UNIVERSIDADE FEDERAL DE GOIÁS

INSTITUTO DE CIÊNCIAS BIOLÓGICAS

PPG-ECOLOGIA E EVOLUÇÃO

Invasões Biológicas:

indo além dos modelos de distribuição na busca de predições realistas sob restrições energéticas

André Felipe Alves de Andrade

Goiânia

2020

UNIVERSIDADE FEDERAL DE GOIÁS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS

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UNIVERSIDADE FEDERAL DE GOIÁS

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ATA DE DEFESA DE TESE

Ata nº **94** da sessão de Defesa de Tese de **André Felipe Alves de Andrade**, que confere o título de **Doutor em Ecologia e Evolução**, na área de concentração em **Ecologia e Evolução**.

Aos **vinte e cinco dias do mês de março de dois mil e vinte (25/03/2020),** a partir das **08h00min**, por **videoconferência, seguindo portaria CAPES no. 36 de 16 de março de 2020 e recomendação da UFG**, realizou-se a sessão pública de Defesa de Tese intitulada **"Invasões Biológicas: indo além dos modelos de distribuição na busca de predições realistas sob restrições energéticas"**. Os trabalhos foram instalados pelo Orientador, **Professor Doutor Paulo De Marco Júnior - DECOL/ICB/UFG,** com a participação dos demais membros da Banca Examinadora: **Professor Doutor José Alexandre Felizola Diniz Filho - DECOL/ICB/UFG,** membro titular interno; **Professora Doutora Alessandra Bertassoni - DECOL/ICB/UFG**, membro suplente interno**; Professor Doutor Marcus Vinícius Vieira - DECOL/UFRJ**, membro titular externo**;** e **Dr. Adriano Pereira Paglia - DBG/UFMG**, membro titular externo. Durante a argüição os membros da banca **não fizeram** sugestão de alteração do título do **trabalho**. A Banca Examinadora reuniu-se em sessão secreta a fim de concluir o julgamento da Tese, tendo sido o candidato aprovado pelos seus membros. Proclamados os resultados pela Professor Doutor **Paulo De Marco Júnior**, Presidente da Banca Examinadora, foram encerrados os trabalhos e, para constar, lavrou-se a presente ata que é assinada pelos Membros da Banca Examinadora, ao(s) **vinte e cinco dias do mês de março de dois mil e vinte (25/03/2020).**

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```
while (1==1) {
   enjoy_the_little_things ()}
```

Agradecimentos

Muito mais do que um p-valor significativo ou um modelo no qual o padrão emergido é exatamente o que se esperava, esta talvez seja a sessão mais importante de uma tese.

Talvez porque é aqui o lugar no qual o doutorado realmente acontece.

Talvez porque o doutorado é muito mais do que artigos publicados e capítulos terminados.

Talvez o doutorado é um período de quatro anos impossível de se percorrer por apenas dois pés.

Talvez por isto os agradecimentos sejam o primeiro tópico de uma tese, e não o último.

Talvez porque esta sessão é muito mais do que simples palavras escritas.

Talvez porque sem todas estas pessoas não existiria todo o resto.

Agradeço inicialmente à minha mãe a ao meu pai, que desde o primeiro momento em que escolhi fazer biologia sempre estiveram ao meu lado. Agora, chegado o final desta primeira etapa, nada mais justo do que dedicar este espaço privilegiado do primeiro parágrafo aos dois. Mesmo observando de longe durante muito tempo, principalmente por observar de longe durante muito tempo, eles são extremamente dignos deste espaço, porque mesmo de longe fizeram questão de estar perto. Colocando em palavras, MUITO OBRIGADO! Obrigado por acreditarem e incentivarem os meus sonhos, obrigado pela confiança, obrigado pela ajuda (que não foi pouca), obrigado pelo carinho, obrigado pelo porto seguro, obrigado pelos exemplos, obrigado pelos puxões de orelha. Se eu defendo hoje o doutorado é porque vocês me deram esta oportunidade. Vocês me apoiam mesmo quando eu era uma criança que sonhava em trabalhar com bichos. Hoje eu sou uma criança um pouco maior e trabalho com bichos que não existem, mas o apoio de vocês jamais deixou de existir. Obrigado!

Dando sequência no núcleo família. Difícil aguentar alguém 24h/dia, mais difícil ainda aguentar um doutorando desesperado no final de sua tese 24h/dia. Ainda mais difícil aguentar um doutorando desesperado no final de sua tese 24h/dia e conseguir proporcionar momentos de leveza, alegria e até mesmo esperança. Este parágrafo é seu mozão. A pessoa com quem eu passo minhas eternas férias, com quem eu divido o café de domingo, a canseira da segunda, os exercícios da terça, as tarefas da casa da quarta, a feira e o bar da quinta, o sextou da sexta e o descanso do sábado, com quem eu começo a formar uma família que inclui a bola de pelo preta mais chata/linda que tem. Obrigado por quase uma década de companhia. Obrigado por quase 2 anos de companhia diária. Obrigado por dividir comigo sonhos, alegrias, angústias e conversas doidas à 1h da manhã. Obrigado pela paciência e carinho, especialmente nestes últimos meses. Obrigado por dividir esta caminhada da vida comigo!

Por fim, ainda no núcleo familiar, muitas pessoas merecem um parágrafo, mas para evitar tirar energia da banca para ler todo o resto (menos importante, admito) da tese e também porque este que vos escreve já não possui mais energias para escreve (um sintoma comum de final de doutorado), sintetizo neste parágrafo algumas pessoas que não podem deixar de aparecer. Peço desculpas pelo espaço físico restrito, mas o carinho e amor que tenho por elas vai muito além destas páginas. À minha irmã mais velha, Juliana, que me aguenta e ensina coisas desde pequeno, a última delas foi me ensinar a ser tio. À minha irmã mais nova, Luciana, que me dá dores de cabeça, alegria e orgulho desde sempre. À minha vó, Vó Grande, que me sempre me deu e dá abraço, colo e bolo. À minha tia, Amiga, que não chama amiga à toa, mas que tem importância de mãe! Ao meu tio, João, que veio lá de Portugal e acabou sendo um segundo pai. À minha prima, irmã, afilhada, Aninha, que de *-inha* já não tem mais quase nada e dá um orgulho danado na gente com as coisas de gente grande que ela faz. À minha sogra e sogro (que nunca foram chamados assim, mas difícil resumir o seu papel em uma palavra), Gislane e Adilson, que me acolheram como um membro da família desde o primeiro momento e pela confiança depositada. Aos meus outros avós e avôs, tios e tias, primos e primas que mesmo distante, fisicamente ou em espírito, carrego sempre comigo e foram essenciais para que eu chegasse até aqui. Muito obrigado!

Talvez não seja do conhecimento de todos, mas uma tese não se faz sem um orientador. E, modéstia à parte, eu tive o melhor, ou pelo menos o único atleticano da EcoEvol, o que dá praticamente na mesma. Chefe, obrigado por responder aquele e-mail a mais de 6 anos, naquele 5 de setembro de 2013, respondido após menos de 1h. Quando você disse naquela mensagem que eu podia vir por que teríamos “MUITA coisa para fazer” você não estava mentindo. O que eu aprendi nestes 6 anos de laboratório foi absurdo! Obrigado por tudo que você me ensinou, pelas conversas (acadêmicas ou não), pelos lamentos com o galo, pelos vários projetos paralelos, pelas portas que você abriu, pela confiança e, claro, pela orientação e a amizade! Obrigado pelo exemplo de pessoa e profissional que você nos dá todo dia com a sua preocupação diária tanto com assuntos burocráticos/administrativos da faculdade quanto e também com a sua sincera preocupação com os problemas de cada um dos seus 3.892.412 orientandos formais e informais espalhados pelo mundo.

Mais do que tudo, um laboratório nada mais é do que um grupo de pessoas que vêm o mundo de forma diferente, colocados para dividir uma mesma sala durante um grande período de tempo, ou seja, quase um Big Brother. Agradeço então a estes heróis que partilharam comigo o confinamento, porque, ao contrário da casa mais vigiada do Brasil, nós infelizmente não tínhamos nem piscina, nem festinhas, então nos distraíamos com conversas (novamente científicas ou não), bolacha Mabel, café (*ad infinitum*) e muita informação banal formadora de caráter. Novamente farei uma síntese, até porque são muitos aqueles que dividiram estes dias comigo. Obrigado à velha guarda (na qual me incluo) que conheci ainda no mestrado, seguiram pelo doutorado, e me acompanham até hoje caçando cachoeiras e cervejarias. Aos coxinhas, grandes amigos que fiz neste doutorado, companheiros de rolês em bares com lugar para sentar, churrascos e até mesmo lanches na tia. A

todos do TheMetaLand, o laboratório mais diverso, louco, barulhento e acolhedor desta UFG (de um ponto de vista nem um pouco enviesado deste que vos fala), e aqui incluo todos que são membros residentes ou transeuntes, já que este laboratório transcende os limites municipais, estaduais, nacionais e até mesmo continentais! Aos amigos dos outros laboratórios, que não por isto deixam de ser menos amigos ou são menos importantes nesta caminhada. Estendo aqui também as fronteiras espaciais do ICB 5 e, quiçá de Goiás, para agradecer também a todos aqueles amigos de fora da graduação/pós-graduação com os quais eu dividi este doutorado. Muitas vezes uma palavra, um abraço, uma cerveja, um futebol ou uma noite de jogatina são eventos muito mais importantes do que ajustar um GLMM para a completude de uma tese. Meu mais sincero obrigado a todos vocês, se este doutorado foi uma experiência divertida e agradável foi porque vocês fizeram parte dele.

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Por fim, mas nunca menos importante, agradeço também à banca que aceitou avaliar estre trabalho: Prof. José Alexandre Diniz-Filho, Prof. Matheus Lima Ribeiro, Prof. Marcus Vinícius Vieira e Prof. Adriano Paglia, também os suplentes Profa. Alessandra Bertassoni, Prof. Luis Mauricio Bini e Prof. Paulo Inácio Prado. Obrigado também a você que dedicou alguns minutos do seu tempo nem que seja para folhear esta tese, já que um texto escrito só ganha propósito quando é lido. Meu muito obrigado!

SUMÁRIO

Apresentação Geral

Como ponto central desta tese exploramos modelos preditivos de invasões biológicas. A pergunta norteadora é: qual a nossa capacidade de predizer uma invasão biológica? A fim de responder esta pergunta nós exploramos diferentes métodos e teorias relacionadas a invasões biológicas e dividimos a tese em duas principais perguntas: i) qual a capacidade preditiva dos modelos comumente utilizados na predição de invasões, e ii) espécies invasoras possuem características em comum que favorecem com que se tornem invasoras?

No primeiro capítulo exploramos a primeira questão e buscamos avaliar a capacidade de modelos de nicho na predição de invasão. Para isto utilizamos espécies virtuais, já que com este método possuímos total controle sobre o nicho fundamental das espécies. A distribuição das espécies foi criada a partir de uma dinâmica populacional realista e a partir desta distribuição foram amostradas ocorrências para os modelos de nicho. Neste capítulo abordamos como a divergência entre o nicho realizado e o nicho fundamental das espécies pode levar a sub- ou super predição das áreas identificadas como adequadas para espécies invasoras.

No segundo e terceiro capítulo abordamos a segunda questão e buscamos responder quais características de uma espécie exótica favorecem para que ela se torne uma espécie invasora. Nestes capítulos construímos modelos baseados em indivíduo, nos quais as regras e processos dos modelos ocorrem sobre os indivíduos e padrões populacionais e gerais do modelo, como a abundância de invasores no sistema, emergem a partir das ações dos indivíduos. Como base para estes modelos, os indivíduos competem pelos recursos no sistema e os alocam para diferentes processos, de acordo com uma ordem de prioridade que varia entre as espécies.

No segundo capítulo buscamos compreender como diferentes estratégias de história de vida são determinantes para a invasão de mamíferos herbívoros. Novamente recorremos a espécies virtuais, mas desta vez agregamos um maior realismo às espécies, já que estas possuíam características de história de vida (número de filhotes, longevidade, tempo de gestação) determinadas por relações alométricas específicas para o grupo.

No terceiro capítulo exploramos como as estratégias de vida se comportam em um cenário realista, com uso do solo e quantidade de recursos variável. Neste capítulo desenvolvemos melhor o modelo do capítulo 2 e buscamos responder perguntas relacionadas à configuração espacial e a co-ocorrência entre espécies, além de testar algumas hipóteses clássicas relacionadas à processos de invasão biológica.

