. A significant test for empty corners in scatter diagrams. Journal of Hydrology, vol. 219, p. 1-6.

BROENNIMANN, O. and GUISAN, A., 2008. Predicting current and future biological invasions: both native and invaded ranges matter. Biology Letters, vol. 4, p. 585-589.

BROENNIMANN, O., TREIER, UA., MULLER-SCHARER, H., THUILLER, W., PETERSON, AT. and GUISAN, A., 2007. Evidence of climatic niche shift during biological invasions. Ecology Letters, vol. 10, p. 701-709.

CAYUELA, L., GOLICHER, DJ., NEWTON, AC., KOLB, M., ALBURQUERQUE, FS., ARETS, EJMM., ALKEMADE, JRM. and PÉREZ, AM., 2009. Species distribution modeling in the tropics: problems, potentialities, and the role of biological data for effective species conservation. Tropical Conservation Science, vol. 2, p. 319-352.

COLOMBO, AF. and JOLY, CA., 2010. Brazilian Atlantic Forest lato sensu: the most ancient Brazilian forest, and a biodiversity hotspot, is highly threatened by climate change. Brazilian Journal of Biology, vol. 70, p. 697-708.

DE’ATH, G. and FABRICIUS, KE., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology, vol. 81, p. 3178-3192.

ELITH, J. and LEATHWICK, JR., 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics, vol. 40, p. 677-697.

ELITH, J., GRAHAM, CH., ANDERSON, RP., DUDIK, M., FERRIER S., GUISAN, A., HIJMANS, RJ., HUETTMANN, F., LEATHWICK, JR., LEHMANN, A., LI, J.,

LOHMANN, LG., LOISELLE, BA., MANION, G., MORITZ, C., NAKAMURA, M., NAKAZAWA, Y., OVERTON, JMcC., PETERSON, AT., PHILLIPS, SJ., RICHARDSON, K., SCACHETTI-PEREIRA, R., SCHAPIRE, RE., SOBERÓN, J., WILLIAMS, S., WISZ, MS. and ZIMMERMANN, NE., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography, vol. 29, p. 129-151.

ENGLER, R., GUISAN, A. and RECHSTEINER, L., 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. Journal of Applied Ecology, vol. 41, p. 263-274.

FAZEY, I., FISCHER, J. and LINDENMAYER, DB., 2005. What do conservation biologists publish? Biological Conservation, vol. 124, p. 63-73.

GARFIELD, E., 2006. The history and meaning of the journal impact factor. Journal of the American Medical Association, vol. 295, p. 90-93.

GOTELLI, NJ. and ENTSMINGER, GL., 2001. EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. Available at: http://homepages.together.net/~gentsmin/ecosim.htm.

GUISAN, A. and THUILLER, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters, vol. 8, p. 993-1009.

HOPKINS, RL., 2009. Use of landscape pattern metrics and multiscale data in aquatic species distribution models: a case study of a freshwater mussel. Landscape Ecology, vol. 24, p. 943-955.

HULME, PE., 2006. Beyond control: wider implications for the management of biological invasions. Journal of Applied Ecology, vol. 43, p. 835-847.

JIMÉNEZ-VALVERDE, A., PETERSON, AT., SOBERÓN, J., OVERTON, JM., ARAGÓN, P. and LOBO, JM., 2011. Use of niche models in invasive species risk assessments. Biological Invasions. DOI: 10.1007/s10530-011-9963-4

KEARNEY, M. and PORTER, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters, vol. 12, p. 1-17.

KENIS, M., AUGER-ROZENBERG, M., ROQUES, A., TIMMS, L., PÉRÉ, C., COCK, MJW., SETTELE, J., AUGUSTIN, S. and LOPEZ-VAAMONDE, C., 2009. Ecological effects of invasive alien insects. Biological Invasions, vol. 11, p. 21-45.

KINGSFORD, RT., WATSON, JEM., LUNDQUIST, CJ., VENTER, O., HUGHES, L., JOHNSON, EL., ATHERTON, J., GAWEL, M., KEITH, DA., MACKEY, BG., MORLEY, C., POSSINGHAM, HP., RAYNOR, B., RECHER, HF. and WILSON, KA., 2009. Major conservation policy issues for biodiversity in Oceania. Conservation Biology, vol. 23, p. 834-840.

KRITICOS, DJ., SUTHERST, RW., BROWN, JR., ADKINS, SW. and MAYWALD, GF., 2003. Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. Journal of Applied Ecology, vol. 40, p. 111-124.

KUMAR, S., SPAULDING, SA., STOHLGREN, TJ., HERMANN, KA., SCHMIDT, TS. and BAHLS, LL., 2009. Potential habitat distribution for the freshwater diatom *Didymosphenia geminata* in the continental US. Frontiers in Ecology and the Environment, vol. **7**, p. 415-420.

LEIMU, R. and KORICHEVA, J., 2005. What determines the citation frequency of ecological papers? Trends in Ecology and Evolution, vol. 20, p. 28-32.

LEUNG, B., LODGE, DM., FINNOFF, D., SHOGREN, JF., LEWIS, MA. and LAMBERTI, G., 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London Series B – Biological Sciences, vol. 269, p. 2407-2413.

MACK, RN., SIMBERLOFF, D., LONSDALE, WM., EVANS, H., CLOUT, M. and BAZZAZ, FA., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications, vol. 10, p. 689-710.

MATEO, RG., FELICÍSIMO, AM. and M, J., 2011. Modelos de distribución de especies: una revision sintética. Revista Chilena de Historia Natural, vol. 84, p. 217-240.

MCNYSET, KM., 2005. Use of ecological niche modeling to predict distributions of freshwater fish species in Kansas. Ecology of Freshwater Fish, vol. 14, p. 243-255.

MELO, AS., BINI, LM. and CARVALHO, P., 2006. Brazilian articles in international journals on Limnology. Scientometrics, vol. 67, p. 187-199.

NUÑEZ, MA. and PAUCHARD, A., 2010. Biological invasions in developing and developed countries: does one model fit all? Biological Invasions, vol. 12, p. 707-714.

OLIVEIRA, MD., HAMILTON, SK., CALHEIROS, DF. and LATINI, RO., 2010. Modeling the potential distribution of the invasive golden mussel *Limnoperna fortunei* in the Upper Paraguay River system using limnological variables. Brazilian Journal of Biology, vol. 70, p. 831-840.

PADIAL, AA., NABOUT, JC., SIQUEIRA, T., BINI, LM. and DINIZ-FILHO, JAF., 2010. Weak evidence for determinants of citation frequency in ecological articles. Scientometrics, vol. 85, p. 1-12.

PEARMAN, PB., GUISAN, A., BROENNIMANN. and RANDIN, CF., 2008. Niche dynamics in space and time. Trends in Ecology and Evolution, vol. 23, p. 149-158.

PEARSON, RG. and DAWSON, TP., 2003. Predicting the impacts of climate change on the distributions of species: are bioclimate models useful? Global Ecology & Biogeography, vol. 12, p. 361-371.

PETERSON, AT., 2003. Predicting the geography of species' invasions via ecological modeling. Quarterly Review of Biology, vol. 78, p. 419-433.

PETERSON, AT. and VIEGLAIS, DA., 2001. Predicting species invasions using ecological niche modeling: New approaches from bioinformatics attack a pressing problem. Bioscience, vol. 51, p. 363-371.

PIMENTEL, D., ZUNIGA, R. and MORRISON, D., 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics, vol. 52, p. 273-288.

PUTH, LM. and POST, DM., 2005. Studying invasion: have we missed the boat? Ecology Letters, vol. 8, p. 715-721.

PYSEK, P., RICHARDSON, DM. and JAROSIK, V., 2006. Who cites who in the invasion zoo: insights from an analysis of the most highly cited papers in invasion ecology. Preslia, vol. 78, p. 437-468.

PYSEK, P., RICHARDSON, DM., PERGL, J., JAROSIK, V., SIXTOVA, Z. and WEBER, E., 2008. Geographical and taxonomic biases in invasion ecology. Trends in Ecology and Evolution, vol. 23, p. 237-244.

QIU, H. and CHEN, Y., 2009. Bibliometric analysis of biological invasions research during the period of 1991 to 2007. Scientometrics, vol. 81, p. 601-610.

R DEVELOPMENT CORE TEAM, 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

READY, J., KASCHNER, K., SOUTH, AB., EASTWOOD, PD., REES, T., RIUS, J., AGBAYANI, E., KULLANDER, S. and FROESE, R., 2010. Predicting the distributions of marine organisms at the global scale. Ecological Modelling, vol. 221, p. 467-478.

RODRÍGUEZ, JP., 2001. Exotic species introductions into South America: an underestimated threat? Biodiversity and Conservation, vol. 10, p. 1983-1996.

SCARANO, FR., DE TONI, K. and AMARANTE, CVG., 2009. A profile of the impact of Acta Botanica Brasilica: reflections on how to improve visibility and recognition of a scientific journal. Acta Botanica Brasilica, vol. 23, p. 606-611.

TERRIBILE, LC., DINIZ-FILHO, JAF. and De MARCO JÚNIOR, P., 2010. How many studies are necessary to compare niche-based models for geographic distributions? Inductive reasoning may fail at the end. Brazilian Journal of Biology, vol. 70, p. 263-269.

THERNEAU, TM. and ATKINSON, B., 2010. rpart: Recursive Partitioning. R port by B. Ripley. R package version 3.1-46. http://CRAN.R-project.org/package=rpart.

THUILLER, W., RICHARDSON, DM., PYSEK, P., MIDGLEY, GF., HUGHES, GO. and ROUGET, M., 2005. Niche-based modeling as tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology, vol. 11, p. 2234-2250.

TSOAR, A., ALLOUCHE, O., STEINITZ, O., ROTEM, D. and KADMON R., 2007. A comparative evaluation of presence-only methods for modeling species distribution. Diversity and Distributions, vol. 13, p. 397-405.

WESTPHAL, MI., BROWNE, M., MACKINNON, K. and NOBLE, I., 2008. The link between international trade and the global distribution of invasive alien species. Biological Invasions, vol. 10, p. 391-398.

ARTIGO II

Predicting the current distribution and potential spread of the exotic grass *Eragrostis plana* Nees in South America and identifying a bioclimatic niche shift during invasion

Predicting the current distribution and potential spread of the exotic grass *Eragrostis plana* Nees in South America and identifying a bioclimatic niche shift during invasion[3,4]

Abstract

Eragrostis plana is a perennial grass introduced from South Africa to the state of Rio Grande do Sul in southern Brazil. Currently it is considered an invasive grass in several regions of the world, including South America, where it has caused negative ecological and socio-economic impacts. Species distribution models, using bioclimatic variables, are often used to predict the potential distribution of invasive species. In this study we prepared two species distribution models for *E. plana* using the Genetic Algorithm for Rule-set Production (GARP), the first based on data from its native region (South Africa) and the second on data from both the native and invaded (South America) regions. We then projected each model onto South America to identify regions vulnerable to invasion by the species, and compared our results with available records of the species in South America. Finally, we explored the model's predictions for the existence of a bioclimatic niche shift during the invasion process of *E. plana* in South America, using multivariate statistical analysis. The model created with native distribution data was only to predict (with high probability) the region of introduction of *E. plana* in South America. However, the current distribution, as well as the region of introduction of the species, were reliably predicted by the model created with data from both native and invaded regions. Our multivariate analysis supports a hypothesis of bioclimatic niche shift during the invasion process of *E. plana* in South America.