Resumo Geral

No antropoceno, invasões biológicas são um dos fatores que mais ameaçam a biodiversidade. A introdução de novas espécies exóticas pode ter gravas consequências às espécies nativas de uma região, levando desde uma alteração das relações bióticas já estabelecidas até mesmo à extinção de espécies. Além das consequências ecológicas, espécies invasoras também possuem um interesse econômico, já que muitas delas alcançam tamanhos populacionais tão expressivos a ponto de causar prejuízos aos mais diversos tipos de atividades econômicas, desde campos agrícolas até mesmo hidrelétricas. Dada a importância ecológica e econômica de espécie invasoras, um ponto essencial para amenizar os impactos consequentes de uma invasão biológica e se antecipar ao processo de invasão e prevenir que uma determinada espécie alcance uma nova área. Para isto, são necessários métodos eficientes na predição de invasões, que conseguem estabelecer regiões alvo com acurácia e também predizer como se dá a interação entre a espécie exótica e a comunidade nativa. Nesta tese nós construímos diversos modelos que buscam melhorar nosso poder de predição de uma invasão nas diferentes etapas do processo. No primeiro capítulo exploramos buscamos avaliar a capacidade de modelos de nicho na identificação de áreas adequadas para um invasor. Modelos de nicho são comumente utilizados para a identificação de áreas de interesse. No entanto, como mostramos neste capítulo, problemas como a divergência entre o nicho realizado e o nicho fundamental das espécies pode levar a sub- ou super predição das áreas identificadas como adequadas para espécies invasoras. No segundo capítulo buscamos compreender como a interação entre diferentes estratégias de história de vida da espécie exótica e da comunidade são determinantes para o sucesso de invasão. Construímos um sistema com indivíduos realistas, no qual estes indivíduos competem por energia e possuem prioridades de alocação desta energia. Encontramos que invasores que possuem uma estratégia comum com as espécies nativas foram os que tiveram sucesso em permanecer no sistema, sendo que a estratégia que possuiu maior retorno foi priorizar o acúmulo de reservas em detrimento da produção de filhotes. No terceiro capítulo exploramos como as estratégias de vida se comportam em um mundo realista, com uso do solo e quantidade de recursos variável. Neste capítulo desenvolvemos melhor o modelo do capítulo 2 e buscamos responder perguntas relacionadas à configuração espacial e a co-ocorrência entre espécies em diferentes níveis de heterogeneidade/distúrbio, além de testar algumas hipóteses clássicas relacionadas à processos de invasão biológica. Avaliamos o sucesso de invasão ao longo de 18 anos em uma paisagem que passa por uma rápida expansão agrícola e encontramos que o sucesso de invasão ao final, quando a paisagem é mais heterogênea e no seu maior percentual de terras agrícolas, foi maior. A expansão agrícola por si só levou à extinção de espécies nativas, além de favorecer o sucesso de invasão e aumentar a co-ocorrência entre as espécies invasoras e as nativas que permaneceram no sistema. Houve uma variação na estratégia de história de vida que levou aos maiores ganhos, de forma que a configuração da paisagem é essencial para determinar o sucesso de invasão.

Keywords: sucesso de invasão; modelo de nicho; modelo baseado em indivíduo; história de vida; co-ocorrência

Abstract

Biological invasions are one of the mains threats to biodiversity in the Anthropocene. The introduction of new exotic species might have serious consequences to native communities, being responsible for modifications to the established biotic relations up to the extinction of native species. Apart from serious ecological consequences, invasive species are also relevant form the economic point of view, as many species reach high populational levels which can lead to losses for several economic activities, such as agriculture and hydroelectric energy generation. Given the relevance of invasive species, an essential aspect to reduce the losses caused by biological invasions is to get ahead of the invasion process and prevent a potential invasive species from ever reaching a new region. In order to reach this goal, the different methods should be effective in anticipating possible invasions, by accurately defining target regions and also how the invasive species will interact with the native community. In this thesis we built and tested several models that seek to improve our capability to anticipate the results of an invasion process in its several stages. In the first chapter we explored the capability of ecological niche models (ENMs) in identifying suitable areas for the occurrence of a potential invasive species. ENMs are commonly used for establishing areas of interest, based on species' suitability. However, as we demonstrate in this first chapter, mismatches between the realized and the fundamental niche may lead to patterns of consistent under-or overprediction of the areas considered as harbouring suitable climatic conditions for an invasive species. At the second chapter we explored how the interaction between the different life-history strategies of invasive species and the native community determine invasion success. We've built a realistic system in which individuals compete for energy and have priorities for allocating the obtained energy. The whole system is regulated by allometric relations and energetic budgets. We found that invaders that share a common life-history strategy with the native species were more successful in establishing in the system, being that the strategy with the higher gains was of living longer, accumulating reserves while reducing the reproductive output (less offspring with longer gestation periods). At the third chapter we explored how those life-history strategies behave under a realistic landscape, with a real land-use and fluctuations in the energy within the system. In this chapter we've improved the chapter developed at the chapter 2 and focused on answering questions related to the landscape configuration and invasive-native co-occurrence under different levels of landscape heterogeneity. We also evaluated our model under classical hypothesis related to the invasion process. We've evaluated invasion success over 18 years in a landscape undergoing a rapid agriculture expansion and found that invasion success was highest at the end of this period, when the landscape is with its highest agriculture coverage. Agriculture expansion, by itself, was responsible for the extinction of native species, besides increasing invasion success and the co-occurrence between invasive and native species. There was also a difference in successful life-history strategies, in a way that the spatial configuration plays a big role in determining invasion success.

Keywords: invasion success; niche model; individual based-model; life-history; co-occurrence

Introdução Geral

Uma das formas de classificar a Terra se baseia em agrupas as regiões de acordo com a sua composição de espécies. Uma das divisões mais conhecidas foi proposta por Alfred Russel Wallace em 1876, uma data que precede a confirmação da Teoria da Tectônica de Placas, que esclareceu a conectividade entre os diferentes continentes. De um ponto de vista evolutivo, as ecorregiões de Wallace representam que um grupo de espécies conviveu em uma mesma região por um período suficiente de tempo a fim de se tornarem mais próximas entre si do que quando comparadas com espécie de outras regiões (Wallace 1876; Elton 1958). Portanto, a possibilidade de agrupar a Terra em regiões devido à similaridade de espécies, assim como a proposta de Wallace e várias outras que a sucederam (e.g. Kreft & Jetz, 2010; Holt et al., 2013), só é viável devido à existência de barreiras físicas/ambientais (e.g. montanhas, desertos, oceanos) que levaram ao isolamento de grupos de espécies em determinadas áreas. Além da sua relevância evolutiva, a divisão da Terra em regiões ria também um conceito que, como ressaltado por Wallace, foi de grande importância para naturalistas modernos, a ideia que espécies são nativas a um local (Wallace 1876). Wallace escreveu seu famoso livro *The Geographical Distribution of Animals* em 1876, uma época na qual o transporte global ainda era incipiente, quando comparado aos níveis de hoje. Após a primeira e a segunda grande guerra o transporte global de pessoas e mercadorias aumentou em quase 50 vezes, dado que só em 2016, 1 bilhão e 240 milhões de turistas visitaram outro país, o que representa aproximadamente 1/7 da população global (Roser 2018). Além de aumentar o transporte de pessoas e cargas, os níveis astronômicos de transporte global levaram a consequências que Wallace não poderia ter previsto em sua época, o grande número de espécies que seria carreada para fora de sua região nativa.

O evento no qual espécies são carreadas para fora de sua região nativa e introduzidas em localidades que extrapolam os limites de sua área de ocorrência cunhou o termo espécies exóticas. Espécies exóticas são aquelas espécies que, intencionalmente ou não, são levadas para fora de sua área nativa e alcançam outras localidades (IUCN 2000; Richardson 2011). O aumento constante no transporte global levou a uma consequência previsível, o aumento destes eventos de introdução, sedo que o número de introduções a cada ano continua aumentando (Hulme 2009; Seebens et al. 2017). Um percentual destas espécies introduzidas consegue se estabelecer e aumentar seus números até o ponto na qual passam a apresentar uma ameaça para a biodiversidade e às atividades econômicas, a estas espécies são dadas o nome de espécies invasoras (IUCN 2000). As consequências são diversas, desde impactos à biodiversidade nativa (McGeoch et al. 2010) e prejuízos econômicos (Born et al. 2005; Simberloff et al. 2013), alcançando até mesmo grandes mudanças biogeográficas, alterando até mesmo as regiões propostas por Wallace (Capinha et al. 2015; Bernardo-Madrid et al. 2019).

Dada a extensão dos impactos causados por espécies invasoras e a relação entre o custo-benefício ao longo do processo de invasão, grande parte dos esforços tem se concentrado em predizer e prever processos de invasão (UNEP, 2002; Simberloff et al., 2013). Teoreticamente, isto poderia ser resolvido ao aplicar o conceito de nicho fundamental de Hutchinson (Hutchinson 1957). Ao identificar todas as condições adequadas para a ocorrência da espécie e, baseando-se na dualidade do nicho (Colwell and Rangel 2009), mapear localidades nas quais estas condições estão presentes, seria simples identificar todas os locais nos quais uma invasão poderia acontecer e tomar medidas a fim de preveni-la. Baseando-se nesta lógica, um vasto número de estudos aplicou modelos de nicho ecológico (ENMs) para identificar áreas com alto potencial de invasão para uma dada espécie (e.g. Broennimann & Guisan, 2008; Menke et al., 2009; Jiménez-Valverde et al., 2011; Riul et al., 2013; de Campos et al., 2014). Em teoria ENMs são totalmente adequados para estas problemáticas, já que suas predições desconsideram capacidades de dispersão e mapeiam o nicho de uma espécie, sendo possível identificar áreas adequadas fora de sua distribuição de origem (Jiménez-Valverde et al. 2011). No entanto, como a real dimensão do nicho fundamental que está expressa dentro da distribuição da espécie é desconhecida, ENMs estão sempre sujeitos a erro no processo de identificação de áreas propensas a sofrer um processo de invasão (Soberón and Arroyo-Peña 2017).

Simultaneamente, um grande esforço tem sido feito com o propósito de desvendar as características biológicas das espécies exóticas e entender porque algumas espécies se tornam invasoras (e.g. Williamson & Fitter, 1996; Hayes & Barry, 2008; Allen et al., 2013; Kempel et al., 2013; Taylor, 2016). Várias hipóteses foram levantadas relacionadas à esta questão, algumas das quais são: i) hipótese da superioridade competitiva (Schultheis and MacGuigan 2018); ii) liberação dos "inimigos" na região nativa (Keane and Crawley 2002; Colautti et al. 2004; Liu and Stiling 2006); iii) alta pressão de propágulo (Simberloff 2009); iv) similaridade com a comunidade nativa/ resistência da comunidade nativa à invasão (Gallien and Carboni 2016); v) estratégias de história de vida (Sol et al. 2012). No entanto, devido à alta complexidade e peculiaridades de cada processo de invasão, não há ainda um consenso sobre a importância das características das espécies para o sucesso ou falha em um processo de invasão (Hayes and Barry 2008; Sol et al. 2012).

Uma informação comumente negligenciada que pode se mostrar fundamental para a solução deste impasse é o registro sobre invasões que falharam ou sobre espécies exóticas que não se tornaram invasoras. Apesar de haver alguma informação sobre invasões que falharam, os números são pouco expressivos e concentrados e os próprios autores reconhecem que este é um tópico que ainda temos muito a avançar (Zenni and Nuñez 2013). Dados sobre falhas (não-significância) geralmente não são reportados ou publicados em ecologia (Koricheva 2003), o que gera uma grande lacuna para análises, em especial métodos correlativos que buscam explicar um padrão, tal como explicar o sucesso de uma invasão ou predizer áreas adequadas para uma espécie por meio de um ENM (Lobo et al. 2010). Na falta destes dados essenciais sobre ausência/falha/não-significância para ajuste de modelos correlativos, uma alternativa é recorrer a modelos mecanístico, já que estes são construídos baseados em bases teóricas já estabelecidas e se mostram úteis para testar as predições

(Clark and Gelfand 2006; Kearney et al. 2008; Kearney and Porter 2009). O lado negative é que tais modelos, geralmente construídos em uma abordagem *bottom-up*, precisam de uma grande quantidade de dados e facilmente alcançam altos níveis de complexidade. A fim de lidar com isto, uma alternativa é recorrer a modelos orientados por padrões (POMs). Tais modelos são construídos tendo como alvo reconstruir padrões verdadeiros e são ancorados em dinâmicas e escalas relevantes àquela simulação. Tal estratégia adiciona realismo ao modelo e permite uma avaliação mais direta ao contrastar os resultados do modelo com o padrão observado no mundo real (Grimm et al. 1996; Wiegand et al. 2003; DeAngelis et al. 2005).

Ecologia é uma ciência fortemente baseada na explicação dos padrões observados (e.g. Dreyer & Puzio, 2001; Bowman et al., 2002; Field et al., 2009; Tittensor & Worm, 2016). Dentre os quais, um que recebe grande destaque é o escalonamento alométrico de vários traços biológicos como por exemplo o número de filhotes, longevidade, idade de maturação sexual (De Marco Jr. 1999), quantidade de comida ingerida (Clauss et al. 2007), tamanho das reservas (Lindstedt and Schaeffer 2002), tamanho do neonato (Martin and MacLarnon 1985). De todas as características que apresentam escalonamento alométrico, talvez a que tenha recebido maior destaque seja a taxa metabólica. Inicialmente proposta por Kleiber como uma lei em 1932, o escalonamento alométrico da taxa metabólica foi amplamente explorada ao longo dos anos, até mesmo em estudos recentes (Nagy et al. 1999; West et al. 2002; Glazier 2015). Duas principais teorias se propõem a explicar os mecanismos por trás deste escalonamento alométrico, o orçamento dinâmico de energia (Kooijman 1993) e a teoria metabólica da ecologia (Brown et al. 2004). Apesar da divergência em relação ao mecanismo responsável por produzir o padrão alométrico, ambas compartilham uma visão comum do mundo, na qual os diferentes processos no indivíduo são regulados pela disponibilidade energética (Maino et al. 2014).

Nesta tese nós nos baseamos nesta forma energética/alométricas de ver o mundo e construímos simulações a fim de explorar fatores que afetam o sucesso de invasão. No primeiro capítulo nós demonstramos que utilizar ENMs para identificar áreas de potencial invasivo possui problemas intrínsecos que necessitam de cuidados durante o processo de modelagem. Para os outros capítulos nós construímos simulações que exploram os processos de invasão a partir de um ponto de vista energético. No capítulo dois nós construímos um mundo mais simples, no qual indivíduos competem com a mesma eficiência pela única fonte de recurso e avaliamos como as estratégias de história de vida são relevantes para o sucesso de uma invasão. Finalmente, no capítulo três, nós exploramos de qual forma as espécies invasoras interagem com uma paisagem realista e com a comunidade nativa a fim de determinar o sucesso de invasão com diferentes níveis de integridade da paisagem. No final, nosso principal objetivo é entender melhor como a interação entre a comunidade nativa, a paisagem e os invasores determinam o sucesso de invasão em uma escala local/regional.

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Chapter 1 - Niche mismatches can impair our ability to predict potential invasions

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Abstract

The accurate anticipation of potential biological invasions is a crucial step toward the control of invasive species. The method used most commonly to identify areas suitable for biological invasion is the construction of Ecological Niche Models (ENMs), although the potential accuracy of this approach may be grossly overestimated. In the present study, we examine how biogeographical, biological, and methodological factors may affect our capacity to identify areas suitable for biological invasion. We created virtual species to investigate the incongruences between the fundamental and available niche in a natural environment. Firstly, we verified how differences in species characteristics (environmental tolerance and dispersal capacity) may hinder our ability to predict invasions using ENMs. We also evaluated how different algorithms behave in the context of these differences. We also measured how prediction accuracy varies in different regions of the world, by evaluating the degree of niche mismatch found in each zoogeographic region. In general, the predictions of the ENMs varied according to species tolerance, dispersal capacity, and the algorithm used to fit the model, although the principal source of variation was the degree to which the algorithms under- or over-estimated the fundamental niche. Some zoogeographic regions did indeed prove to be more error-prone than others, due to the variation in the levels of climatic incompleteness and the representation of the fundamental niche within a species' distribution. We demonstrate that the prediction of potential biological invasions using ENMs may incur errors in niche estimation, which may result in suitable locations being overlooked. This reinforces the need for caution in the prediction of biological invasions, given that the fundamental niche may not be expressed adequately within the native range of the species, as determined fundamentally by its biological characteristics.

Introduction

The distinction between the fundamental and the realised niche, as proposed by Hutchinson (1957), is one of the root concepts of modern ecology (Jackson and Overpeck 2000; Soberón 2007), although it is also one of the most controversial and misused (Silvertown 2004; Silvertown et al. 2006; Holt 2009; Peterson et al. 2012). Hutchinson defined the fundamental niche as the volume of a hyperspace, delimited by environmental variables, within which a species will encounter the conditions in which it can exist indefinitely. The realised niche is a subset of the fundamental niche, which is limited by the presence of other species, preventing the occupation of the entire fundamental niche (Hutchinson 1957). However, as it is difficult to define niche limits, Hutchinson's concept may be inadequate for discussing questions on a global scale, and this definition does, in fact, neglect other key factors that also prevent a species from occupying its fundamental niche fully, including dispersal limitations, niche evolution, density-dependence processes, and feedbacks (Jackson and Overpeck 2000; Soberón 2007; Holt 2009).

A more recent theoretical framework, the BAM concept, focuses on the understanding of species distributions on a broad scale (Soberón and Peterson 2005; Soberón and Nakamura 2009). The BAM model, based on the Grinnelian and Eltonian niche concepts, emphasizes the abiotic and biotic components, respectively, of the ecological niche, together with a third component, which represents the restrictions on the dispersal of the species. On a broad geographical scale, that is, over a large area or at a coarse resolution, scenopoetic variables and dispersal restrictions are expected to have a more decisive influence on species distributions, while the biotic component plays a more important role at finer resolutions, as in the Eltonian Noise Hypothesis (Soberón & Nakamura, 2009; see also Willis, 2002; Pearson & Dawson, 2003; Hortal et al., 2010). Even so, biotic interactions cannot be overlooked entirely, given their potential contribution to the prediction of the distribution of a species, even at a broad scale (e.g. Heikkinen et al. 2007; Silva et al. 2014; Staniczenko et al. 2017).

Species invasions are complex, idiosyncratic processes, which means that every invasion is unique (Theoharides and Dukes 2007; Hoberg 2010). In general, however, preventing the colonisation of an area is seen the most effective way of deterring an invasive species (Myers et al. 2000; Puth and Post 2005). To achieve this, it is essential to identify the conditions most suitable for the target species, that is, its fundamental niche, and determine the distribution of these conditions in the environment (Mack et al. 2000; Nentwig 2007). It is impossible to describe the fundamental niche of a species in full, although it is necessary to at least define subsets of this niche. This can be done using two principal approaches, that is, empirical observations or experiments (in the field or laboratory), both of which have their strengths and weaknesses (Holt 2009). While an experiment approach permits the control of environmental variables and the testing of a wide range of conditions, providing a more accurate definition of the tolerance limits of a species, experiments are resource-intensive and organism-specific, limiting the potential for generalisations. Even so, tolerance limits have been estimated reasonably accurately from laboratory experiments in a number of cases of well-studied invasion processes (e.g., Kearney et al., 2008; Mccann et al., 2014; Magozzi & Calosi, 2015). The alternative, empirical approach is to estimate niche limits from occurrence records and statistical models, a framework known as ecological niche modelling (ENM: Peterson et al. 2012). While this method is straightforward, it is subject to a number of intrinsic limitations that that may lead to errors in the estimation of niche parameters, due to either (i) the absence of suitable climate within the native region (climatic incompleteness) or (ii) the inability of the species to reach areas with suitable climate (climatic non-equilibrium).

Scenarios of this type can be interpreted in the context of the recently-proposed concepts of fundamental, existing and realised niche (Soberón and Arroyo-Peña 2017). The fundamental niche encompasses all the conditions in which a species can survive, as proposed by Hutchinson (1957), while the existing niche is a subset of this fundamental niche, and is defined as the conditions of the fundamental niche that actually exist in a given space and time, and the realised niche encompasses the areas actually occupied by the species (Soberón and Arroyo-Peña 2017). On every continent, the existing set of combinations of possible conditions may not correspond to all the possible combinations of these variables (Jackson and Overpeck 2000; Guisan et al. 2014). In this case, while a species may be capable of surviving within a given combination of climatic variables (e.g., mean temperature > 25oC and annual precipitation < 550 mm), these conditions may not be found currently within its native region of occurrence, which means that its fundamental niche is not expressed completely within its existing niche. This incompleteness constitutes a problem for the description of a niche based on empirical occurrence data, given that conditions suitable for the species may not necessarily be observed (Figure 1, see the red areas in the Climatic Incompleteness panels). Climatic non-equilibrium is potentially more problematic, and refers to the existence of appropriate combinations of climate within the native region that are not occupied due to dispersal limitations, geographic barriers or local exclusion through biological interactions, such as the presence of a superior competitor or the absence of a mutualist (Guisan et al., 2014; Qiao et al., 2017; Figure 1, see red areas in the Climatic Non-equilibrium panels). In this framework, situations of this type represent a mismatch between the existing and realised niches (Soberón and Arroyo-Peña 2017), and an ENM may identify these areas as lacking suitable climate, which would result in the fundamental niche being underestimated, with similar limitations for the identification of potential areas of species occurrence (Jackson & Overpeck, 2000; Qiao et al., 2017).

Despite those issues, ENMs are used extensively to identify areas suitable for potential biological invasions (e.g., Cássia et al. 2014; Rodrigues et al. 2016; Oliveira et al. 2018; Zemanova et al. 2018), although the accuracy of this approach may be overestimated, given the shortcomings outlined above. In the present study, we apply a virtual species framework to investigate how the incorrect estimation of the fundamental niche of a species affects the potential for the identification by ENMs of areas suitable for biological invasions. We verified how different algorithms estimate the fundamental niche and suitable areas of occurrence in different biological scenarios (based on environmental tolerance and dispersal capacity), and how different zoogeographical regions are affected by climatic incompleteness and non-equilibrium.

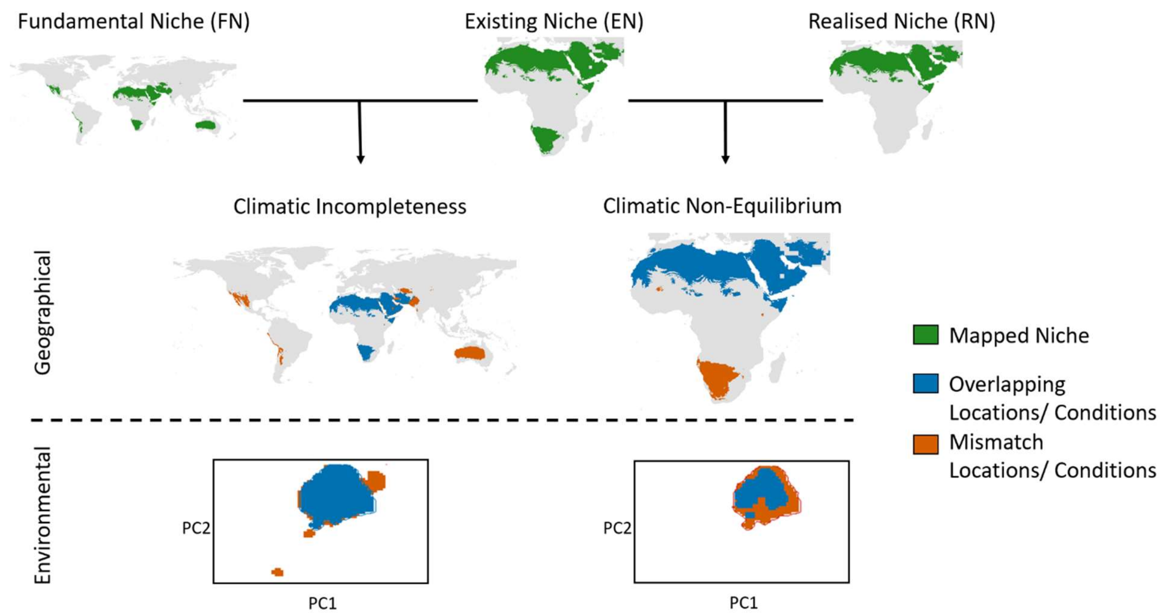

Figure 1: Sources of niche misestimation regarding climatic incompleteness and non-equilibrium in the environmental and geographic space. On top, the three niches proposed by Soberón and Arroyo-Peña (2017): fundamental, existing and realised niche. Under the niches, left panels represent the overlap between the fundamental and existing niche and right panels the overlap between the existing and the realised niche. Blue areas/conditions signify the niches overlap and in red areas/conditions the niches mismatch. The mismatch between the fundamental and existing niche creates situations of climatic incompleteness, in which there are suitable conditions for species occurrence that do not exist on its native zoogeographic region (red areas, left panels). The mismatch between the existing and realised niche creates situations of climatic non-equilibrium, in which there are suitable conditions for the species occurrence within the zoogeographic region, but the species fail to occupy those areas due to dispersal limitations or biotic interactions (red areas, right panels).