---

[3] Com colaboração de Valério D. Pillar, Anthony Palmer & Adriano S. Melo

Keywords: invasive grass, species distribution model, GARP, native pasture

---

[4] Capítulo submetido à publicação no periódico Austral Ecology em 15 de agosto de 2011

Introduction

Biological invasions by exotic grasses are a threat to the maintenance of biodiversity (D'Antonio and Vitousek 1992; Pivello et al. 1999). They can negatively affect the native community structure (Brewer 2008; Hoffmann and Haridasan 2008; Yoshioka et al. 2010) and ecosystem properties and processes (Williams and Baruch 2000; Holly et al. 2009), as well as cause many negative impacts on human economic activities (Pimentel et al. 2001).

Species of African grasses have been introduced accidentally or intentionally in different parts of the world (Filgueiras 1990; D'Antonio and Vitousek 1992; Pivello et al. 1999; Williams and Baruch 2000). In many instances, these grasses spread successfully and displaced native plants (Pivello et al. 1999; Brewer 2008) and caused problems for native herbivores (Yoshioka et al. 2010). South America harbors several invasive grasses native to South Africa, including *Digitaria decumbens* Stent., *Eragrostis ciliaris* (L.) R. Brown, *Eragrostis plana* Nees, *Hyparrhenia rufa* (Nees) Stapf., *Panicum coloratum* L., *Panicum maximum* Jacq., and *Rhynchelytrum repens* (Willd.) C.E.Hubb. (Filgueiras 1990; Williams and Baruch 2000).

Eragrostis plana, known as fan lovegrass (or capim-annoni in Brazil), is a perennial grass (Kissmann 1991; Bredenkamp et al. 1996) native to South Africa (Reis and Coelho 2000; Medeiros et al. 2004). It was introduced into the state of Rio Grande do Sul in southern Brazil in 1957 (Reis and Coelho 2000), as a contaminant of forage seed (*Chloris gayana* Kunth and *Eragrostis curvula* Schrader) imported from South Africa (Ferreira et al. 2008a, b). In 1971, the species was identified as a high-potential forage species and was propagated and marketed as seed in several regions of Rio Grande do Sul and other states of Brazil (Paraná, Mato Grosso and Santa Catarina States) (Medeiros et al. 2009).

Eragrostis plana has low forage quality compared to native species that are abundant in natural grasslands in southern Brazil (Reis and Coelho 2000; Medeiros and Focht 2007; Medeiros et al 2009). In addition, the species has various undesirable effects of an invasive grass that confer a competitive advantage over local species, sometimes resulting in a monoculture (Reis and Coelho 2000), including rapid growth, a long reproductive phase (Reis and Coelho 2000; Lisboa et al. 2009), a potential allelopathic effect (Ferreira et al. 2008a), a persistent seed bank (Kissmann 1991; Ferreira et al. 2008b), and a high capacity to colonize native pastures, roadsides, and farmlands (Medeiros et al. 2004). In 1979, the sale of seeds and seedlings of the species was banned in Rio Grande do Sul by the Brazilian Ministry of Agriculture (Reis and Coelho 2000). The species is currently an invasive grass in several regions of Asia, India, South America, and the United States (Boechat and Longhi-Wagner 2000; USDA 2009). Because of the ecological and socio-economic threat, as well as the difficulty of control or eradication once it has become established (Reis and Coelho 2000; Medeiros et al. 2009), it is important to explore the potential of *E. plana* to invade new areas.

In recent years, studies have evaluated species distribution models (SDM) based on bioclimatic variables to predict the potential distribution of invasive plants (Peterson et al. 2003; Thuiller et al. 2005; Broennimann et al. 2007; Broennimann and Guisan 2008). These models combine species presence and absence records and bioclimatic spatial response surfaces to create a predictive model of a species’ requirements for the predictors examined.

The resulting model is then projected onto a new geographical space, as a map of the potential distribution of the species (Peterson and Vieglais 2001; Peterson 2003).

Models are usually created with occurrence records and bioclimatic predictors of the native region of a plant species, to predict its invasive potential (Peterson et al. 2003; Fonseca et al. 2006; Raimundo et al. 2007), assuming climatic niche conservation across space and time. However, some models created with occurrence records and bioclimatic predictors of the native region have been able to predict regions of introduction, but not the total region of invasion (Broennimann et al. 2007; Estrada-Peña et al. 2007), raising the possibility that a species may alter its climatic niche during the invasion process. Accordingly, studies have suggested that a better alternative for prediction of potential regions subject to species invasions is the use of occurrence records and bioclimatic predictors from both native and invaded regions to create species-distribution models (Welk 2004; Mau-Crimmins et al. 2006; Broennimann and Guisan 2008). Studies of species-distribution models have used additional analyses, such as measures of niche overlap and multivariate statistical analysis, to evaluate the hypothesis that a species may alter its climatic niche during the invasion process (Broennimann et al. 2007; Broennimann and Guisan 2008; Beaumont et al. 2009; Mata et al. 2010).

In the present study, we developed two species-distribution models based on bioclimatic predictors for *Eragrostis plana.* The first model included occurrence records (presence-absence) from its native region (South Africa), and the second included occurrence records (presence-absence) from its native region and presence records from invaded regions in South America. We projected each bioclimatic model onto South America to identify regions vulnerable to invasion by the species, and compared our results with available records of this grass in South America. Further, we explored the possibility of a bioclimatic niche shift during the invasion process of *Eragrostis plana* in South America, using multivariate statistical analysis.

Methods

Occurrence records of *Eragrostis plana* and bioclimatic predictors

We obtained 4816 georeferenced occurrence records of *E. plana* in its native range in South Africa. The dataset comprised 2780 presence and 2036 absence records (Fig. 1). Data from invaded regions in South America included 438 georeferenced presence records of the current distribution of *E. plana*. This dataset comprised 417 presence records from Brazil, 20 from Uruguay, and one from Argentina (Fig. 1). The occurrence records were obtained from field surveys in South Africa and Brazil and from databases maintained by the Global Biodiversity Information Facility – GBIF (http://www.gbif.org), Instituto Hórus (http://www.institutohorus.org.br), and South African Biodiversity Institute – SANBI (http://www.sanbi.org/).

We initially considered 19 bioclimatic variables as possible predictors. These were: i) annual mean temperature, ii) mean temperature diurnal range (mean of the monthly difference of the maximum and minimum temperatures), iii) isothermality, iv) temperature seasonality, v) maximum temperature of the warmest month, vi) minimum temperature of the coldest month, vii) temperature annual range, viii) mean temperature of the wettest quarter, ix) mean temperature of the driest quarter, x) mean temperature of the warmest quarter, xi) mean temperature of the coldest quarter, xii) annual precipitation, xiii) precipitation in the wettest month, xiv) precipitation in the driest month, xv) precipitation seasonality, xvi) precipitation in the wettest quarter, xvii) precipitation in the driest quarter, xviii) precipitation in the warmest quarter, and xix) precipitation in the coldest quarter. The bioclimatic data were obtained from the Worldclim database (Hijmans et al. 2005; available at http://www.worldclim.org) with a spatial resolution of 30 arc seconds (ca. 1 km^2).

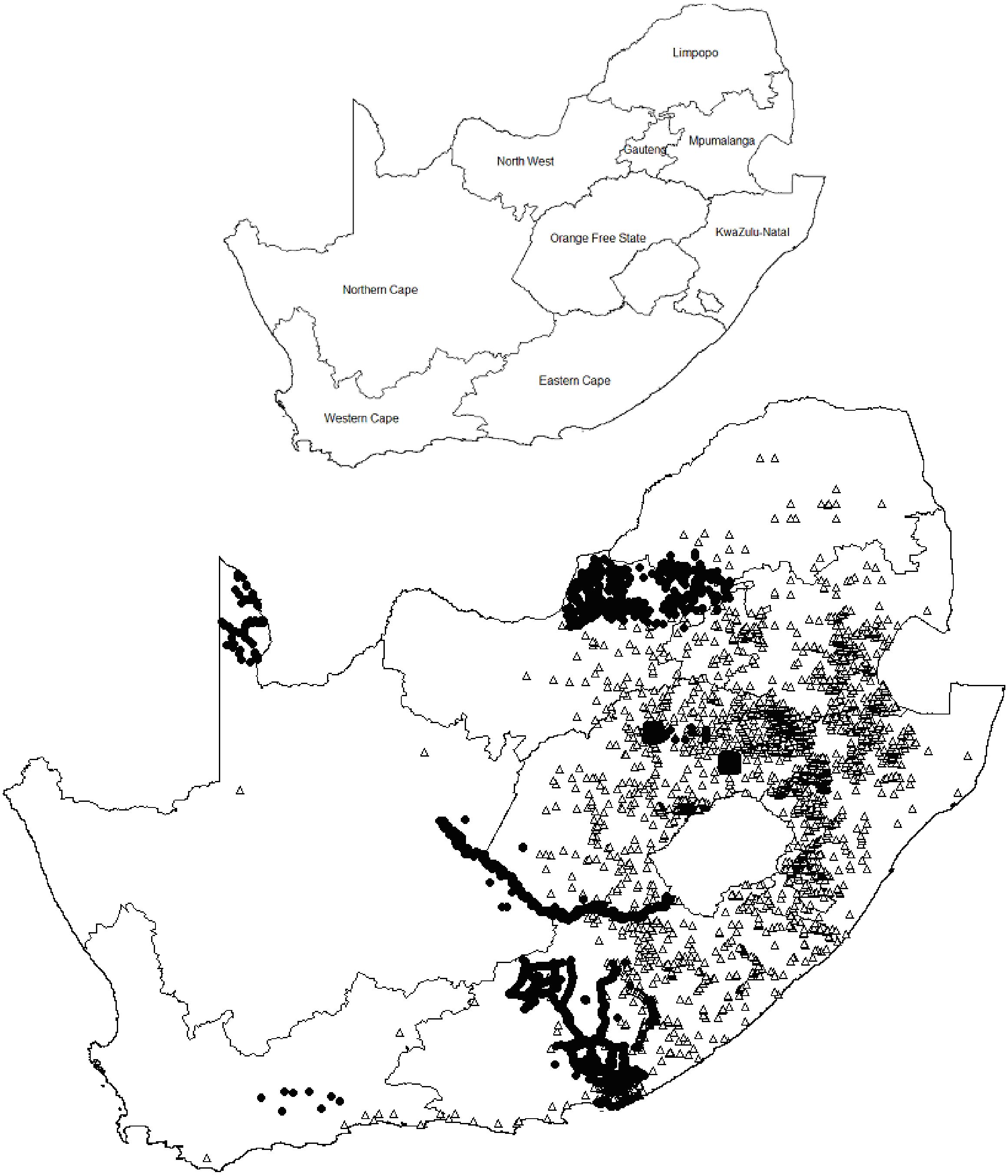


Fig. 1 Presence and absence records of *Eragrostis plana* in its native region of occurrence (South Africa) used to create species distribution models. △ = presence records and ● = absence records

Pre-processing of bioclimatic predictors

We employed regression tree analysis and Spearman correlations to reduce the original set of bioclimatic predictors to those predictors that provided the highest predictive power and that were not strongly correlated with each other. We evaluated the relationship between the occurrence records (presence and absence) of *E. plana* in South Africa and bioclimatic variables, using a regression tree (De'ath and Fabricius 2000). We selected eight bioclimatic variables included in the first nodes of the resulting tree model: i) temperature seasonality, ii) maximum temperature of the warmest month, iii) minimum temperature of the coldest month, iv) mean temperature of the wettest quarter, v) annual precipitation, vi) precipitation in the wettest month, vii) precipitation seasonality, and viii) precipitation in the wettest quarter. Additionally, Spearman correlations among these eight bioclimatic variables were employed to avoid strong colinearity among predictors. We excluded one of the variables in variable pairs that had a coefficient of correlation higher than 0.8. The reduced set of bioclimatic variables used to model the distribution of *E. plana* comprised: i) temperature seasonality, ii) minimum temperature of the coldest month, iii) mean temperature of the wettest quarter, iv) precipitation seasonality, and v) precipitation in the wettest quarter.