Methods

Methodological Overview

Our general approach in the present study was to generate virtual species distributions using a cellular automaton to simulate population dynamics and colonisation/extinction processes, based on a known set of responses to climatic conditions. We created virtual species with different characteristics to demonstrate how variations in the environmental tolerance and dispersal capacity of a species affect the predictions based on ENMs (for a detailed explanation of the creation of the virtual species, see Supporting Information 1). To begin with, we created fundamental niches (FNs) with two different degrees of environmental tolerance (Fig. 2a; Supporting Information 1). We simulated the occupancy of suitable areas by projecting the FN onto geographic space, considering two levels dispersal capacity (Fig. 2b; Supporting Information 1). To represent long-term stability in the distribution of the species and obtain a more realistic, cohesive pattern, we established a minimum threshold of 0.5, below which the species cannot survive in the cell (De Marco Jr. et al. 2008). We interpreted the environmental conditions found within the distribution of the species as the realised niche (RN), which can be defined as the "climates in localities where a species has been observed" (Soberón and Arroyo-Peña 2017). A high dispersal capacity may increase the chances that all the suitable areas are accessed during the iterations (De Marco Jr. et al. 2008), although our simulations include two potential barriers to the dispersal of the species, even those with a high dispersal capacity, that is, oceans and extensive areas of unsuitable climate. Finally, we defined the existing niche (EN) as the portions of the FN within all zoogeographical regions occupied by the species during the cellular automaton process. To evaluate the potential interaction between environmental tolerance and dispersal capacity, we created 100 species for each combination of species-climate specificity and dispersal, with a final total of 400 virtual species.

We extracted random points from the distribution of each species as occurrence data for the ENMs and fitted models using a set of algorithms (envelope, logistic regression, machine learning, Bayesian) chosen to represent the variation in the complexity of these scenarios and the different input data requirements (presence only, presence/pseudo-absence, and presence/background; Elith & Graham, 2009; Figs. 2c; Supporting Information 1). We sampled only presence data, but created pseudo-absence/background data whenever necessary, as this is the type of dataset most commonly used for ENM modelling. The niche estimated by the ENMs (Predicted Niche; PN) was delimited as the set of environmental conditions at locations above the maximum specificity and sensitivity thresholds, a criterion that balances omission and commission errors and is commonly used in ENM modelling (Jiménez-Valverde & Lobo, 2007; Fig 2d). To further evaluate the effects of these thresholds on our results, we also investigated the effects of delimiting the PN as a set of conditions above the threshold that maximizes the Jaccard index (Supporting Information 2; Leroy et al. 2018).

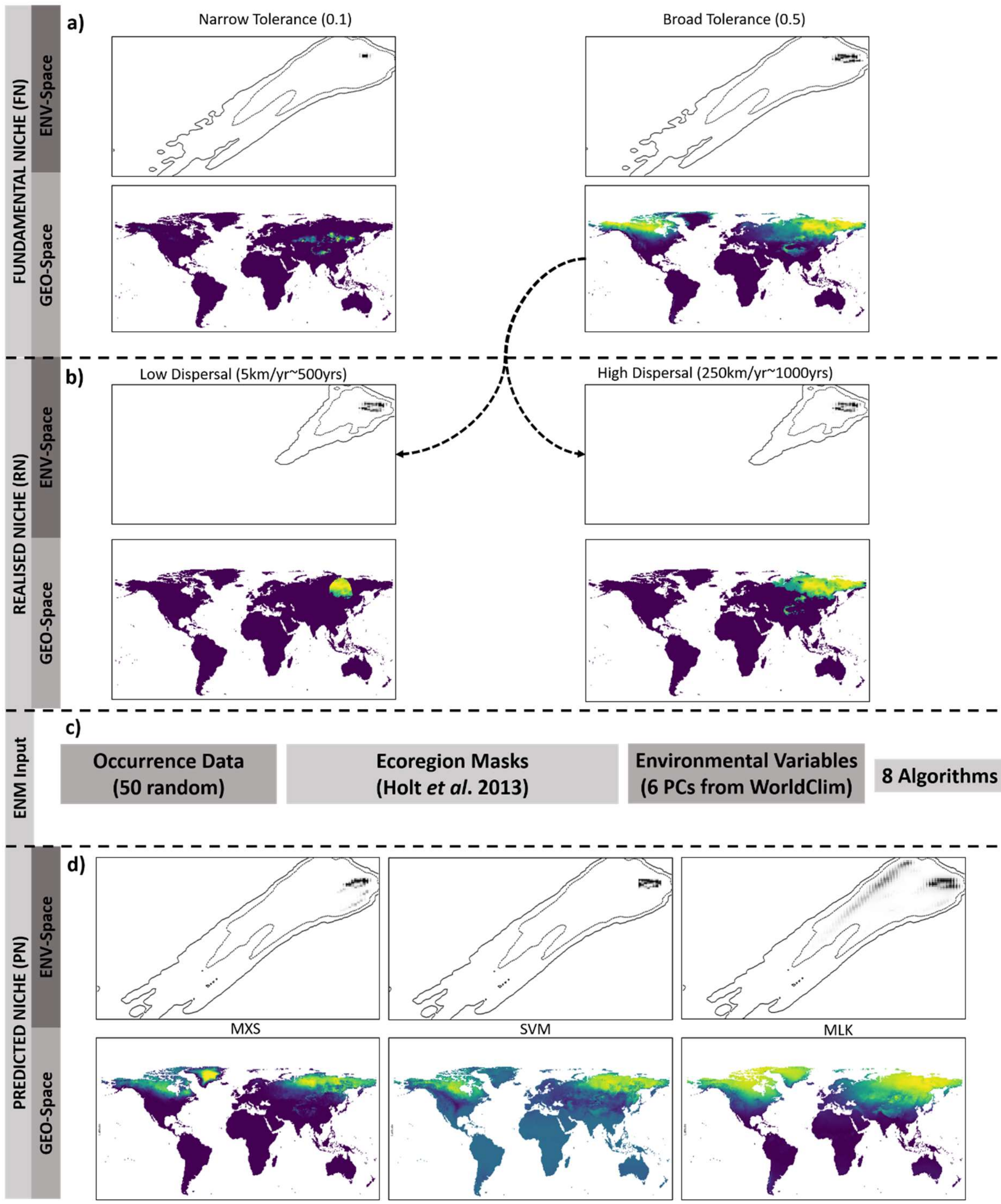

Figure 2: Methodological overview. In the first level, it is possible to observe how differences in the width of the environmental tolerance affect the geographical distribution of suitable areas or the fundamental niche (FN; 2a). From the niche, we select a highly suitable cell (>0.95) and simulate species distributions with two levels of dispersal, this may generate species that share the same FN, but have distinct distributions. We extracted the environmental conditions within the distribution to delimit the realised niche (RN; 2b). From the distribution, we extracted occurrence data and created zoogeographic masks to restrict pseudo-absence/background sampling. We used the occurrence and pseudo-absence data, along with principal components derived from WorldClim bioclimatic variables, as input for ENM (2c). We used eight algorithms (three of which are

exemplified in the figure) to fit ENMs and evaluated its predictions both in the geographical and environmental space. Predictions in the geographic space identify suitable areas for occupancy, while the environmental space represents the niche as predicted by ENMs (PN; 2d).

Climatic Incompleteness and Non-Equilibrium

The mismatch between the fundamental (FN) and existing (EN) niches or between the existing (EN) and realised (RN) niches can be used to investigate the two principal factors that contribute to inaccurate niche estimates, that is, climatic incompleteness and climatic non-equilibrium, respectively. We also investigated how these questions are structured on a global scale. We used the zoogeographic regions of Holt et. al. (2013) to evaluate whether different regions have different levels of representativeness of species FNs, as this may result in a systematic modelling bias. We expect that natural differences in climate heterogeneity and the size of the different zoogeographic regions may cause differences in the expression of climatic incompleteness and non-equilibrium, around the globe (e.g., Australian vs. Afrotropical realms).

For climatic non-equilibrium, we measured the EN by extracting environmental conditions (the first two axes of a Principal Components Analysis (PCA) run on global 19 Worldclim bioclimatic variables v.2.0; Fick and Hijmans 2017) for cells with a suitability of over 0.5 (the threshold for a species' FN) within a species' native zoogeographical regions. For the RN, we extracted the environmental conditions (the same first two PCA axes) of every cell occupied in the cellular automata. We then used a modified version of the framework proposed by Broennimann et al. (2012) and Guisan (2014), implemented in the ecospat package (Di Cola et al. 2017), to quantify niche stability, expansion, and unfilling between the EN and the RN. As we had complete knowledge of the fundamental niche of each species, and a substantial number of data points, we did not consider the density profile in niche comparisons, as this would cause errors in the calculations due to a major bias toward some niche conditions. This framework characterises the niches from the data of the first two axes of a PCA run on the predictors and fits a kernel density to the points, constructing a density distribution for each niche. Regions in which the polygons overlap are considered to be areas of stability, with all others being considered areas of expansion or unfilling. Niche stability is determined by the overlap between the EN and the RN, which means that a species with greater niche stability has its EN well represented within its geographic distribution. Areas of expansion represent sets of conditions found within the EN that are not represented within the RN or areas of climatic non-equilibrium. We did not evaluate the unfilling component in this step because it is impossible for the RN to have conditions that are not encompassed by the EN, given that the RN is a subset of the EN.

Climatic incompleteness was estimated by quantifying how much of the FN is represented within the EN. We used the same framework to evaluate stability, expansion, and unfilling between the FN and the EN. In this scenario, niche stability refers to the conditions of the FN found within the native zoogeographic region, while the unfilling is the set of conditions of the FN that do not exist within the native region, representing climatic incompleteness. As the EN is a subset of the FN, we did not evaluate the expansion component, as it will always be zero.

Prediction Success of the ENM

We evaluated the prediction success of the ENMs in both environmental (how successfully the models predict the FN of the species in the environment) and geographical space (how successful they predict the potential distribution of the species). We used the same framework developed to measure climate incompleteness and non-equilibrium (as above) for the analysis of environmental space. We compared the predicted niche (PN) with the FN to assess the accuracy of the models. Here, stability is the portions of the FN encompassed by the model, expansion quantifies the over-prediction of the fundamental niche by the model, while unfilling quantifies its under-prediction. We transformed both true suitability and ENM predictions into presence-absence maps for the analysis of geographic space, and used a confusion matrix to quantify the accuracy of the ENMs (Allouche et al. 2006). We used two thresholds to define areas of presence or absence in the ENMs: (i) maximum specificity and sensitivity, and (ii) the maximisation of the Jaccard index. For fundamental suitability, on the other hand, we applied the established threshold of 0.5 to create the true potential distribution of the virtual species. A confusion matrix allowed us to identify regions of stability (true positives - TPos), over-prediction (false positives - FPos), and under-prediction (false negatives - FNeg) between models predicting the potential distribution and the actual potential distribution. We excluded the locations at which the species cannot occur due to real low suitability and where it was classified as absent by the ENMs (true negatives - TNeg), given that this can inflate model accuracy and that these localities are not focal areas in our study (Leroy et al. 2018). We calculated ratios for these metrics as for the environmental space, by dividing the number of cells in the target metric by the total number of cells in all three metrics (e.g. TPos rate= TPos/ (TPos+FPos+FNeg)). We also derived error metrics based on patterns of suitability. We calculated the Rooted Mean Square Error (RMSE) between the suitability predictions of the ENMs and the real suitability to estimate the degree to which the different algorithms represented the real suitability pattern. Values of RMSE closer to zero denote a better performance of the ENM.