The regression tree analysis was carried out using the package rpart (Therneau and Atkinson 2008) run under the R environment, version 2.7.2 (The R Development Core Team 2008). We used the class method, appropriate for our binary response data (presence-absence records).

Species Distribution Models

We used the Genetic Algorithm for Rule-set Production (GARP) (Stockwell and Noble 1992; Stockwell and Peters 1999) to create the two species-distribution models. The use of GARP to predict potential areas subjected to species invasions was discussed by Peterson and Vieglais (2001) and Peterson (2003). We used presence and absence records of *E. plana* in its native range (South Africa) and presence records in the invaded range (South America). For each dataset (native region or native plus non-native regions), we divided equally and randomly the occurrence records into training (to create the model) and testing (to evaluate the model) datasets (Fielding and Bell 1997; Anderson et al. 2003; Araújo et al. 2005). The species distribution modeling was conducted using the algorithm GARP with best subsets (Anderson et al. 2003) run under the openModeller Desktop version 1.0.8 (http://openmodeller.sourceforge.net/) (Sutton et al. 2007).

We used the area under the curve (AUC) of a receiver operating characteristic (ROC) to evaluate the predictive accuracy of fitted models (Fielding and Bell, 1997; Lobo et al. 2008). The AUC, a criterion independent of a threshold (Lobo et al. 2008), ranges from 0.5 (random accuracy) to a maximum value of 1.0 (perfect discrimination). The AUC values were interpreted using the classification of Pearce and Ferrier (2000): excellent AUC > 0.90; reasonable 0.70 < AUC < 0.90; and poor 0.50 < AUC < 0.70.

We projected the fitted models onto South America using five classes of probability of occurrence. Additionally, we included in the resulting probability maps the currently known presence records in South America. These maps enabled us to evaluate whether the predictions matched the actual occurrences, and to identify regions with a high probability of invasion.

Bioclimatic niche shift

We explored the similarity between presence records from native and invaded regions in terms of bioclimatic variables using Principal Components Analysis (PCA). Additionally, we tested the hypothesis of no difference in bioclimatic niches in the native and invaded regions, using a distance-based Multivariate Analysis of Variance (MANOVA) with randomization testing.

The PCA was carried out using the package ade4 (Dray and Dufour 2007), run under the R environment, version 2.7.2 (The R Development Core Team 2008). The MANOVA was performed using the software MULTIV version 2.4 (Pillar 2006). We opted for the sum of squares between groups (Qb statistic according to Pillar 2006) as a criterion to assess whether the difference between groups was significant (Pillar and Orlóci 1996). This analysis was carried out using the Euclidean distance, obtained from bioclimatic variables of the presence records used in modeling, and the data were previously transformed by centering and normalization. The randomization test was run with 1000 iterations.

Results

The evaluation of the model within the native range of *E. plana* showed an AUC of 0.89 and 0.88 for the training and the test data, respectively, suggesting reasonable predictive power of the model. The projection of the model fitted to the data from the native region onto South

America showed a high probability of occurrence in regions including the present distribution of *E. plana* in the region of Mesopotamia (Corrientes Province) in Argentina, southern and northeastern Brazil, and Uruguay (Fig. 2). The model also indicated high probabilities of occurrence in the lowlands along the Andes, Pampas region (Buenos Aires, Cordoba, and Santa Fe Province) in Argentina, Bolivia, and Paraguay, where no presence records are currently available. A few records from central-western Brazil were located in regions predicted by the model as having a low probability of occurrence (Fig. 2).

The model built for the invaded range of *E. plana* in South America using data from both native and invaded regions showed an AUC of 0.92 and 0.91 for the training and the test data, respectively, suggesting excellent predictive power of the model. The projection of the model onto South America showed a high probability of occurrence of *E. plana* in all regions where it is currently recorded (the Mesopotamia region in northeastern Argentina, southern Brazil, and Uruguay), including the few records in central-western Brazil that were not predicted by the previous model (Fig. 3). The model also predicted a high probability of occurrence of *E. plana* in regions where it is currently known to be absent, such as in the state of Rondônia (Brazil), including parts of regions identified with the previous model (Fig. 3). Given the proximity to southern Brazil, where the species is widespread, these regions are likely to be invaded by the species in the future. In relation to the model fitted to the data from the native region alone, there was an increase in the region suitable for the spread of the species. In particular, many areas of savanna (Cerrado), in the center of South America, are now predicted to have a high probability of occurrence. The detached area of savanna north of the Amazon Forest (the state of Roraima in Brazil, close to Venezuela) was also predicted to be suitable for *E. plana*.

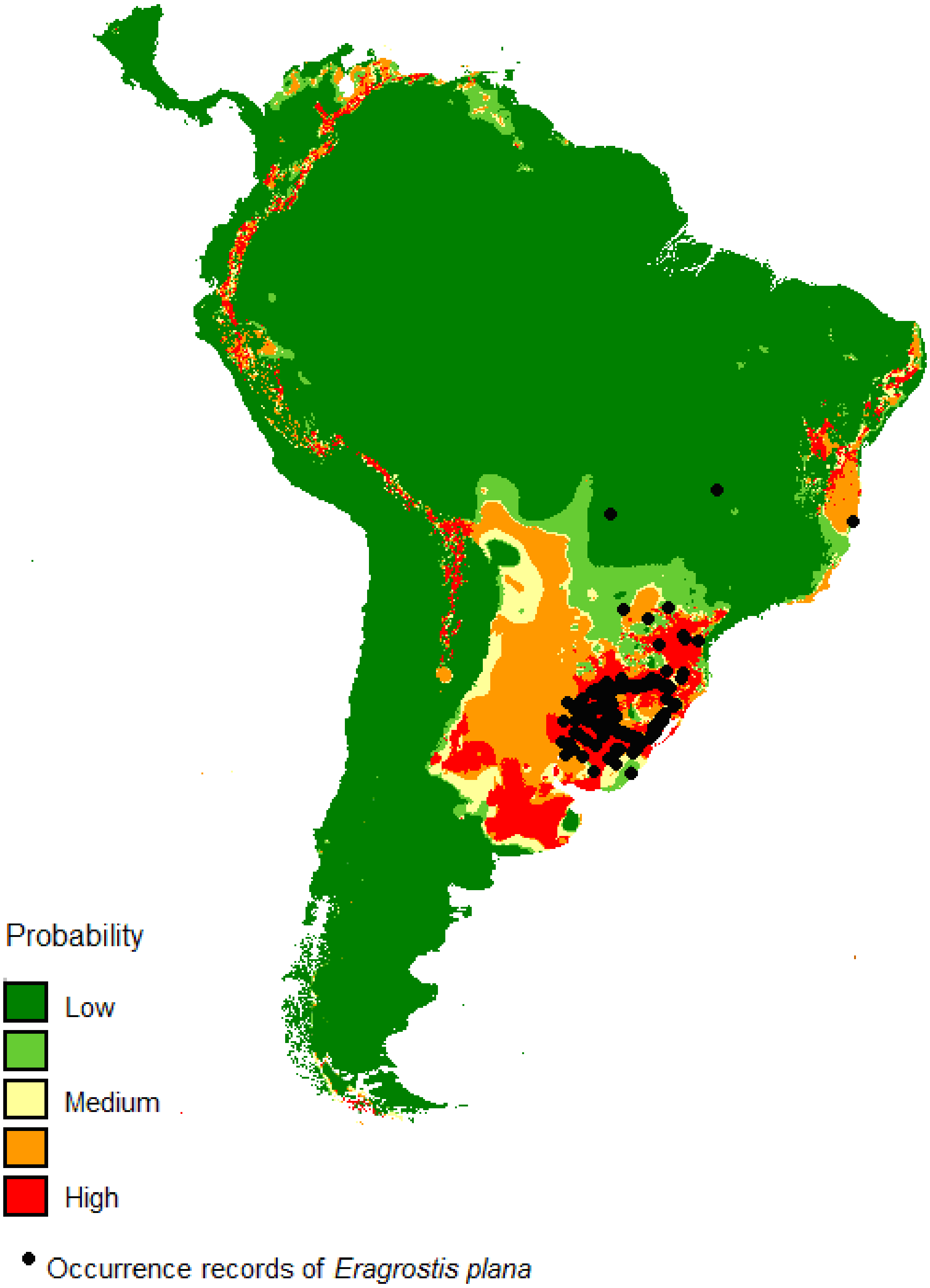


Fig. 2 Probability map of the model fitted to the distribution data of *Eragrostis plana* in South Africa projected onto South America. Dots indicate presence records of the species

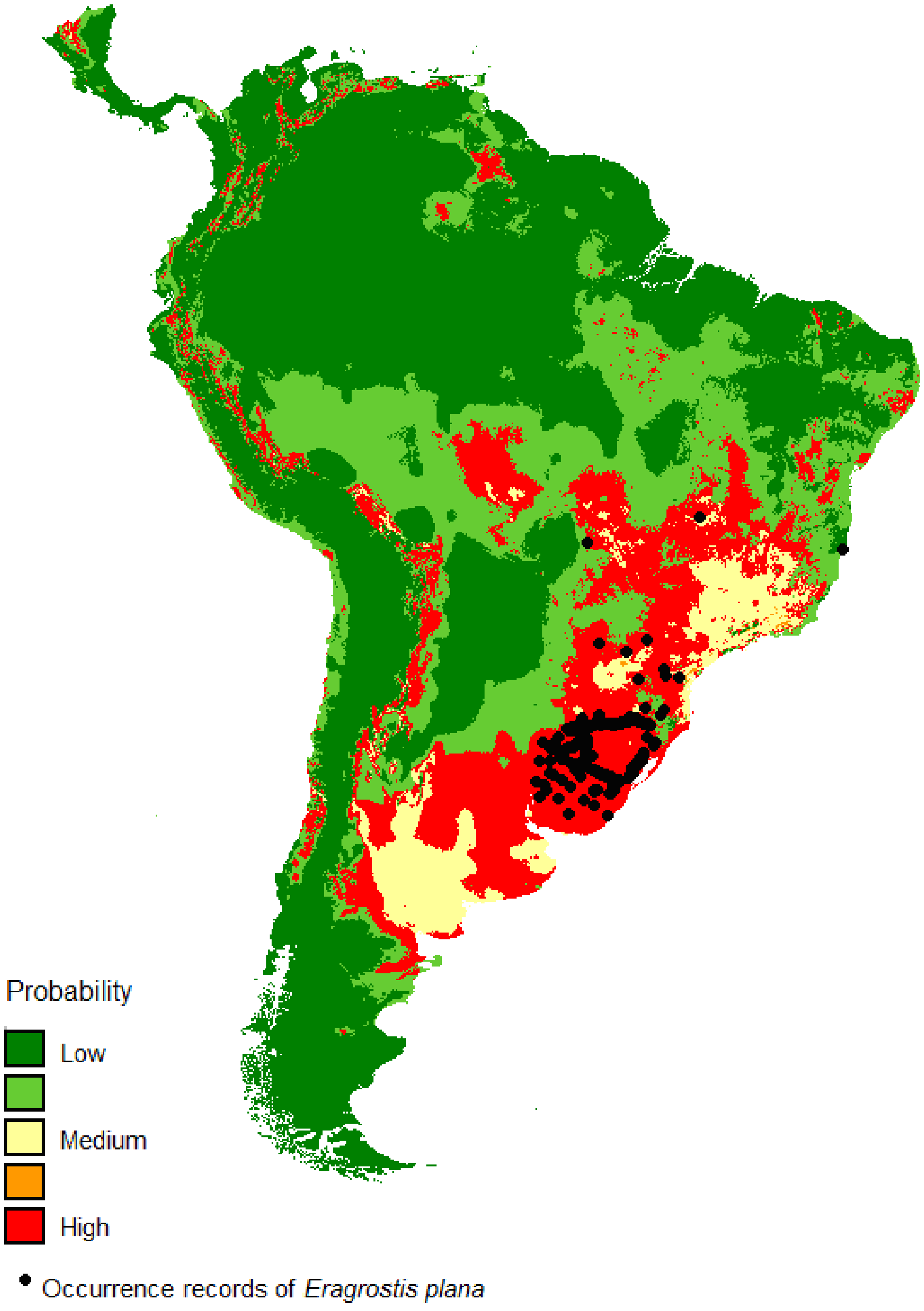


Fig. 3 Probability map of the model fitted to the distribution data of *Eragrostis plana* in South Africa and South America, projected onto South America. Dots indicate presence records of the species

The PCA indicated different bioclimatic conditions between the presence records in South Africa and in South America (Fig. 4). The MANOVA test rejected the hypothesis of no difference in the bioclimatic niches in South Africa and South America (p = 0.001).

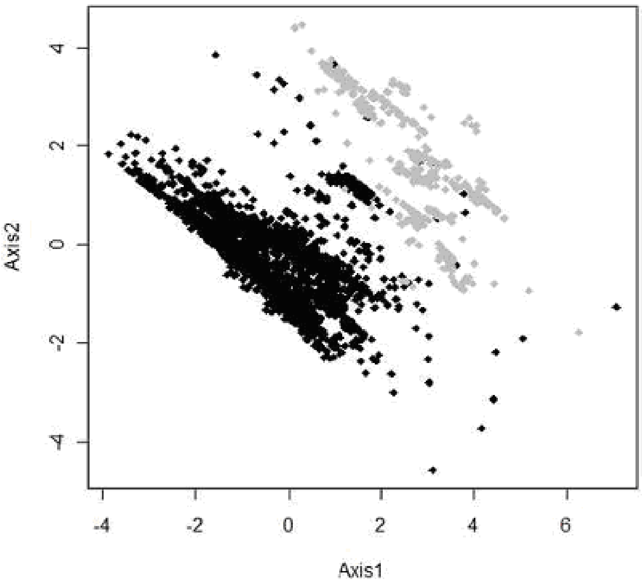


Fig. 4 Principal Components Analysis (PCA) of the bioclimatic conditions for the presence records of *Eragrostis plana* in its native (South Africa) and invaded (South America) regions. Black dots indicate records in the native bioclimatic niche, and gray dots indicate invaded bioclimatic niche

Discussion

The bioclimatic predictors and the GARP algorithm used to build the models performed very well in predicting the distribution of *E. plana* in South America. It is widely recognized that bioclimatic variables, particularly temperature and precipitation, play an important role in the prediction of the potential distribution of plant species at large scales (Thuiller et al. 2005; Broennimann et al. 2007). Our results support previous studies that reported the successful use of GARP and bioclimatic variables in the prediction of the potential distributions of invasive plant species (Peterson 2003; Peterson et al. 2003; Fonseca et al. 2006).

The model created with occurrence records and bioclimatic predictors from the native region (South Africa) was able to predict, with a high degree of probability, the region of introduction of *E. plana* in South America (Rio Grande do Sul, southern Brazil), but not its current enlarged distribution. Similarly, previous studies have shown that models created with data from the native regions were able to predict region of introduction, but not the total region of invasion (Broennimann et al. 2007; Fitzpatrick et al. 2007; Loo et al. 2007, Beaumont et al. 2009). Broennimann et al. (2007), for example, used occurrence records from the native region (Europe) of an invasive weed (*Centaurea maculosa* Lam.) in North America, and showed that the models were able to correctly predict region of introduction in the United States, but not the full extent of the occupied region after invasion.

The current distribution and the region of introduction (Rio Grande do Sul, Brazil) of *E. plana* are predicted with a high level of probability by our model created with occurrence records and bioclimatic predictors from both native (South Africa) and invaded (South America) regions. This result is consistent with that of Broennimann and Guisan (2008), who found better prediction of the distribution of an invasive weed using models created with both native and invaded ranges than with models created with only the native range. Models created with both native and invaded ranges may better represent the range of bioclimatic conditions under which the species can spread (Welk 2004; Mau-Crimmins et al. 2006;

Broennimann & Guisan 2008; Beaumont et al. 2009), because a species may shift its bioclimatic niche during the invasion process (Broennimann et al. 2007).

Previous studies of species-distribution models using additional analyses, such as measures of niche overlap and multivariate statistical analysis, have shown evidence of a bioclimatic niche shift during the invasion process of species (Broennimann et al. 2007; Broennimann and Guisan 2008; Beaumont et al. 2009; Mata et al. 2010; Medley 2010). Our multivariate analysis supports a hypothesis of a bioclimatic niche shift during the invasion of *E. plana* into South America. This niche shift may be a consequence of various processes, including the absence of enemies and competitors from its native range in the invaded region and/or a rapid evolutionary change after introduction. In the former case, previous studies have concluded that the absence of native herbivores, pathogens, and predators may explain the invasion and spread of plant species (Keane and Crawley 2002; Mitchell and Power 2003; DeWalt et al. 2004; Vila et al. 2005). In the latter case, founding effects and evolutionary processes associated with small populations may lead to rapid adaptive evolutionary changes during the invasion process (Lee 2002; Parker et al. 2003; Lavergne and Molofsky 2007).

Eradication and/or control of an invasive species after its establishment is costly and often difficult to implement (Pimentel et al. 2001; Simberloff 2003). Prevention is the best management strategy, and is often the most cost-effective approach (DiTomaso 2000; Davies and Sheley 2007). Our model indicated uninvaded regions in South America that have favorable conditions for the establishment of *E. plana*. Parts of these regions are near presently infested areas. These regions need effective programs to prevent the spread of the species by monitoring and control of its main routes of dispersal, and developing better practices of pasture management (Medeiros et al. 2009).

References

Anderson RP, Lew D, Peterson AT (2003) Evaluating predictive models of species distributions: criteria for selecting optimal models. Ecol Model 162:211-232

Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. Glob Chang Biol 11:1504-1513

Beaumont LJ, Gallagher RV, Thuiller W, Downey PO, Leishman MR, Hughes L (2009) Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. Divers Distrib 15:409-420

Boechat SC, Longhi-Wagner HM (2000) Padrões de distribuição geográfica dos táxons brasileiros de *Eragrostis* (Poacea, Chloridoideae). Rev Bras Bot 23:177-194

Bredenkamp GJ, Ed Granger J, Hoffman MT, Low AB, Lubke RA, McKenzie B, Rebelo AG, van Rooyen N (1996) Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria. Available at: http://www.ngo.grida.no/soesa/nsoer/Data/vegrsa/vegstart.htm

Brewer S (2008) Declines in plant species richness and endemic plant species in longleaf pine savannas invaded by *Imperata cylindrica*. Biol Invasions 10:1257-1264

Broennimann O, Treier UA, Muller-Scharer H, Thuiller W, Peterson AT, Guisan A (2007) Evidence of climatic niche shift during biological invasion. Ecol Lett 10:701-709

Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native and invaded ranges matter. Biol Lett 4:585-589

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle and global change. Ann Rev Ecol Syst 23:63-87

Davies KW, Sheley RL (2007) A conceptual framework for preventing the spatial dispersal of invasive plants. Weed Sci 55:178-184

De'ath G, Fabricius KE (2000) Classification and Regression Trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178-3192

DeWalt SJ, Denslow JS, Ickes K (2004) Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. Ecology 85:471-483

DiTomaso JM (2000) Invasive weeds in rangelands: species, impacts, and management. Weed Sci 48:255-265

Dray S, Dufour A-B (2007) The ade4 package: implementing the duality diagram for ecologists. J Stat Soft 22:1-20

Estrada-Peña G, Pegram RG, Barré N, Venzal JM (2007) Using invaded range data to model the climate suitability for *Amblyomma variegatum* (Acari: Ixodidae) in the New World. Exp Appl Acarol 41:203-214

Ferreira NR, Medeiros RB, Soares GLG (2008a) Potencial alelopático do capim-annoni-2 (*Eragrostis plana* Nees) na germinação de sementes de gramíneas perenes estivais. Rev Bras Sementes 30:43-50

Ferreira NR, Medeiros RB, Favreto R (2008b) Banco de sementes do solo de margem viária dominada por capim-annoni-2 e sujeito ao controle com distúrbios no solo e introdução de gramíneas. Rev Bras Sementes 30:54-63

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38-49

Filgueiras TS (1990) Africanas no Brasil: Gramíneas introduzidas da África. Cad Geocienc 5:57-63

Fitzpatrick MC, Weltzin JF, Sanders NJ, Dunn RR (2007) The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? Glob Ecol Biogeogr 16:24-33

Fonseca RL, Guimarães PR, Morbiolo SR, Scachetti-Pereira R, Peterson AT (2006) Predicting invasive potential of smooth crotalaria (*Crotalaria pallida*) in Brazilian national parks based on African records. Weed Sci 54:458-463

Hijmans RJ, Cameron SE, Para JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global areas. Int J Climatol 25:1965-1978

Hoffmann WA, Haridasan M (2008) The invasive grass, *Melinis minutiflora*, inhibits tree regeneration in a Neotropical savanna. Aust Ecol 33:29-36

Holly DC, Ervin GN, Jackson CR, Diehl SV, Kirker GT (2009) Effect of an invasive grass on ambient rates of decomposition and microbial community structure: a search for causality. Biol Invasions 11:1855-1868

Keane RM, Crawley, MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164-170

Kissmann KG (1991) *Eragrostis plana* Nees. In: Kissmann KG (ed) Plantas infestantes e nocivas: plantas inferiores – monocotiledôneas. BASF, São Paulo, v.1, pp 420-423

Lavergne S, Molofsky J (2007) Increased genetic variation and evolutionary potential drive the success of an invasive grass. Proc Natl Acad Sci USA 104:3883-3888

Lee CE (2002) Evolutionary genetics of invasive species. Trends Ecol Evol 17:386-391