Data Analysis

We used generalised linear mixed models (GLMM) to test the effects of different algorithms, environmental tolerance, and species dispersal capacity on the predictive capacity of the ENM approach to the estimation of the FN in environmental and geographical space. Fixed effects, included as factors, were parameterised up to a triple interaction between predictor variables. The structure of random effects permitted the inclusion of random shifts around the intercept and slope based on virtual species and the dispersal capacity of the species, respectively. We inspected the normality and homoscedasticity of the model residuals, and whenever necessary, the data were root-square transformed to either normalize the data or eliminate outliers. We used Wald's Chi-square to verify the effect of each factor. As the analyses are derived from simulations, we based our interpretation on the values of the Chi-square rather than the p value (White et al. 2014). We used the lme4 (Bates et al. 2015), car (Fox and Weisberg 2011) and lsmeans (Lenth 2016) packages to fit the mixed models, run Wald's test, and estimate the means and confidence intervals.

As we did not control for the origin of a species when creating it, we observed considerable variation in the number of species native to a given zoogeographical region, with some combinations not even being observed. For example, no species with a narrow environmental tolerance and low dispersal capacity were observed in Oceanian, Panamanian or Oriental zoogeographic regions. Given this, the results of the analyses of climatic incompleteness and non-equilibrium are interpreted based on the visual evaluation of the confidence intervals, and no statistical tests were run on these metrics.

Results

ENM Prediction Success

We measured prediction success of the ENM of the FN in both environmental (predicted niche versus fundamental niche; Fig. 3; Tables 1 and 3; Figure S2 in Supporting Information 2) and geographical space (predicted potential distribution versus actual potential distribution; Fig. 4; Tables 2 and 4; Figures S3 in Supporting Information 2). The complexity of the relationships affecting these results is expressed systematically by the existence of statistical interactions among the biological factors and the different algorithms (Tables S1, S2, S3, and S4).

In environmental space, the algorithms obtained varying levels of accuracy according to the environmental tolerance or dispersal capacity of the species (Tables S1 and S3). However, when the FN was both over- and underestimated, the algorithms were the primary source of variation, with some algorithms consistently overestimating the FN and others consistently underestimating the FN (Figures 3 and S2). We established three groups of algorithms based on the levels of under- or over-estimation: (i) algorithms with very broad predictions, beyond the FN of the species (high overestimation and low underestimation; Generalised Linear Model (GLM) and Maximum Likelihood, MLK), (ii) algorithms with very restricted predictions, which underestimate the FN of a species (low overestimation and high underestimation; Bioclim (BIO), Random Forests (RDF) and Support Vector Machine, SVM), and (iii) algorithms with balanced predictions (mean over- and under-estimation; Maxent (MXS), Bayesian-Gaussian (GAU), and the Generalised Additive Model, GAM).

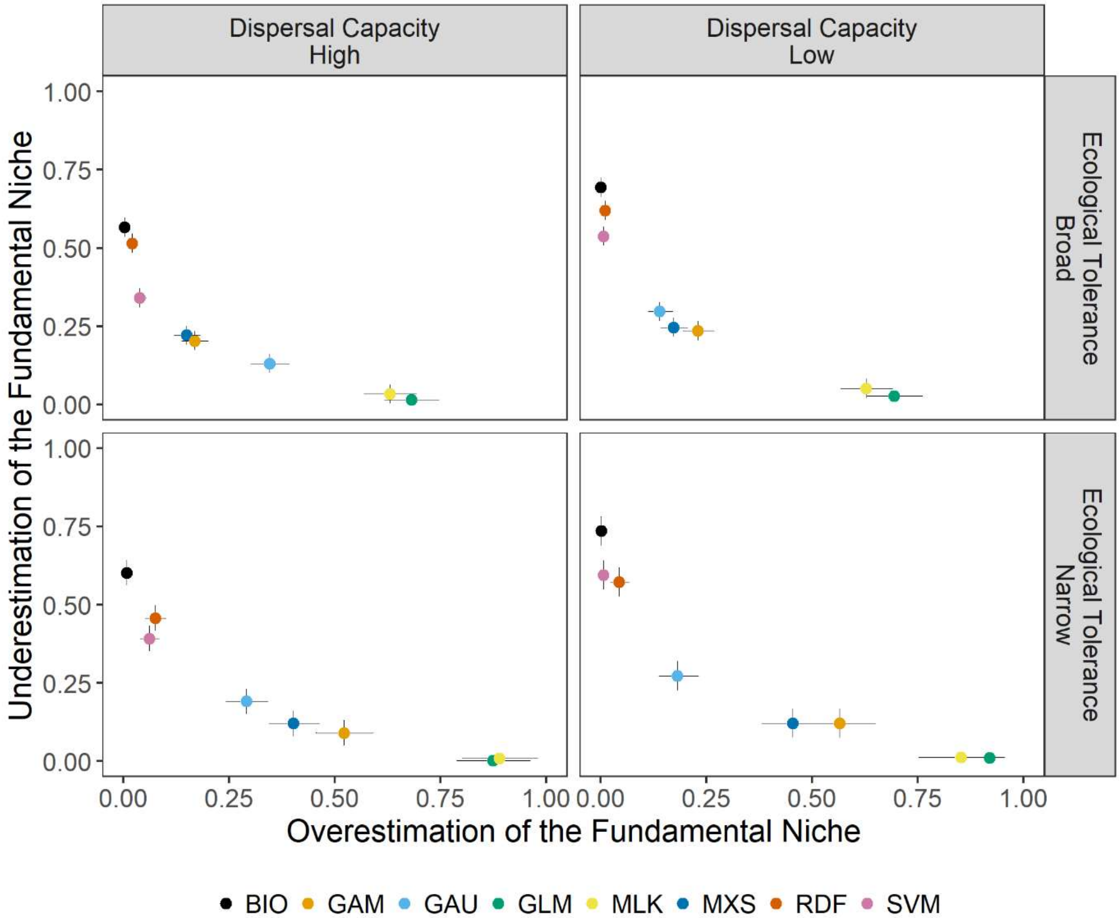

Figure 3: Niche overestimation and underestimation between species' fundamental niche (FN) and the niche predicted by the different ENM algorithms (colours) for species with different levels of environmental tolerance (rows) and dispersal capacity (columns) under the maximum specificity and sensitivity threshold. The closer an algorithm is to {0,0}, the higher its accuracy on estimating the fundamental niche. Higher values in the X-axis and Y-axis are caused by ENMs overestimating and underestimating species' fundamental niche respectively. Algorithms acronyms: Bioclim (BIO), Generalised Additive Model (GAM), Bayesian-Gaussian (GAU), Generalised Linear Model (GLM), Maximum Likelihood (MLK), Maxent (MXS), Random Forests (RDF) and Support Vector Machine (SVM).

The algorithms also tended to consistently over- or under-estimate the potential distribution of a species in geographical space, but without the formation of clear clusters (Figures 4 and S3). The effects of the biological characteristics were more pronounced, however, and even surpassed the effect of the different algorithms in some cases. The environmental tolerance of the species was a factor determining the over-prediction of an algorithm, with species characterised by a narrow tolerance having higher levels of over-prediction for most algorithms, in particular in the species with a high dispersal capacity. On the other hand, the degree of under-prediction of an algorithm was influenced primarily by the dispersal capacity of the species. In this case, the potential distribution of the species with a low dispersal capacity was underestimated to a higher degree (Tables S2 and S4). This pattern was found in the case of both thresholds, although predictions based on the Jaccard index had lower errors of over-prediction (Figures 4 and S3).

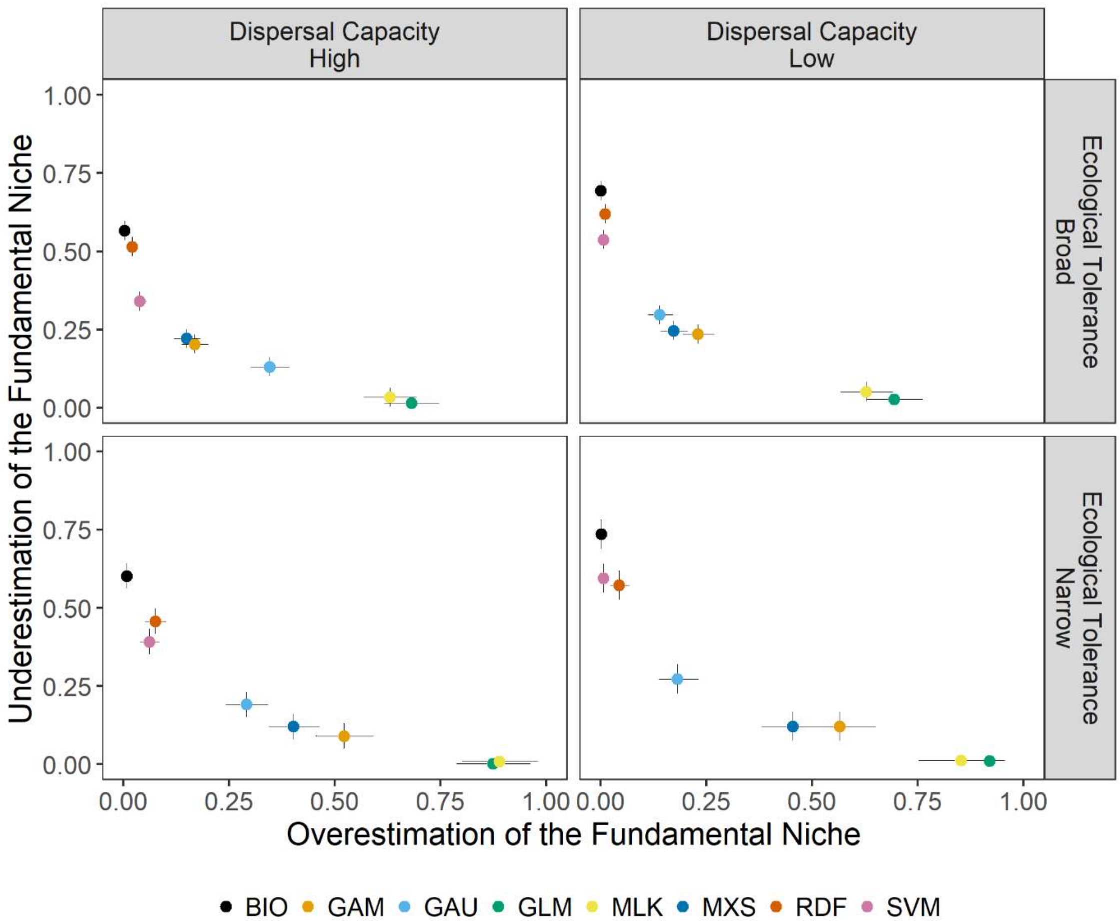

Figure 4: Over-and underprediction rates of the different ENM algorithms (colours) when compared to the real potential distribution of a species with different levels of environmental tolerance (rows) and dispersal capacity (columns) under the the maximum specificity and sensitivity threshold. The closer an algorithm is to {0,0}, the higher its accuracy on estimating potential occurrence. Higher values in the X-axis and Y-axis are caused by ENMs overestimating and underestimating the suitable locations for occurrence respectively. Algorithms acronyms: Bioclim (BIO), Generalised Additive Model (GAM), Bayesian-Gaussian (GAU), Generalised Linear Model (GLM), Maximum Likelihood (MLK), Maxent (MXS), Random Forests (RDF) and Support Vector Machine (SVM).

Differences in suitability, as evaluated by the RMSE, hampered the evaluation of the degree of under- and over-prediction of the different algorithms, although they did help to evaluate how far the algorithms deviated from the original species suitability (Fig. 5). In general, the BIO algorithm performed well for species with narrow tolerance, which can also be confirmed by the evaluation of geographical space based on this algorithm (Figures 4 and S3). The MXS, RFS, and SVM algorithms also had low levels of error for species with narrow tolerance. On the other hand, Maxent was the best algorithm for species with broad tolerance, especially when these species had a high dispersal capacity. The RDF, SVM, and BIO algorithms also presented satisfactory results. The worst-case scenario for all the algorithms was found for the species with broad environmental tolerance, but poor dispersal capacity.