Lisboa CAV, Medeiros RB, Azevedo EB, Patino HO, Carlotto SB, Garcia PA (2009) Poder germinativo de sementes de capim-annoni-2 (*Eragrostis plana* Nees) recuperadas em fezes de bovinos. Rev Bras Zootec 38:405-410

Lobo JM, Jiménez-Valverde A, Real R (2008) AUC: a misleading measure of the performance of predictive distribution models. Glob Ecol Biogeogr 17:145-151

Loo SE, Nally RC, Lake PS (2007) Forecasting New Zealand mudsnail invasion range: model comparisons using native and invaded ranges. Ecol Appl 17:181-189

Mata RA, Tidon R, Côrtes LG, De Marco P, Diniz-Filho JAF. 2010. Invasive and flexible: niche shift in the drosophilid *Zaprionus indianus* (Insecta, Diptera). Biol Invasions 12:1231-1241

Mau-Crimmins TM, Schussman HR, Geiger EL (2006) Can the invaded range of a species be predicted sufficiently using only native-range data? Ecol Model 193:736-746

Medeiros RB, Pillar VP, Reis JCL (2004) Expansão de *Eragrostis plana* Nees (capim-annoni-2) no Rio Grande do Sul e indicativos de controle. Reunión del grupo técnico regional del Cono Sur em mejoramiento y utilización de los recursos forrajeros del área tropical y subtropical. Grupo Campos 20:208-211

Medeiros RB, Focht T (2007) Invasão, prevenção, controle e utilização do capim-annoni-2 (*Eragrostis plana* Nees) no Rio Grande do Sul, Brasil. Pesqui Agropecu Gaúch 13:105-114

Medeiros RB, Saibros JC, Focht T (2009) Invasão de capim-annoni (*Eragrostis plana* Nees) no bioma Pampa do Rio Grande do Sul. In: Pillar VP, Müller SC, Castilhos ZMS, Jacques AVA (eds) Campos Sulinos – conservação e uso sustentável da biodiversidade. Brasília, Ministério do Meio Ambiente, pp 319-330

Medley KA (2010) Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. Glob Ecol Biogeogr 19:122-133

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421:625-627

Parker IM, Rodriguez J, Loik ME (2003) An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. Conserv Biol 17:59-72

Pearce J, Ferrier S (2000) Evaluating the predictive performance of habitat models developed using logistic regression. Ecol Model 133:225-245

Peterson AT, Vieglais DA (2001) Predicting species invasions using ecological niche modeling new approaches from bioinformatics attack a pressing problem. BioScience 51:363-371

Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modelling. Q Rev Biol 78:419-433

Peterson AT, Papes M, Kluza DA (2003) Predicting the potential invasive distributions of four alien plant species in North America. Weed Sci 51:863-868

Pillar VD, Orlóci L (1996) On randomization testing in vegetation science: multifactor comparisons of relevé groups. J Veg Sci 7:585-592

Pillar VD (2006) MULTIV: Multivariate exploratory analysis, randomization testing and bootstrap resampling. User's Guide v. 2.4. Departamento de Ecologia, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Brasil. Available at http://ecoqua.ecologia.ufrgs.br

Pimentel D, McNair S, Janecka S, Wightman J, Simmonds C, O'Connel C, Wong E, Russel L, Zern J, Aquino T, Tsomondo T (2001) Economic and environmental threats of alien plant, animal and microbe invasions. Agric Ecosyst Environ 84:1-20

Pivello VR, Shida CN, Meirelles ST (1999) Alien grasses in Brazilian savannas: a threat to the Biodiversity. Biodivers Conserv 8:1281-1294

Raimundo RLG, Fonseca RL, Schachetti-Pereira R, Peterson AT, Lewinsohn TM (2007) Native and exotic distributions of Siamweed (*Chromolaena odorata*) modeled using the Genetic Algorithm for Rule-Set Production. Weed Sci 55:41-48

Reis JCL, Coelho RW (2000) Controle do capim-annoni-2 em campos naturais e pastagens. Pelotas: EMBRAPA Clima Temperado, Circular Técnica, 21p.

Simberloff D (2003) Eradication – preventing invasions at the outset. Weed Sci 51:247-253

Stockwell DRB, Noble IR (1992) Induction of sets of rules from animal distribution data: a robust and informative method of analysis. Math Comput Simul 33:385-390

Stockwell DRB, Peters DP (1999) The GARP modelling system: problems and solutions to automated spatial prediction. Int J Geogr Inf Sci 13:143-158

Sutton T, Giovani R, Siqueira MF (2007) Introducing openModeller. OSGeo J 1:1-6

The R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at http://www.r-project.org

Therneau TM, Atkinson B (2008) rpart: Recursive partitioning. R port by B. Ripley. R package version 3.1-41. Available at http://www.r-project.org

Thuiller W, Richardson DM, Pysek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-based modelling as tool for predicting the risk of alien plant invasions at a global scale. Glob Chang Biol 11:2234-2250

United States Department of Agriculture (USDA) (2009) PLANTS Database (Version 3.5). Available at http://plants.usda.gov. Accessed January 2009

Vila M, Maron JL, Marco L (2005) Evidence for the enemy release hypothesis in *Hypericum perforatum*. Oecologia 142:474-479

Welk E (2004) Constraints in range predictions of invasive plant species due to non-equilibrium distribution patterns: purple loosestrife (*Lythrum salicaria*) in North America. Ecol Model 179:551-567

Williams DG, Baruch Z (2000) African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. Biol Invasions 2:123-140

Yoshioka A, Kadoya T, Suda S, Washitani I (2010) Invasion of weeping lovegrass reduces native food and habitat resource of *Eusphingonotus japonicus* (Saussure). Biol Invasions 12:2789-2796

ARTIGO III

Impact of climate changes on the distributions of invasive African grasses in the Americas: predicted scenarios from ensemble forecast

Impact of climate changes on the distributions of invasive African grasses in the Americas: predicted scenarios from ensemble forecast[5,6]

ABSTRACT

Aim We explore the impact of climate change on the distributions of five invasive African grasses in the Americas.

Location *Chloris gayana, Hyparrhenia rufa, Panicum maximum, Pennisetum ciliare and Urochloa mutica* are native in the Africa and invasive in Americas.

Methods We created ensembles forecasting consisting of projections derived from five niche models (ANN, CTA, GAM, MDA, and MARS) available in the BIOMOD package. Current and future (2080) American distributions for each invasive grass species were modeled using the atmosphere-ocean general circulation model (HadDCM3) and two gas emission scenarios (A2a and B2a).

Results In the general, our ensembles forecasting using average consensus method showed excellent predictive performance. The species *C. gayana* and *P. maximum* have high probabilities to disappear of some regions currently occupied. The species *H. rufa*, *P. ciliare,* and *U. mutica* should reduce slightly their spatial distributions.

---

[5] Com colaboração de Miguel B. Araújo & Adriano S. Melo

[6] As referências bibliográficas seguem as regras do período Global Change Biology

Main conclusions The future disappearance of *C. gayana* and *P. maximum* from many areas is associated mainly with precipitation conditions. Restoration opportunities may arise due to potential reduction in distributions of these five invasive African grasses in the Americas under climate changes.

Keywords: biological invasions, climate warming, consensus method and species distributions models

INTRODUCTION

Biological invasions have been recognized as one of the greatest global challenges for species conservation in the last centuries (Mack *et al*., 2000). Introductions, accidental or intentional, of exotic species into new environments are commonly associated with increased global trade and transport (Hulme, 2009). In the new environment some exotic species have become invasive causing significant ecological and economic damage (Mack *et al*., 2000; Pimentel *et al*., 2001). Invasive plant species threaten native biodiversity (Mack *et al*., 2000) and change ecosystem function (Mack & D'Antonio, 1998). In addition, invasive plants have caused enormous economic impacts, with costs (pest management and restoration of invaded ecosystems) reaching billions of dollars (Pimentel *et al*., 2001).

Among the invasive plants, grasses are especially important because many species: i) have high seed production, germination, and survival rate, ii) rapid growth, iii) can spread very easily, iv) tolerate fire, and v) are able to modify severely the environment where they dominate (D'Antonio & Vitousek, 1992). In the Americas, many African exotic grasses were introduced intentionally for degraded grasslands restoration, forage or ornamental purposes and accidentally through contaminated crop seeds (Williams & Baruch, 2000). Some of these exotic grasses have escaped from cultivated areas and invaded anthropogenic and natural regions (Williams & Baruch, 2000) causing serious ecological impacts (see Williams & Baruch, 2000 for review).

Invasions by exotic plants may amount to other global challenges (see Bradley *et al*., 2010a for review) such as climate change or climate warming (e.g., rising temperatures and altered precipitation regimes) (Dukes & Mooney, 1999; Walther *et al*., 2009). Climate change may affect many aspects of invasive plants: i) modify the impact of invasive species on native species and ecosystem, ii) facilitate the establishment and spread of invasive species into new regions, and iii) altered effectiveness of control/eradication strategies (Hellmann *et al*., 2008, Bradley *et al*., 2010a). Long-term observational and experimental studies suggest that climate change favors invasive plant species over native species (Dukes & Mooney, 1999; Buckland *et al*., 2001; Verlinden & Nijs, 2010).

Predictive models have been developed and applied for assessing the impacts of climate change on invasive plants (Thuiller *et al*., 2007; Bradley *et al*., 2010a). In the last decade, species distribution models have become important tools to predict the potential distribution of invasive grasses under global climate change scenarios (Beaumont *et al*., 2009; Bradley, 2009; Bradley *et al*., 2009; Parker-Allie *et al*., 2009; Bradley *et al*., 2010b). Species distribution models, also termed bioclimatic envelope modelling or ecological niche modelling, are constructed using a modelling method (see Guisan & Thuiller, 2005; Elith *et al*., 2006; and Heikkinen *et al*., 2006 to available modelling methods) that combines presence/absence or presence-only data of a species at a given geographical space with a series of spatial environmental data (see Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005 to review). The resulting model is then projected in the same geographical space under a scenario of future climate or onto a new space, showing the potential distribution of the species (Peterson & Vieglais, 2001; Peterson, 2003).

Species distribution models are created assuming that species distribution is in equilibrium with current environmental conditions (Guisan & Zimmermann, 2000; Guisan and Thuiller, 2005) and that the environmental niche of the species is conserved spatially and temporally (Pearman *et al.*, 2008). A recent study, however, showed that invasive species may shift its environmental niche during the invasion process (Broennimann *et al.*, 2007). Therefore, multivariate statistical analyses and niche overlap have been used to evaluate the hypothesis that invasive species may alter its environmental niche during the invasion process (Broennimann & Guisan, 2008; Mata *et al.*, 2010; Medley *et al.*, 2010).

Currently, the potential applications of species distribution models in distinct ecological issues is immense (Guisan & Thuiller, 2005), as well as the number of modelling methods available to create these models (see Guisan & Thuiller, 2005; Elith *et al.*, 2006 to modelling methods available). In addition, a number of studies have demonstrated differences in performance among modelling methods (Segurado & Araújo, 2004; Elith *et al.*, 2006; Tsoar *et al.*, 2007) and there is no consensus on the appropriate method to create the species distribution models (Pearson *et al.*, 2006). In this context, Araújo & New (2007) suggested the use of ensemble forecasting as a potential alternative for reducing uncertainty among modelling methods. Ensembles forecasting are created using the combination of predictions produced by different modelling methods (Araújo & New, 2007). Ensembles forecasting have been applied to predict the impact of climate change on biodiversity patterns (Coetzee *et al.*, 2009; Diniz-Filho *et al.*, 2010; Marini *et al.*, 2010), including biological invasions (Roura-Pascual *et al.*, 2009; Bradley *et al.*, 2010b; Stohlgren *et al.*, 2010).