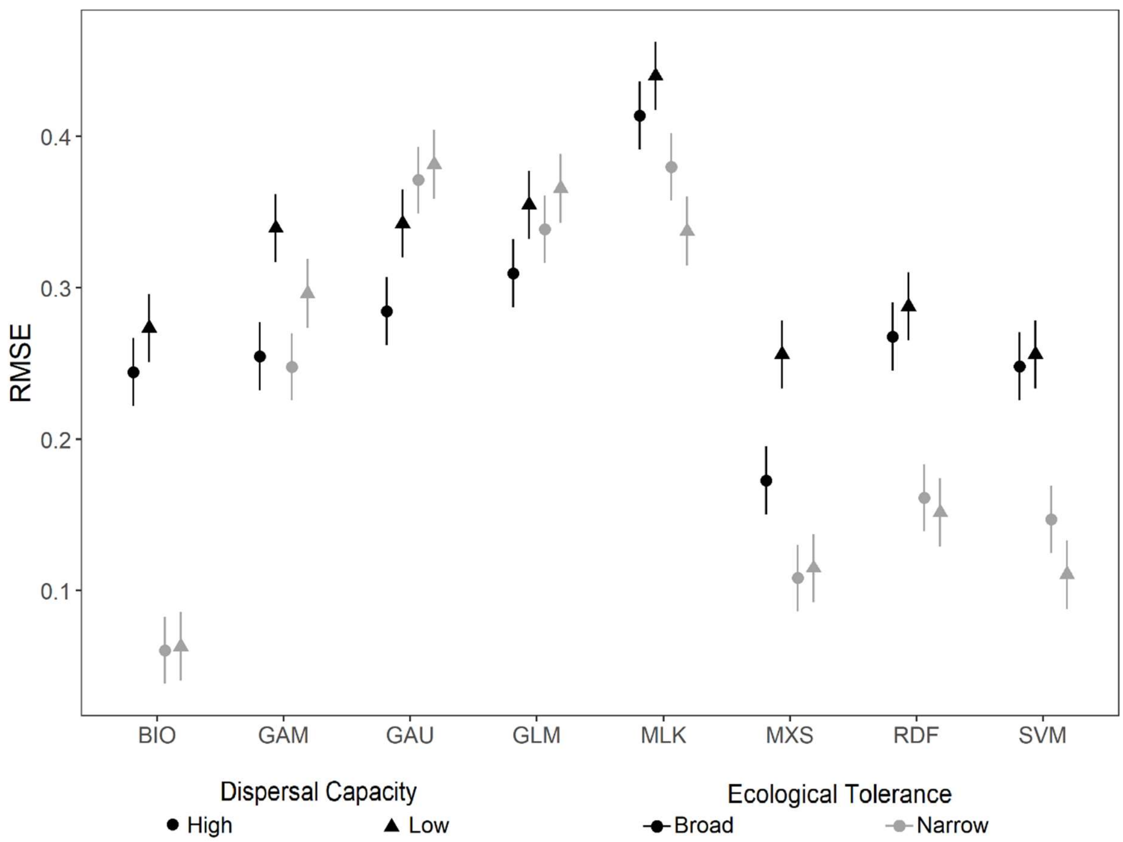

Figure 5: Rooted Mean Square Error (RMSE) between different ENM algorithms and species fundamental suitability. Different colours (black, grey) represent the different levels of species' environmental tolerance (broad and narrow, respectively), while different shapes (circles, triangles) are the different levels of dispersal capacity (high and low, respectively). The lowest the RMSE value, the closer the algorithm is to the real fundamental suitability. Algorithms acronyms: Bioclim (BIO), Generalised Additive Model (GAM), Bayesian-Gaussian (GAU), Generalised Linear Model (GLM), Maximum Likelihood (MLK), Maxent (MXS), Random Forests (RDF) and Support Vector Machine (SVM).

Climatic Incompleteness and Non-Equilibrium

The ranges of the variance in climatic incompleteness and non-equilibrium make it clear that the primary source of uncertainty was derived from the species not being in climatic equilibrium (0~0.95; Fig. 6), rather than climatic incompleteness within the native region (0~0.29; Fig. 6). Two clear patterns of climatic incompleteness are apparent in the data: (i) species with a narrow range of environmental tolerance were rarely affected by climatic incompleteness, and (ii) incompleteness appeared to be more relevant in the Australian region (Fig. 6). Incompleteness was found in species with narrow tolerance only in the Australian region (~10% FN-EN mismatch), reaching the highest level (~20% FN-EN mismatch) for species with broad tolerance. Some degree of incompleteness in species of broad tolerance was found in all the regions analysed, with certain regions having very low maximum levels, as in the case of the Palaeartic and Oceania, in which no scenario had FN-EN incompleteness of more than 10%. Other regions, including the Neotropical, Afrotropical, and Australian regions, had higher maximum values, with scenarios close to or exceeding 20% FN-EN incompleteness, with the Australian region reaching 30%, and no region having less than 20% (Figure 6).

In the case of climatic non-equilibrium, when we considered only the biological characteristics of the species, the taxa with poor dispersal capacity and broad environmental tolerance had the highest levels of non-equilibrium (Figure 6). When we included the geographical origin of the species, the same pattern is found in all zoogeographic regions, albeit at varying levels (Figure 6). Given the different sample sizes available for each combination, we could not establish systematic comparisons and rank the zoogeographical regions, but rather, we opted to highlight the most pertinent patterns. The dispersal capacity of the species appeared to be more significant in the taxa with narrow tolerance in regions such as the Sino-Japanese and Neotropical regions, while it had much less influence in the Nearctic region. In species with broad tolerance, the variation in dispersal capacity was greater in regions such as the Nearctic and Palaearctic, providing more reliable insights into when a species reaches climatic equilibrium (Figure 6).

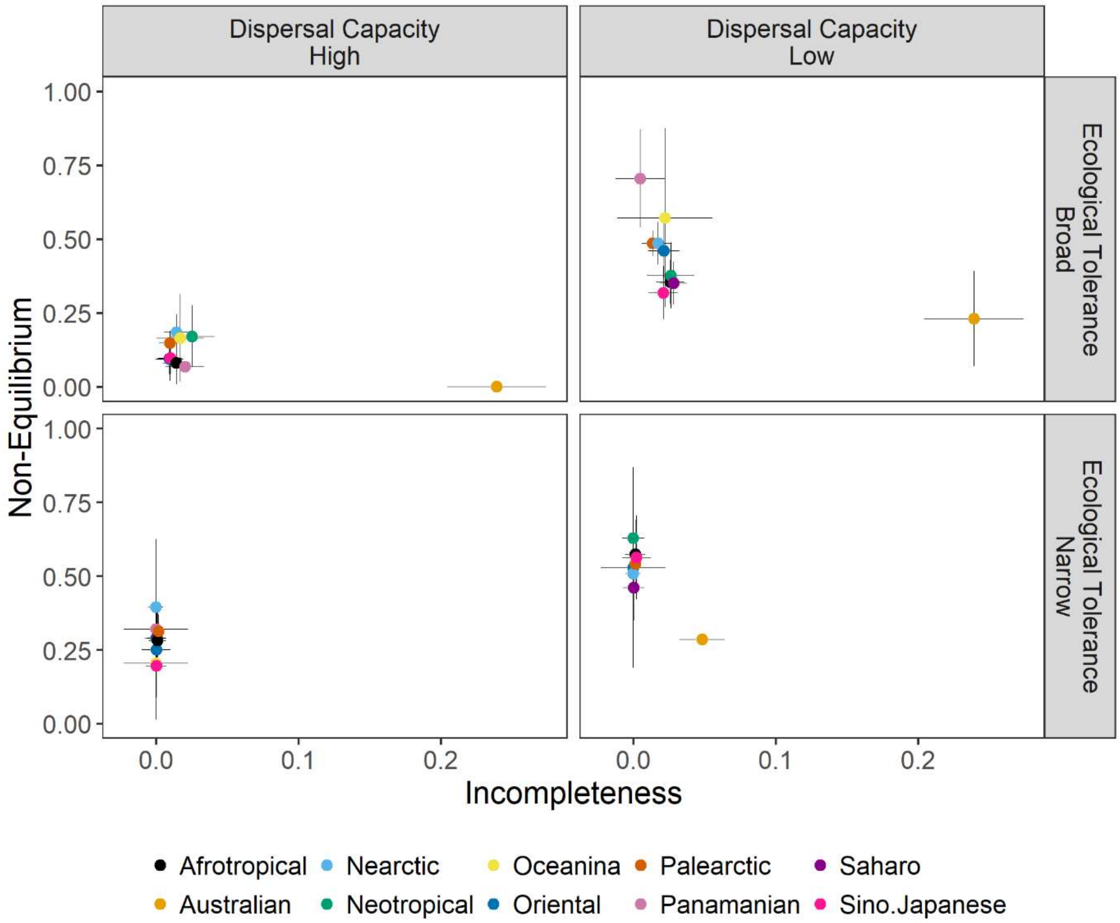

Figure 6: Climatic incompleteness (conditions of species' fundamental niche that do not exist in its native zoogeographic region; FN-EN mismatch) and non-equilibrium rates (conditions of the fundamental niche that exist in the native zoogeographic region but are not encompassed by species' distribution; EN-RN mismatch) in the different zoogeographic regions (colours). Species are classified by their environmental tolerance according to species' environmental tolerance (rows) and dispersal capacity (columns). Zoogeographic regions closer to (0,0) are more likely to have all conditions of the fundamental niche expressed within species distribution.

Discussion

In the present study, we evaluated the potential for the accurate identification of areas suitable for biological invasions using ENMs, one of the most widely used approaches to this question (e.g., Broennimann and Guisan 2008b, Bradley 2013, Guimapi et al. 2016, Turbelin et al. 2016). We identified a number of severe limitations in the capacity of ENMs to identify these areas, which varied according to the specific algorithm and the biological characteristics of the species. We identified three groups of algorithms, based on their degree of over- and under-prediction of the fundamental niche

(FN). The GLM and MLK algorithms overestimated both the FN and potential distribution, whereas BIO, RDF, and SVM underestimated the FN and potential distribution, and MXS, GAM, and GAU returned intermediate levels of error in both cases. We also verified how problems of climatic incompleteness and non-equilibrium affect species from different zoogeographic regions. Although climatic non-equilibrium was an important question in all regions, especially for the species with low dispersal capacity, climatic incompleteness was much less relevant, even for species with broad environmental tolerance.

The role of the different algorithms in the variance of the results is not a novel finding for the ENM approach. A number of previous studies obtained similar findings when the uncertainty of the predictions of a model were partitioned (Diniz-Filho et al. 2009; Watling et al. 2015). We expected to find this pattern here, given that the models make different assumptions and fit curves with different levels of complexity (Elith and Graham 2009), and the fact that no single ENM model will normally be optimal for all situations or, as Qiao et al. (2015) put it, there is no "free lunch". Even so, anticipating the behaviour of an algorithm can be vital to the interpretation of the results of a model and the selection of the algorithms most appropriate for a given study. Depending on the objectives of the study, algorithms that either over- or under-predict may be more or less appropriate (Peterson, 2006; Jiménez-Valverde et al., 2011).

In general, it is well known that niche models based on empirical evidence of occurrence are poor predictors of the fundamental niche (Soberón 2007; Jiménez-Valverde et al. 2008; Soberón and Arroyo-Peña 2017). Qiao et al. (2015) evaluated how different algorithms affect the estimation of the FN of virtual species in geographical space, and also found that different algorithms behaved in distinct ways, but despite its similar methodological framework, the results of the present study indicated a different pattern. Qiao et al. (2015) found low levels of over-prediction in all algorithms, with under-prediction being the primary driver of the variation between algorithms, whereas in the present study, we found high levels of both over- and under-prediction in the different algorithms. We conclude that this difference is related to three principal factors: (i) the total amount of geographical and related environmental variation included in each study, (ii) the process adopted to create the distributions of the species, and (iii) the environmental heterogeneity among zoogeographical regions. In the present study, we focused on how algorithms behave when predicting global invasions, whereas Qiao et al. (2015) focused specifically on the variation in species niches and distribution in Southeast Asia. Our global approach provided a broader, and in many ways, novel set of environmental conditions, resulting in higher levels of error in both over- and under-prediction. This difference in the two approaches, together with our more realistic simulation of population dynamics, may have resulted in the greater divergence between the FNs and the RNs. While Qiao et al. (2015) did confirm that the performance of the algorithms varies according to the scenario, as shown in our study, we feel that our findings support more reliable generalisations, given our more realistic approach to broad-scale climatic variation.

We also determined how niche mismatch can hamper predictions by causing climatic incompleteness or non-equilibrium. In all zoogeographic regions, the FN of resident species may not be contained entirely within its native range, although the amount of incompleteness will vary according to the dispersal capacity and environmental tolerance of the species, with species of broad tolerance being more prone to FN incompleteness. In practice, this translates to models being fitted to conditions that represent a subset of the species' niche. Any ENM approach can do no more than adjust its response curves to the conditions to which it was fitted, with any conditions beyond these limits being included by extrapolation (Fitzpatrick and Hargrove 2009; Elith et al. 2010; Owens et al. 2013). Model extrapolation can be considered to be a "disease without a cure", given that the problem can be circumvented, but not resolved completely. Models will inevitably include some extrapolation when identifying potential areas for biological invasions around the world, given that no one zoogeographic region will encompass all possible climatic combinations. When a model fit encompasses the whole of the FN, extrapolations are likely to be unsuitable for the occurrence of the species. When the FN is incomplete, however, some of these areas may represent suitable localities that were not available within the native region of the species. As even the most effective analysis is unlikely to characterise the whole FN, the most effective approach to this question is to identify areas of extrapolation, and treat these areas with caution, given that they may not be suitable for potential biological invasions (Owens et al. 2013). While our findings indicate that climatic incompleteness may be a minor problem, it clearly cannot be overlooked. Hutchinson's (1957) niche concept determines that any set of conditions in environmental space may be expressed by more than a single location in geographical space. Any such duality in the expression of the niche, however minor it may seem, should always be taken into account, to avoid the incorrect evaluation of the effects of incompleteness of the geographical space, even when it appears to be irrelevant in ecological space (Hutchinson 1957; Colwell and Rangel 2009).

Climatic non-equilibrium is more preoccupying, however, as it contradicts one of the basic assumptions of niche modelling (De Marco Jr. et al. 2008; Peterson et al. 2012). This question has been discussed extensively, and a number of different solutions, i.e., how to allocate pseudo-absences in the invasive region to reflect non-equilibrium correctly, have been proposed (Elith et al. 2010; Gallien et al. 2012; Hattab et al. 2017). We recognize non-equilibrium as a significant problem that must be dealt with systematically, but not only with reference to the invaded range, but also to the native region, given that our results indicate that this problem is the rule, rather than an exception (Svenning and Skov 2004; Araújo et al. 2005; Early and Sax 2014; Menuz et al. 2015). While there is no guaranteed solution, the careful allocation of pseudo-absences and the selection of accessible areas are effective measures to limit this problem. The careful delimitation of the area that must be accessed to reach a quasi-equilibrium state (Acevedo et al. 2012), together with the adoption of measures that restrict pseudo-absence sampling to locations that are environmentally distinct within this area (Wisz and Guisan 2009; Hattab et al. 2017), currently appears to be the best way of minimising the problem of non-equilibrium. We would thus recommend that a framework, such as that developed by Hattab et al. (2017), should be applied to both the invaded and the native ranges. The impact of these steps on the results of a model may vary depending on how closely the species meets the equilibrium assumption. Even so, we emphasise the fact that scenarios of perfect equilibrium within the native region appear to be the exception, rather than the rule, even in species with a high dispersal capacity.

There is an ongoing debate as to whether biological invasions are accompanied by a shift in the niche (Broennimann et al. 2007; González-Moreno et al. 2015; Parravicini et al. 2015; Chapman et al. 2017; Qiao et al. 2017). While we do not intend to finalize this discussion, we would urge caution for the identification of niche shifts, given that they may be the result of the under-representation of the FN of a species within its native distribution (Peterson and Nakazawa 2008; Peterson 2011; Qiao et al. 2017). While some evidence of niche evolution exists (Pearman et al. 2008; Kearney and Porter 2009; McCann et al. 2014), it cannot be determined solely by ENM predictions, given that ENMs will always include some degree of error and uncertainty in the definition of the niche, and the fact that empirical models are unlikely to estimate the FN correctly.

The present study did not encompass some factors known to influence the outcome of an ENM analysis, including the number of occurrence records (Stockwell and Peterson 2002; Moudrý and Šímová 2012; Liu et al. 2018), geographical sampling bias (Lobo and Tognelli 2011; Beck et al. 2014), and the strategy adopted for the allocation of pseudo-absence (Stokland et al. 2011; Barbet-Massin et al. 2012; Liu et al. 2018). While this may have placed some limitations on the applicability of the results of the present study, we feel confident that the inclusion of none of these factors would have led to significant improvements in the analyses. A universal pattern is that model accuracy increases with sample size (Stockwell and Peterson 2002; Moudrý and Šímová 2012; Liu et al. 2018) and, while we decided to limit our models to a single sample of 50 occurrences, this is a reliable number, according to the analysis of Stockwell and Peterson (2002). While we may have obtained some improvement by increasing sample size, especially in the case of species with high prevalence (Liu et al. 2018), this would not have resolved the problems caused by climatic incompleteness and non-equilibrium. Overall, the optimal number of occurrences will also be influenced by the quality of the data. In the present study, we sampled each species randomly throughout its distribution, which is close to the ideal approach. Real data are likely to be affected by sampling bias and spatial heterogeneity, which means that models based on a real dataset of the same size would likely yield less reliable results (Rondinini et al. 2006; Lobo 2008; Maldonado et al. 2015). Geographical sampling bias is widely known to decrease the predictive capacity of ENMs by overfitting the data, leading to under-prediction (Lobo and Tognelli 2011; Beck et al. 2014). Despite this, algorithms with high levels of over-prediction in all scenarios (GLM and MLK) may in fact benefit from biased data, although this requires a more systematic evaluation. Finally, the strategy adopted for the allocation of pseudo-absence is also known to affect algorithms in different ways (Stokland et al. 2011; Barbet-Massin et al. 2012; Liu et al. 2018), although environmental restrictions on this allocation, such as that suggested by Barbet-Massin et al. (2012), may reduce the influence of non-equilibrium, by not allocating pseudo-absence to non-accessible areas that are similar to those in which the species occur.

Soberón and Arroyo-Peña (2017) recently demonstrated the mismatch between the FN, EN, and the RN by contrasting occurrence data with physiological experiments. In the present study, we verified how this mismatch affects our ability to indicate potential biological invasions, and conclude that it must always be taken into account, and that modellers must be aware of its effects on predictions, and interpret the results appropriately. Obviously, biological systems are much more complex than the artificial system we created here, and any realistic scenario will become increasingly intricate if factors such as within-species niche variation (Vital et al. 2012), source-sink dynamics (Pulliam 2000), and niche evolution (Franks et al. 2014) are taken into account. Even so, anticipating the behaviour of algorithms and understanding how different factors may cause niche mismatches are essential first steps for the improvement of the accuracy and reliability of these models.

Data Availability

Due to the large size of files (all the raster files were over 40GB), we will make available at Pangaea the occurrence data used for model fitting and the tables used for niche and geographical analysis (under-and overprediction). The mentioned data is available at Pangaea database through the link https://doi.pangaea.de/10.1594/PANGAEA.892658.

For the remaining data (species' fundamental niche and distribution and models' results), please contact the corresponding author.

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Chapter 2 – Life-history strategies of successful invaders: a case study with mammalian herbivore

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Abstract

Fitness is one of the key concepts in ecology, with both ecological and evolutionary consequences. Life-history theory states that species have different strategies that compete to obtain the best return from the available resources within the environment, or the maximization of fitness. In the evolutionary time, communities move towards an equilibrium, in which remaining species are an optimal sub-sample of a wider set of life-history strategies previously available. Biological invasions are events in which this equilibrium is disturbed, and a new strategy is inserted in the community. Examined from this standpoint, a simple question that arises is if there is a common life-history strategy for successful invaders. In this study we created a mechanistic individual-based model to explore the success of different invaders (and life-history strategies) that are arriving in a new community and competing for the available resources. We simulated the invasion of herbivore mammals and recurred to an allometric scaling of life-history characteristics in order to create realistic individuals. We evaluated how the different life-history strategies (reproduction, survival and growth) and body size determine the likelihood of invader presence, abundance and the number of cells occupied by the invader of the system. Within a homogeneous environment, in which resources are refilled daily, successful invaders were the ones with a large body size who prioritize investments in survival, at the expense of investing in reproduction. This strategy was the same predominant strategy within the native community. This is a deviation of the common expectation that invasive species are the ones with a large reproductive effort. Nevertheless, this result may be due our overly simplified system. We demonstrate here that a realistic mechanistic model based on resource competition and life-history theory is viable to simulate and explore different invasion processes and allows for an experiment in which both failed and successful invasions are always taken into account.

Introduction

What is the meaning of life? This question has been haunting mankind throughout its existence. Nevertheless, if you ask this same question for evolutionists and ecologists, there is a high chance that most of them would answer without hesitation "maximize fitness". There is no single formal definition of the term fitness, but it could be traced back to the origins of modern ecology with the definition of Herberth Spencer of "survival of the fittest" in response to Darwin`s *On the Origin of Species* (Darwin 1859; Spencer 1864). In practical terms, the fittest individual is the one that leaves the most descendants throughout its life. For example, an individual that reaches sexual maturity very early, survives for a very long period and have a high number of offspring per brood is likely to have a very high fitness. However, the existence of such “Darwinian Demons” is merely hypothetical, as individuals have a limited amount of energy and must make allocation priorities (Williams 1966; Gadgil and Bossert 1970; Law 1979). The existence of different energy allocation strategies and the trade-offs that emerge from those turn this situation, from an evolutionary perspective, in a competition for which life-history strategy results in the highest fitness (Stearns 1976, 1989; Kuzawa 2007).

Although the existence of a “Darwinian Demons” is questionable, invasive species have been proposed as the ones that most closely resemble the characteristics of this mythological demon (Shea et al. 2005). Despite that, even them are subject to trade-offs in energy allocation. Given the relevance of biological invasions and their ecological, social and economic impacts (e.g. Perrings et al., 2005; Nentwig, 2007; Simberloff et al., 2013), several studies have focused on finding the existence of an optimal life-history strategy in invaders (e.g. Shea et al., 2005; Theoharides & Dukes, 2007; Blackburn et al., 2009; Sol et al., 2012). Simultaneously, several hypotheses were proposed to explain invaders success based on their interactions with native species. Among those hypotheses, a large number was focused on the competition between invaders and native species. A competitive superiority of invaders has been proposed due to factors such as larger size, more rapidly growth, better response to resource fluctuations or even more efficient allocation strategies (Simberloff and Rejmánek 2011). Nevertheless, the existence of consistent predictors that explain invasion success is still highly debated (Hayes and Barry 2008; Sol et al. 2012). The inexistence of a “general theory for invasion” is not exclusive to the invasion biology field. Ecology is a complex science in which general theories, even more laws, are an exception (Marquet et al. 2014). Even though, there are some noteworthy exceptions that propose explanations for the general operation of the world, such as the theory of natural selection (Darwin 1859), niche theory (Vandermeer 1972; Chase and Leibold 2003), neutral theory (Hubbell 2001) and metabolic theories (Kooijman 1993; Brown et al. 2004).

Metabolic theories stand out as an interesting foundation to investigate invasion success based on competing life-history strategies. Built upon previously known laws, such as Kleiber’s Law of the allometric scaling of metabolism (Kleiber 1932), metabolic theories describe the world from an energetic point of view, in which individual’s metabolic requirements scale with body size. If any given characteristic scales with body size it is considered as allometric scaling, and this is not exclusive to metabolism, being that several life-history parameters were also established to scale allometrically (e.g. Peters, 1983; Peters & Wassenberg, 1983; Speakman, 2005; Clauss et al., 2007). In addition, there is a recent focus in Ecology to gather known existent data in major datasets, also known as data-papers (e.g. Ernest, 2003; Jones et al., 2009; Rodrigues et al., 2019), which opens the possibility to explore the allometric scaling of those parameters (Reichman et al. 2011; Hampton et al. 2013). In addition to scaling allometrically, species’ characteristics are also affected by their life-history strategy and their priorities in allocating the obtained resources (Stearns 1976; Sibly and Calow 1986). This is a possible explanation of why two animals with close body sizes, for example the two Suidae wild boar (*Sus scrofa*, Linnaeus 1758) and babirusa (*Babyrousa babyrussa*, Angas 1849), have large differences in the average litter size (5.76 and 1.4, respectively), sexual maturity (9.77 and 18.0 months) and life expectancy (252 and 188 months). At the end, metabolic theory opens up the possibility to analyze biological invasions from an energetic viewpoint and based on life-history theory, in which species with different resource allocation priorities are competing for the resources available at the environment.

In this study we seek to simulate this energetic world in which species with different life-histories compete for resources and evaluate invasion success based on the strategies for resource allocation in a virtual space that follows metabolic rules and the allometric scaling of parameters. We recur to the previously established allometric scaling of parameters and data based on biological characteristics to build a simulation model to evaluate the success of different life- history strategies, and evaluate the effect on invasion success of four major points: i) is there an optimal resource allocation strategy for invaders; ii) how body size affects all those elements; and iii) does successful invaders share the same successful life-history strategy that is dominant in native communities.