In the present study, we will assess the potential impact of climate changes on the distributions of invasive African grasses in the Americas. As the invasive species were mostly from tropical areas in Africa, our general expectation was an increase in the area occupied by species toward temperate regions of the America. For this purpose, we generated ensembles forecasting to current and to future potential distributions of each grass species. We selected five invasive African C_4 grass species considered aggressive and widespread in the Americas: *Chloris gayana* Kunth (common name Rhodes grass), *Hyparrhenia rufa* (Nees) Stapf (common name Jaraguá), *Panicum maximum* Jacq. (common name Guinea grass and capim colonião), *Pennisetum ciliare* (L.) Link. (syn. *Cenchrus ciliaris* L., common name Buffel grass), and *Urochloa mutica* (Forsk.) Stapf (syn. *Brachiaria mutica*, common name Pará grass and capim angola) (Williams & Baruch, 2000).

METHODS

Species of study

The species *C. gayana* was intentionally introduced in native tropical savanna and cleared forest to improve pasture but escaped from areas planted and invaded natural habitats (Williams & Baruch, 2000). The grass *H. rufa, P. maximum,* and *U. mutica* were introduced in the humid tropics of Central and South America to improve forage quality but escaped from areas planted and invaded natural habitats (Williams & Baruch, 2000). *Hyparrhenia rufa* was intentionally introduced, whereas *P. maximum,* and *U. mutica* were accidentally introduced trough the slave ships in the Brazil (Parsons, 1972; Filgueiras, 1990). *Pennisetum ciliare* is drought resistant, present high biomass productivity (Sanderson *et al.*, 1999) and was intentionally introduced in the arid and semi-arid regions of North and South America for degraded grasslands restoration and rangeland improvement (D'Antonio & Vitousek, 1992; Williams & Baruch, 2000). However, the species escaped from the planted areas and become invasive in natural habitats causing threat to native species (D'Antonio & Vitousek, 1992; De la Barrera, 2008).

Williams & Baruch (2000) shows the distribution of these five African grasses in Americas. The species *C. gayana* occur in humid tropics and sub-tropics, *H. rufa* in humid and sub-humid tropics, Central and South America, *P. maximum* in tropics of Central and South America, and South Eastern United States, *P. ciliare* in arid and semi-arid tropics and sub-tropics, North Mexico, and southwestern United States, and *U. mutica* in humid tropics and sub-tropics.

Species and climate data

We obtained the occurrence records of the five invasive grasses in different online databases, including the Global Biodiversity Information Facility – GBIF (http://www.gbif.org), Instituto Hórus (http://www.institutohorus.org.br), SpeciesLink (http://splink.cria.org.br), and Tropicos (http://www.tropicos.org). A total of 292 presence records were compiled for *C. gayana* (103 native in Africa and 189 invasive in Americas), 619 for *H. rufa* (77 native in Africa and 542 invasive in Americas), 785 for *P. maximum* (159 native in Africa and 626 invasive in Americas), 488 for *P. ciliare* (162 native in Africa and 326 invasive in Americas), and 175 for *U. mutica* (92 native in Africa and 83 invasive in Americas).

We used the annual average of maximum and minimum temperature and annual total precipitation to both current and future conditions. The annual averages of maximum and minimum temperatures were extracted from monthly averages of maximum and minimum temperatures and the annual total precipitation from monthly total precipitation at a resolution of 20 km x 20 km (10 arc-minute) from the WorldClim database (http://ww.worldclim.org) (Hijmans *et al*., 2005). Current climate conditions are the result of interpolation of climate data recorded between 1950 and 2000 (Hijmans et al. 2005). Future climate conditions for the year 2080 (estimated 2070 - 2099 interval) were obtained from HadCM3 global circulation model as well as two gas emission scenarios: i) A2a and ii) B2a (IPCC 2001). The A2 scenario is considered more pessimistic than B2, with higher emissions of greenhouse gases (IPCC, 2001).

Climatic niche shift

Invasive species may shift its climatic niche during the invasion process (Broennimann et al. 2007). Therefore, we tested the hypothesis of difference in climatic niches in the native (Africa) and invaded (Americas) regions for each species using distance-based Multivariate Analysis of Variance (db-MANOVA) with randomization testing.

The db-MANOVA tests were performed using the software MULTIV version 2.4 (Pillar, 2006), using the sum of squares between groups (Qb statistic according to Pillar, 2006) as criterion (Pillar & Orlóci, 1996). These analysis were carried out using the Euclidean distance, obtained from current climate variables of the presence records both in native and invaded regions. Data were previously transformed by centering and normalization. The randomization test was run with 1000 iterations.

Difference in climatic niche in the native and invaded regions was evident only for *C. gayana* (p = 0.027). Thus, we used presence records and current climate variables from both native and invaded regions to create the species distribution models of *C. gayana*. For *H. rufa*, *P. maximum*, *P. ciliare,* and *U. mutica*, species that are at equilibrium with their environment, we created models using presence records and current climatic variables from the invaded region.

Species distribution models

For each of the five species, we created species distribution models using five modelling methods: i) Artificial Neural Networks (ANN), ii) Classification Tree Analysis (CTA), iii) Generalized Additive Models (GAM), iv) Multiple Adaptive Regression Splines (MARS), and v) Mixture Discriminant Analysis (MDA). ANN is a machine learning method, CTA and MDA are classification methods, and GAM and MARS are regression methods (see Elith *et al*., 2006 and Heikkinen *et al*., 2006 to description of each modelling method). The species distribution models were created using the package BIOMOD (Thuiller *et al*., 2009) run under the R environment, version 2.8.1 (The R Development Core Team, 2008). All models require presence and absence records and thus we created pseudo-absences for each species by using the 'random strategy' in BIOMOD. The number of pseudo-absences created equaled the number of presence records for each species multiplied by 10 (Jensen *et al*., 2008; Beaumont *et al*., 2009). Moreover, all species distribution models were created using default parameters of BIOMOD.

To evaluate the predictive performance of each model described above, we randomly separated 70% of the occurrence records as training data (calibration) and 30% for testing (evaluation) the model, and this procedure was repeated 10 times. We used the average area under the curve (AUC) derived from receiver operating characteristic (ROC) plot of the crossvalidation to evaluate the predictive performance of models (Fielding & Bell, 1997). The AUC values were interpreted using the classification of Pearce & Ferrier (2000): excellent AUC > 0.90; reasonable 0.70 > AUC < 0.90; and poor 0.50 > AUC < 0.70.

We used 100% of available presence records to make a final calibration of the models. Subsequently, we projected the models calibrated onto current climate conditions of Americas, as well as future American climate conditions for 2080. For each of the five species, we created five current predictions (with different modelling methods) and 10 projections of future potential distributions (combination of five modelling methods, one global circulation model and two gas emission scenarios) for 2080, in a total of 15 models per species.

Ensemble forecasting

For each of the five considered grass species, we generated an ensemble forecasting to current predictions and to projections of future potential distributions of each gas emission scenarios (A2 and B2) for year 2008. For this purpose, we used average consensus method based on AUC values (Araújo & New, 2007; Marmion *et al*., 2009).

For each ensemble forecasting, we create a distribution map using five probability of occurrence classes. On the current distribution map of each species, we included the known presence records of the species. These maps allowed us to examine the impact of climate changes on the current presence records of the species. In addition, in order to assess reduction or increase in the potential distribution of each species under climate changes, we calculate the percentage of grid cells where each species is predicted to occur with high probability in the current and future climate (year of 2080) under gas emission scenarios (A2a and B2a).

RESULTS

The average consensus method based on values AUC for *C. gayana*, *H. rufa, P. maximum,* and *P. ciliare* was 0.903, 0.911, 0.901, and 0.915 respectively, indicating excellent performance of ensemble forecasting. However, for the species *U. mutica* the average consensus method was 0.840, indicating reasonable performance.

The ensembles forecasting of the invasive grasses showed that some species have low probabilities of persistence and may be locally extinct in 2080 from areas currently occupied (Figure 1). In this study, we consider high probabilities of disappearance the two classes of low probability of occurrence and probabilities of the species remain the others classes. Thus, *C. gayana* shows a high probability to disappear from northeast Brazil and decrease its extent of occurrence in areas far from the Atlantic coast (Figure 1a). The results for *H. rufa* shows that the species should remain in most of the areas currently occupied (Figure 1b). The predicted areas occupied by *P. maximum* are very dependent on the scenario used (Figure 1c). For the B2a model, it should remain in most of the areas currently occupied. However, for the scenario A2a the species has high probability of disappearance of countries of the northwest of the South American, although new areas may be colonized in central and south of Argentina (Figure 1c). The area occupied by *P. ciliare* should decrease slightly in both scenarios, particularly in Central Brazil (Figure 1d). *Urochloa mutica* should have its distribution drastically reduced, remaining mostly restricted to small areas in northwest South America (Figure 1e).

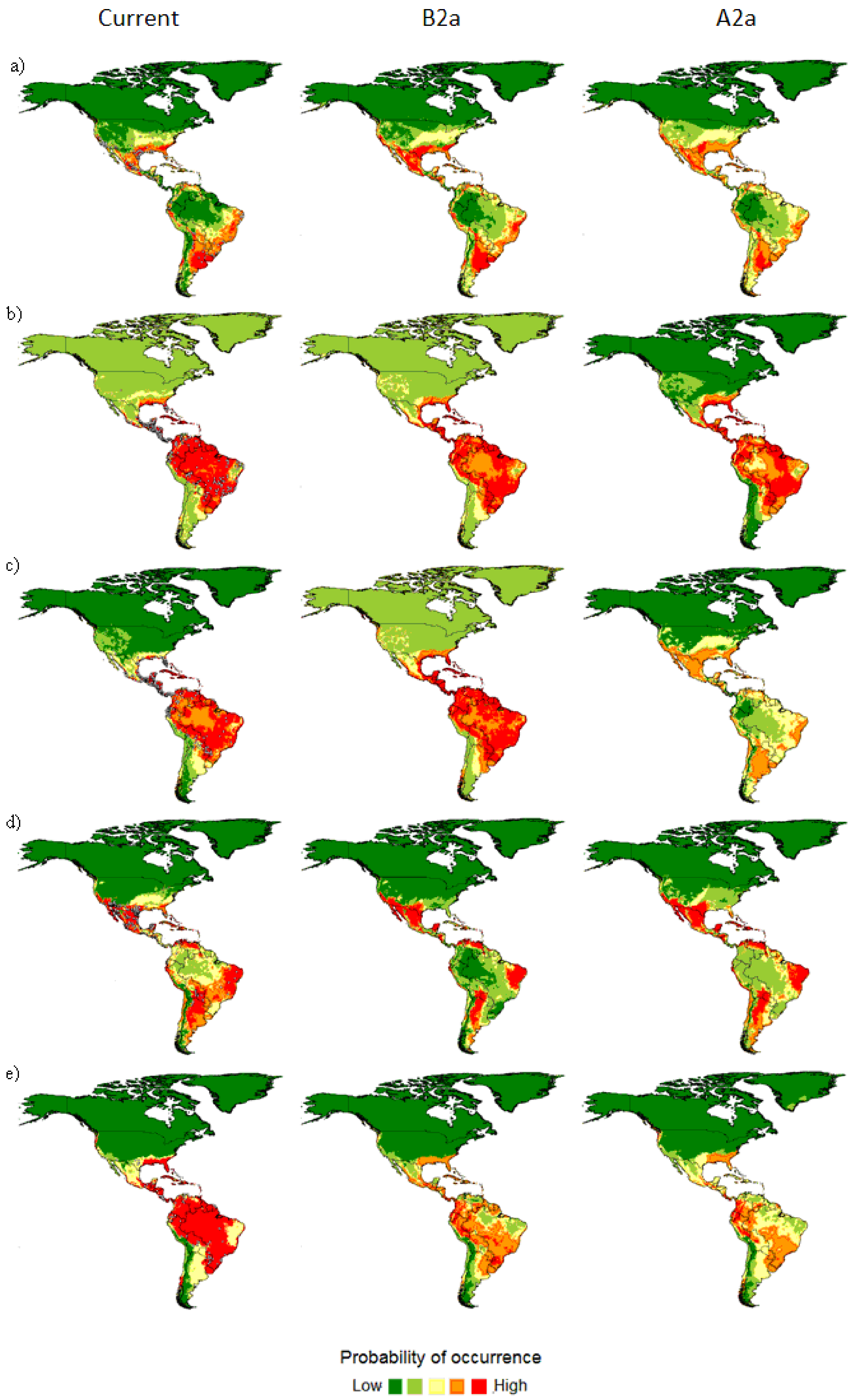

Current
B2a
A2a
a)
b)
c)
d)
e)
Probability of occurrence
Low
High

Figure 1. Occurrence probabilities at current climate and future scenario (2080) for five invasive grasses in Americas: (a) *C. gayana*, (b) *H. rufa*, (c) *P. maximum*, (d) *P. ciliare*, and (e) *U. mutica* obtained with ensemble forecasting

The current potential distribution of all five invasive grass species will decrease in 2080. In the general, the decrease will be greater in A2a than in the B2a scenario (Table 1).

Table 1. Invasive grass species, percentage of grid cells where each species is predicted to occur with high probability in the current and future climatic (year of 2008) under gas emission scenarios (B2a and A2a).

Species	**Current**	**2080**	
		B2a	**A2a**
Chloris gayana	4.46%	6.41%	2.66%
Hyparrhenia rufa	20.61%	14.98%	13.44%
Panicum maximum	19.12%	18.18%	0%
Pennisetum ciliare	10.27%	7.84%	9.40%
Urochloa mutica	21.60%	2.77%	1.66%

DISCUSSION

To reduce uncertainty of modelling methods, ensembles forecasting have been applied to assess the potential impact of climatic change on biodiversity, including endemic amphibians and reptiles (Carvalho *et al*., 2010), endemic and rare birds (Coetzee *et al*., 2009, Marini *et* *al*., 2009), endemic and rare plant (Lomba *et al*., 2010), invasive plants (Beaumont *et al*., 2009; Stohlgren *et al*., 2010) and insects (Diniz-Filho *et al*., 2010). These ensembles forecasting are generated using different consensus methods (see Marmion *et al*., 2009 to a recent evaluation of the methods available) including the average consensus employed in our study. In our study, the average consensus method of the ensemble forecasting procedure produced excellent predictive performance, corroborating results of a previous study (Marmion *et al*., 2009). However, the predictive performance of ensemble forecasting for *U. mutica* was reasonable. Studies have evaluated the effects of sample size on the predictive performance of species distribution models (Stockwell & Peterson, 2002; Hernandez *et al*., 2006), including models created with some modelling methods used in this study, as such GAM, MARS and MDA (McPherson *et al*., 2004; Wisz *et al*., 2008). For example, Wisz *et al*., (2008) found that, generally, the performance of the models decreased with decreasing number of available occurrence records. In the present study, the species *U. mutica* had the lowest number of presence records. Thus, the reasonable model performance for *U. mutica* can be due to the small sample size.

Previous studies have demonstrated that invasive grasses may disappear of regions currently occupied (Bradley *et al*., 2009; Parker-Allie *et al*., 2009). An example is provided by *B. tectorum* (cheatgrass), which is predicted to disappear of regions of southern Nevada and southern Utah (Bradley *et al*., 2009). In the present study, the grasses *C. gayana* and *P. maximum* have high probability of disappear of many regions in 2080. The climate projections generated by the HadCM3 model show anomalies of precipitation and temperature in northeast Brazil and anomalies of precipitation in South American (coast of Peru and

Ecuador) in 2080 (Nobre *et al*., 2008). For northeast Brazil the model predicts increase of temperature and decrease of annual total precipitation (less than 500 mm) in 2080. For the northwest of the South America (coast of Peru and Ecuador) the model predicts increase of annual total precipitation, with anomalies slightly more intense in the A2a scenario (Nobre *et al*., 2008). *Chloris gayana* has high probability of disappear of northeast Brazil. In fact, the climate variable most important for *C. gayana* was annual total precipitation (Appendix S1). Thus, the decrease of precipitation appear to be the main reason for the disappearance of *C. gayana* in northeast Brazil. Previous work have highlighted that the species is only able to maintain viable populations in areas with 600-1500 mm of annual precipitation (Ponsens *et al*., 2010). *Panicum maximum* predominates in regions with annual precipitation usually in excess of 1000 mm (Skerman & Riveros, 1992), has low tolerance to low temperatures (Brotel *et al*., 2002), and only tolerates flooding for short periods (Skerman & Riveros, 1992). Currently the northwest of the South American shows high values of annual total precipitation. For *P. maximum*, the climate variable most important was annual total precipitation followed by annual average of minimum temperature (Appendix S1). Increases in precipitation may cause excessive flooding of the soil (Dias-Filho & Carvalho, 2000). Thus, the disappearance of *P. maximum* in northwest of the South American (coast of Peru and Ecuador) may be associated with increase of annual total precipitation, since the species only tolerates short periods of flooding (Skerman & Riveros, 1992). The species does not tolerate low temperatures (Skerman & Riveros, 1992) and thus potential colonization of new areas in central and south Argentina may be due to the increase in annual average of minimum temperature.

According to Bardley *et al.* (2009), some studies have used only temperature conditions to predict the impact of climate changes on potential distribution of invasive species (e.g. Beerling, 1993). On the other hand, the potential distribution of species under climate changes has been predicted using both future conditions of precipitation and temperature (Kriticos *et al.*, 2003; Parker-Allie *et al.*, 2009; Bradley *et al.*, 2010). In the present study, the future disappearance in several regions of *C. gayana* and *P. maximum* is associated mostly with precipitation conditions, corroborating the study by Bradley (2009) that demonstrated the importance of precipitation conditions on future distribution of *Bromus tectorum* (cheatgrass), an invasive annual grass, in the western North America.

The results of ensemble forecasts showed that the species *H. rufa*, *P. ciliare* and *U. mutica* have the potential to remain in mostly of the areas currently occupied. These results are due to the physiological characteristics of these species, usually able to resist or tolerate the climate changes predicted for 2080. For instance, *H. rufa* is resistant to drought (Baruch & Fernández, 1993). *Pennisetum ciliare* is a species that survives in semi-arid and arid climate, with annual precipitations in the range 200 to 1200 mm (Cox *et al.*, 1988, Ibarra *et al.*, 1995). *Urochloa mutica* survives in warm and high precipitation conditions in the tropics and subtropics (Smithsonian Marine Station at Fort Pierce 2010 – http://www.sms.si.edu/irlspec/), and is tolerant to flooding (Baruch, 1994; Mattos *et al.*, 2005). In addition, the C_4 grasses have physiological characteristics that confer them a tolerance to high temperatures (Collatz *et al.*, 1998; Ward, 1999). For *P. ciliare* and *U. mutica*, the climate variable most important was annual average of minimum temperature, and for *H. rufa* was annual total precipitation followed by annual average of minimum temperature (Appendix S1).

Studies have used species distribution models to predict the impact of climate changes on potential distribution of invasive grass species (Bradley *et al*., 2009; Parker-Allie *et al.*, 2009; Bradley *et al*., 2010b). Our results suggest that the climate changes will reduce the current areas of high probability of occurrence for the five invasive grass species studied, coinciding with results of other models constructed for Eurasian invasive grass in the North America (Bradley, 2009; Bradley *et al*., 2009) and for invasive Eurasian C_3 and C_4 grasses in South Africa (Parker-Allie *et al*., 2009), with reductions greater under the A2a than the B2a scenario.

According to Bradley *et al*. (2009), restoration opportunities may arise in the locations subjected to reductions or eliminations of invasive species under climate changes. For instance, it would allow traditional restoration with native species present originally (Bradley *et al*., 2009) or a transformative restoration with the introduction of new native species (see Bradley & Wilcove, 2009 to more details). Active restoration programs are highly desirable in these areas because locations no longer suitable for previous invaders may be occupied by others new invasive species. In this context, modelling and experimental studies are needed to assess the impact of climate changes on native species and other new native species in the locations unsuitable for each of the five grass species considered in the present study. The results of these studies can be used in restoration plans in the locations that in the future should become unsuitable for the invasive grass species.

REFERENCES

Araújo MB, New M (2007) Ensemble forecasting of species distributions. *Trends in Ecological and Evolution*, **22,** 42-47.

Baruch Z (1994) Responses to drought and flooding in tropical forage grasses I. Biomass allocation, leaf growth and mineral nutrients. *Plant and Soil*, **164**, 87-96.

Beaumont LJ, Gallagher RV, Downey PO, Thuiller W, Leishman MR, Hughes L (2009) Modelling the impact of *Hieracium* spp. on protected areas in Australia under future climates. *Ecography,* **32**, 757-764.

Beerling DJ (1993) The impact of temperature on the Northern distribution-limits of the introduced species *Fallopia japonica* and *Impatiens glandulifera* in North West Europe. *Journal of Biogeography*, **20**, 45-53.

Bradley BA (2009) Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. *Global Change Biology*, **15**, 196-208.

Bradley BA, Oppenheimer M, Wilcove DS (2009) Climate change and plant invasions: restoration opportunities ahead? *Global Change Biology,* **15**, 1511-1521.

Bradley BA, Blumenthal DM, Wilcove DS, Ziska LH (2010a) Predicting plant invasions in an era of global change. *Trends in Ecology and Evolution*, **25**, 310-318.

Bradley BA, Wilcove DS, Oppenheimer M (2010b) Climate change increases risk of plant invasion in the Eastern United States. *Biological Invasions,* **12**, 1855-1872.

Broennimann O, Treier UA, Muller-Scharer H, Thuiller W, Peterson AT, Guisan A (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**, 701-709.

Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native and invaded ranges matter. *Biology Letters*, **4**, 585-589.

Brotel MD, Alvim MJ, Ferreira RP, Xavier DF (2002) Potencial forrageiro de gramíneas em condições de baixas temperaturas e altitude elevada. *Pesquisa Agropecuária Brasileira*, **37**, 393-398.

Buckland SM, Thompson K, Hodgson JG, Grime JP (2001) Grassland invasions: effects of manipulations of climate and management. *Journal of Applied Ecology*, **38**, 301-309.

Carvalho SB, Brito JC, Crespo EJ, Possingham HP (2010) From climate change predictions to actions – conserving vulnerable animal groups in hotspots at a regional scale. *Global Change Biology*, **16**, 3257-3270.

Coetzee BWT, Robertson MP, Erasmus BFN, van Rensburg BJ, Thuiller W (2009) Ensemble models predict important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Global Ecology and Biogeography*, **18**, 701-710.

Collatz GJ, Berry JA, Clark JS (1998) Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C_4 grasses: present, past, and future. *Oecologia*, **114**, 441-454.

D’Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass-fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63-87.

De la Barrera E (2008) Recent invasion of buffel grass (*Cenchrus ciliaris*) of a natural protected area from the southern Sonoran Desert. *Revista Mexicana de Bidoversidad*, **79**, 385-392.

Dias-Filho MB, Carvalho CJR (2000) Physiological and morphological responses of *Brachiaria* spp. to flooding. *Pesquisa Agropecuária Brasileira*, **35**, 1959-1966.

Diniz-Filho JAF, Nabout JC, Bini LM, Loyola RD, Rangel TF, Nogues-Bravo D, Araújo MB (2010) Ensemble forecasting shifts in climatically suitable areas for *Tropidacris cristala* (Orthoptera: Acridoidea: Romaleidae). *Insect Conservation and Diversity*, **3**, 213-221.

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? *Trends in Ecology and Evolution*, **14**, 135-139.

Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton J, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129-151.

Fielding AH, Bell JF (2006) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38-49.

Filgueiras TS (1990) Africanas no Brasil: Gramíneas introduzidas da África. *Cadernos de Geociências*, **5**, 57-63

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147-186.

Guisan A, Thuiller W (2005) Predicting species distribution more than simple habitat models. *Ecology Letters*, **8**, 993-1009.

Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and uncertainties in bioclimatic envelope modeling under climate change. *Progress in Physical Geography*, **30**, 751-777.

Hellmann JJ, Byers JE, Bierwagen BG, Dukes JS (2008) Five potential consequences of climate change for invasive species. *Conservation Biology*, **22**, 534-543.

Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, **29**, 773-785.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Journal of Climatology*, **25**, 1965-1978.

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, **46**, 10-18.

International Panel on Climate Change (IPCC) (2001) *Climate change 2001: synthesis report*. Cambridge University Press, London.

Jensen RA, Madsen J, O’Connell M, Wisz MS, Tommervik H, Mehlum FF (2008) Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario. *Global Change Biology*, **14**, 1-10.

Kriticos DJ, Sutherst RW, Brown JR, Adkins SW, Maywald GF (2003) Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. *Journal of Applied Ecology*, **40**, 111-124.

Lomba A, Pellissier L, Randin C, Vicente J, Moreira F, Honrado J, Guisan A (2010) Overcoming the rare species modelling paradox: A novel hierarchical framework applied to an Iberian endemic plant. *Biological Conservation*, **143**, 2647-2657.

Mack RN (1981) Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems*, **7**, 145-165.

Mack MC, D’Antonio CM (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution*, **13**, 195-198.

Mack RN, Simberlof D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689-710.

Marini MA, Massin-Barbet M, Lopes LE, Jiguet F (2009) Major current and future gaps of Brazilian reserves to protect Neotropical savanna birds. *Biological Conservation*, **142**, 3039-3050.

Marini MA, Massin MB, Lopes LE, Jiguet F (2010) Predicting the occurrence of rare Brazilian birds with species distribution models. *Journal of Ornithology*, **151**, 857-866.

Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2019) Evaluation of consensus methods in predictive species distribution modeling. *Diversity and Distributions*, **15**, 59-69.

Mata RA, Tidon R, Côrtez LG, De Marco P, Diniz-Filho JÁ (2010) Invasive and flexible: niche shift in the drosophilid *Zaprionus indianus* (Insecta, Díptera). *Biological Invasions*, **12**, 1231-1241.

McPherson JM, Jetz W, Rogers DJ (2004) The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *Journal of Applied Ecology*, **41**, 811-823.

Medley KA (2010) Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. *Global Ecology and Biogeography*, **19**, 122-133.

Nobre CA, Sampaio G, Salazar L (2008) Cenários de mudança climática para a América do Sul para o final do século 21. *Parcerias Estratégicas*, **27**, 19-42.

Parsons JJ (1972) Spread of African grasses to the American tropics. *Journal of Range Management*, **25**, 12-17.

Parker-Allie F, Musil CF, Thuiller W (2009) Effects of climate warming on the distributions of invasive Eurasian annual grasses: a South African perspective. *Climatic Change*, **94**, 87-103.

Pearce J, Ferrier S (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225-245.

Pearman PB, Guisan A, Broennimann O, Randin CF (2008) Niche dynamics in space and time. *Trends in Ecology and Evolution*, **21**, 149-158.

Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, Miles L, Segurado P, Dawson TP, Lees DC (2006) Model-based uncertainty in species range prediction. *Journal of Biogeography*, **33**, 1704-1711.

Peterson AT, Vieglais DA (2001) Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *Bioscience*, **51**, 363-371.

Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modelling. *The Quarterly Review of Biology*, **78**, 419-433.

Pillar VD, Orlóci L (1996) On randomization testing in vegetation science: multifactor comparisons of relevé groups. *Journal of Vegetation Science*, **7**, 585-592.

Pillar VD (2006) MULTIV: Multivariate exploratory analysis, randomization testing and bootstrap resampling. User's Guide v. 2.4. Departamento de Ecologia, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Brasil. Available at http://ecoqua.ecologia.ufrgs.br.

Pimentel D, McNair S, Janecka S, Wightman J, Simmonds C, O'Connel C, Wong E, Russel L, Zern J, Aquino T, Tsomondo T (2001) Economic and environmental threats of alien plant, animal and microbe invasions. *Agriculture, Ecosystems & Environment*, **84**, 1-20.

Ponsens J, Hanson J, Schellberg J, Moeseler BM (2010) Characterization of phenotypic diversity, yield and response to drought stress in a collection of Rhodes grass (*Chloris gayana* Kunth) accessions. *Field Crops Research*, **118**, 57-72.

Roura-Pascual N, Brotons L, Peterson AT, Thuiller W (2009) Consensual predictions of potential distributional areas for invasive species: a case study of Argentine ants in the Iberian Peninsula. *Biological Invasions*, **11**, 1017-1031.

Segurado P, Araújo MB (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography*, **31**, 1555-1568.

Skerman PJ, Riveros F (1992) *Gramínea tropicales*. Roma: FAO. 849p.

Smithsonian Marine Station at Fort Pierce (2010) The Indian River Lagoon Species Inventory. Available at http://www.sms.si.edu/irlspec/.

Stohlgren TJ, Ma P, Kumar S, Rocca M, Monsette JT, Jarnevich CS, Benson N (2010) Ensemble habitat mapping of invasive plant species. *Risk Analysis*, **30**, 224-235.

Stockwell DRB, Peterson AT (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, **148**, 1-13.

The R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Viena, Austria. ISBN ISBN 3-900051-07-0. Available at http://www.r-project.org.

Thuiller W, Richardson DM, Midgley GF (2007) Will climate change promote alien plant invasions? In: *Biological Invasions, Ecological Studies*. (eds. Nentwig W), pp. 197-211. Vol. 193. Springer-Verlag, Berlin Heidelberg.

Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD – a platform for ensemble forescating of species distributions. *Ecography*, **32**, 369-373.

Tsoar A, Allouche O, Steinitz O, Rotem D, Kadmon R (2007) A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and Distributions*, **13**, 397-405.

Verlinden M, Nijs I (2010) Alien plant species favored over congeneric natives under experimental climate warming in temperate Belgian climate. *Biological Invasions*, **12**, 2777-2787.

Walther G-R, Roques A, Hulme PE, Sykes MT, Pysek P, Kuhn I, Zobel M (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology and Evolution*, **24**, 686-693.

Williams DG, Baruch Z (2000) African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biological Invasions*, **2**, 123-140.

Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A, NCEAS Predicting Species Distributions Working Group (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, **14**, 763-773.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this paper:

Appendix S1. Importance of each climate variable in the models created for each species grass and the average importance of each variable.

	Methods	Annual total precipitation	Annual average of maximum temperature	Annual average of minimum temperature
Chloris gayana	ANN	0.531	0.405	0.381
	CTA	0.689	0.058	0.368
	GAM	0.769	0	0.147
	MARS	1.341	0.522	0.359
	MDA	0.472	0.324	0.219
	Average	0.7604	0.2618	0.2948
Hyparrhenia rufa	ANN	0.611	0.134	0.809
	CTA	0.585	0	0.46
	GAM	0.443	0.319	0.273
	MARS	0.540	1.212	0.594
	MDA	0.632	0.031	0.403
	Average	0.5622	0.3392	0.5078

Continuation of Appendix S1.

Panicum maximum	ANN	0.336	0.215	0.598
	CTA	0.528	0.300	0.401
	GAM	0.473	0.220	0.305
	MARS	1.325	0.129	0.792
	MDA	0.240	0.531	0.185
	Average	0.5804	0.279	0.4562
Pennisetum ciliare	ANN	0.442	0.297	0.340
	CTA	0.389	0.287	0.470
	GAM	0	0.518	0.316
	MARS	0.544	0.013	0.799
	MDA	0	0.048	0.944
	Average	0.275	0.2326	0.5738
Urochloa mutica	ANN	0.017	0.26	1.076
	CTA	0	0	0.986
	GAM	0.076	0	0.879
	MARS	0.94	1.152	1.211
	MDA	0.587	0.034	0.713

Continuation of Appendix S1.

Average	0.324	0.2892	0.973

The importance of each climate variable was obtained using the function “VarImportance” in BIOMOD (see Thuiller *et al.*, 2009 for details). This function gets the value of importance of each variable for each modelling method used to create the models. Therefore, we use the average value of each variable of the methods.

3. CONSIDERAÇÕES FINAIS

O uso de modelos de distribuição de espécies para predizer a distribuição potencial de espécies invasoras aumentou especialmente nas últimas duas décadas. Entretanto, algumas lacunas precisam ser preenchidas, tais como o número relativamente pequeno de estudos realizados em países em desenvolvimento e ambientes aquáticos.

O modelo de distribuição de espécie criado com dados da área nativa e invadida foi mais robusto para predizer a distribuição atual de *Eragrostis plana* na América do Sul do que o modelo criado com dados somente da área nativa. Além disso, *E. plana* alterou seu nicho bioclimático durante o processo de invasão na América do Sul.

Os modelos de distribuição de espécies criados para *E. plana* indicam regiões favoráveis ao seu estabelecimento na América do Sul. Assim, estas informações podem ser usadas em ações de planejamento ambiental e nas tomadas de decisão de forma direcionada para as regiões favoráveis ao estabelecimento de E. *plana* na America do Sul.

As mudanças climáticas globais irão alterar a distribuição potencial das cinco gramíneas Africanas invasoras nas Américas. As espécies *Chloris gayana* e *Panicum maximum* apresentam alta probabilidade de desaparecerem das regiões que ocupam atualmente, devido principalmente as mudanças nas condições de precipitação. Tanto o desaparecimento quanto a contração da distribuição potencial das gramíneas podem ocasionar futuramente oportunidades de restauração nas regiões impróprias para estas gramíneas nas Américas.