Methods

Model overview

We present here a general description of our system, for a more detailed description of the model, following the ODD (overview, design concepts and details) protocol (Grimm et al. 2006, 2010), see the Appendix 1. The model is implemented in MatLab and the code is available at GitHub (https://github.com/andrefaa/energy-ibm).

The model to evaluate how different life-history strategies determine invasion success is based on three major theories: allometric relations (Peters 1983; Lindstedt and Schaeffer 2002), energy budgets (Sibly and Calow 1986; Sibly et al. 2013) and life-history theory (Stearns 1976, 1989, 2000).

Allometric relations are the basal rule that regulates all the processes in the model. Species have a maximum body size and individuals have their body size curve determined by a Gompertz Growth Model. Individual/species body size regulates all other parameters (*e.g.* such as basal metabolic rate, distance traveled, maximum ingested food, litter size, neonate body size, gestation period). Other than that, many parameters are also affected by species' life history-strategy. Investment in growth affects species' maximum body size and adult growth rate; investments in survival increases species' maximum reserves and longevity; while investments in reproduction reduces gestation time and the age of first reproduction and also increases the litter size.

Regarding the relation between energy budgets and life-history strategies, we considered as life-history strategies the species' priority to allocate energy to three processes: growth, reproduction and survival. Species allocate energy to all processes, but the order of this allocation is given according to its priority. Life-history priority is calculated as a proportion, the sum of all strategies is always one, and each species has different proportions randomly allocated to each strategy (e.g. a species with its priorities distributed as 0.8 to reproduction, 0.1 to growth and 0.1 to survival is a species with a strategy to prioritize its reproduction effort). Aside from the order of allocation, the degree of priority also affects different life-history parameters. Energy invested in reproduction affects species' litter size, age of sexual maturity and gestation period; allocating energy for growth results in larger maximum body size, which affects individual's maximum dispersal capacity and gives a slight advantage in competing for resources; finally, energy allocated for survival increases the size of individuals' energy reserve and their lifespan (Fig.1, Energy allocation module).

Body size and life-history strategies are the ground rules for the model. Nevertheless, the whole system is dependent on individuals' ability to consume resources from the system and energy intake. Individuals forage daily and, according to its priority to life-history strategy, allocate the energy to one of three processes: daily growth, fill fat reserves and feed offspring/younglings. For example, an individual that has a higher degree of priority for survival, followed by growth and reproduction will first fill its reserves, followed by investing in their daily grow and finally feeding offspring/younglings. Energetic Reserves have an important role in the model as individuals may use it to supplement their own demands. Individuals forage in a pattern that simulates the idea of a home-range (Burt 1943) and move in a semi-conscious way, trying to increase their energetic gains. Foraging follows an herbivore functional response in which intake is regulated by bite mass and is limited by individuals' daily movement and maximum intake capacity (Fig.1; Foraging module; Spalinger and Hobbs 1992).

The whole model can be divided in four major modules: main module, foraging, energy allocation and reproduction. At the model initialization the virtual space is created in a round shape, without boundaries, and species and individuals are created and distributed throughout the system. The species pool is composed of a large number of species with different life-history strategies and body sizes. At the initial stage, colonizing individuals are all female adults, but as the model progresses those adults generate offspring which, in turn, as born as younglings. At the main module the order of resource consumptions is determined, and individuals forage according to the foraging module. As a result of this step individuals can be placed in one of two categories: i) individuals that foraged successfully and have energy to supply their basal necessities and; ii) individuals who failed to forage or did not reach their basal necessities. Individuals in the first set allocate any extra energy according to their life-history priorities and stay at the same location they ended the foraging step. Individuals in the second set may disperse and forage to supply their basal necessities, if they have not already done so. If those individuals that dispersed foraged successfully, they are now placed among the first set and can allocate any extra energy. Otherwise, if they failed to forage, they may use energy stored in the reserves to supply their basal needs. If there is no energy in the reserves those individuals die. At the end of each day individuals' reproduction timer reduces and the energy in the system is restored (Fig.1, Main module).

As the model advances, individuals' reproduction timer will eventually reach zero. At that time, that individual produces offspring, which are embryos supplied by their mother. The number of offspring and the gestation length are determined by allometric relations and the degree of reproduction priority. Pregnant adults have the limit of their maximum reserves increased by 50%, a fact common in mammals, as they need to storage energy for lactation time (Hudson and White 1985; Gittleman and Thompson 1988; Speakman 2008a; Heldstab et al. 2017). We chose not to establish an allometric scaling at this step as we found no evidence of this in the literature. When the gestation period is over, surviving offspring become younglings, which rely on mothers' milk as the only sour of nutrition. Lactation is possibly the greatest energetic burden upon mothers, with reports of food intake increasing by 1.5~2.5 times (Gittleman and Thompson 1988; Rogowitz 1996; Speakman 2008a). We represent this in a simplified way in our model, by increasing the limits for both daily movement and maximum food ingested by 50% in lactating females. Once more we chose not to establish allometric relations due to the lack of evidence. When younglings reach the weaning mass, they become adults and stop relying on their mother for food. At this step younglings disperse away from their mothers and establish a new position (Fig.1, Reproduction module).

The simulation starts with the creation of the species pool, with 300 different species of herbivore mammals, with body size ranging from 10g-100kg, being allocated throughout the world at random. The native community is left undisturbed for a period of ten years (3650 days), a period in which the system approaches equilibrium. At this point we introduce a new species, which is created in the same way as any other species in the system, to represent the arrival of an exotic species (Fig. 2). Each native community was invaded by 50 individuals of 50 different species, with different life-history strategies that were a random sample from all possible combinations. After introducing the invader, the system runs for 10 years of a successful invasion or when the invasion fails. After this time, we reset the native community to the state right before the invasion (time=3650) and started a new invasion process. This process ensures that different invaders will meet the same native community and makes it possible to compare its invasion success. We created 20 different native community, each one being invaded by 50 different invaders, which means that in total we had 1000 different invasion events.

Figure 1: Flowchart of the individual-based model to test invasion success for different life-history strategies. Different colors in the box are related to variables that affect a given process. If the process box contains more than one color it is affected by more than one variable. Brown boxes represent processes affected by allometric relations; green boxes are the ones affected by energy allocated to growth; yellow boxes are affected by energy allocated to survival; and blue boxes are processes affected by energy allocated to reproduction. The model can be divided in four major modules: a main module, in which all other three modules are inserted; a foraging module; a energy allocation module and a reproduction module. Model daily dynamics occur in the main module, in which individuals remove resources from the environment, and disperse to gather more resources if necessary. Foraging follows a set of rules, determined within the foraging module, in which individuals have a maximum movement of ingestion budget. After all individuals foraged, those who acquired the necessary resources allocate any extra energy for growth, survival or reproduction following a priority order. Allocating energy to each of the three strategies have immediate consequences (i.e. allocating energy for growth is necessary for individuals to increase their body size in that day), but also have long-term effects (i.e. individuals that prioritize growth reach a greater maximum body size and higher growth rate). Individuals that did not obtain the necessary resources to sustain the basic metabolic needs are allowed to disperse once and go through another foraging event. If those individuals still do not reach the necessary amount of energy, they can remove the daily necessary energy from the reserves. Individuals only leave the system (death), if their reserves are not enough to sustain their basic metabolic needs or if they`ve reached the maximum lifespan. New individuals are inserted in the system through the reproduction module. Individuals have a reproduction timer that decreases daily. After this timer reaches zero the individual is pregnant and goes through a gestation period in which it needs to provide sustenance for the offspring. When the gestation period is over the offspring is inserted in the system initially as juveniles, which still rely on their mothers for energy intake. When juveniles reach their species-specific weaning mass they are considered adults and join the others in the daily competition for food in the environment.

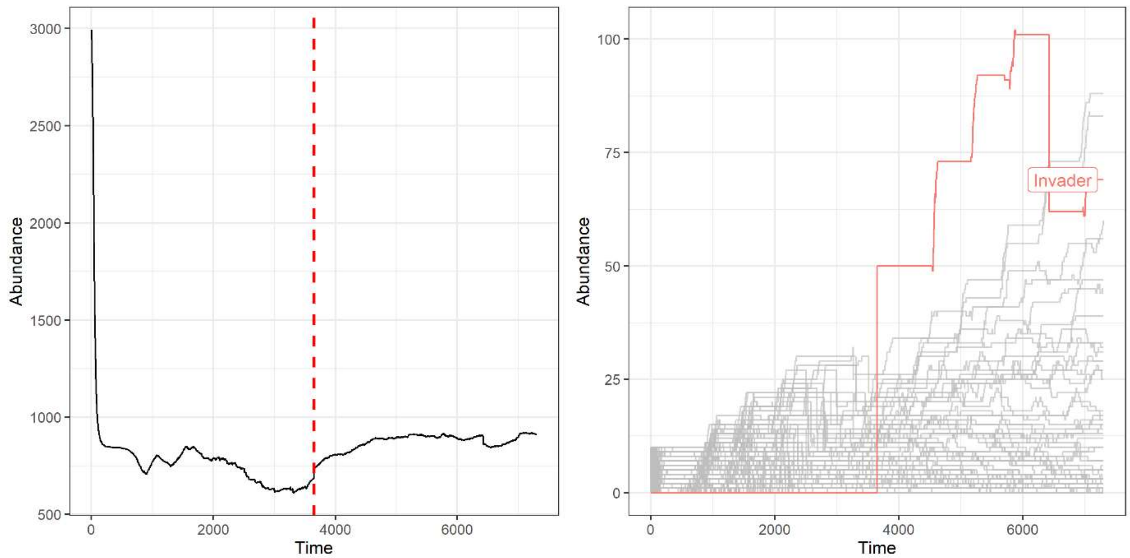

Figure 2: Abundance of individuals in the system at each time-step. The left panel curve represents the total abundance of individuals, with the red dashed line indicating the time of invasion. On the right panel the different curves represent the species-specific abundance, with the black arrow pointing to the time of invasion and invader's curve.

Life-history strategy and invasion success

We use three metrics to measure invasion success: invaders' presence (Eq.1) and abundance (Eq.2) in the system after 10 years of the species' introduction and the number of communities (cells) occupied by the invader (Eq.3). We used Generalised Linear Mixed Models (GLMMs) to evaluate the effect of different life-history strategies – Energy allocated for reproduction ($E_{REPR.}$), Energy allocated for growth ($E_{GRWT.}$) and Energy allocated for survival ($E_{SURV.}$) – and their interactions with maximum body size (BS) in determining invasion success. We consider invader's centre of origin for the invasion(ORI), which is nested within replicates, a random effect as the composition of the native community in the centre of origin also affects the invasion success. We also consider failed invasions in our analysis, as they represent life-history strategies that were not successful.

$$\boldsymbol{Presence} \sim (\boldsymbol{BS} * \boldsymbol{Erepr}) + (\boldsymbol{BS} * \boldsymbol{Esurv}) + (\mathbf{1}|\boldsymbol{Replicate}/\boldsymbol{ORI}) \qquad \text{(Eq.1)}$$

$$\boldsymbol{Abundance} \sim (\boldsymbol{BS} * \boldsymbol{Erepr}) + (\boldsymbol{BS} * \boldsymbol{Esurv}) + (\mathbf{1}|\boldsymbol{Replicate}/\boldsymbol{ORI}) \qquad \text{(Eq.2)}$$

$$\%_{INVADED\ COMMUNITIES} \sim (\boldsymbol{BS} * \boldsymbol{Erepr}) + (\boldsymbol{BS} * \boldsymbol{Esurv}) \ + \ (\boldsymbol{1}|\boldsymbol{Replicate}/\boldsymbol{ORI}) \quad \text{(Eq.3)}$$

We are aware the use of statistical testing for simulations has received critics and should be approached with care (White et al. 2014). Therefore, we avoid basing our assumption on the p-value, focusing instead on the estimated values for the metrics and their contribution for the patterns produced. Nevertheless, our experimental design falls upon one of the situation the author believe hypothesis testing can be applied to simulations, as we use our simulation to test experimental approaches in a system with known mechanics and we do not have many replicates, given the complexity of our simulations.

Invasion outcome and life-history similarity to native community

We also evaluated if invaders that were successful in establishing themselves in the native community had similar or different life-history strategies as the native community individuals. We performed a PERMANOVA with Euclidian distance and 9999 repetitions to contrast each one of the native communities' individuals and successful and unsuccessful invaders at the community. We tested for homogeneity of multivariate dispersions prior to conducting the PERMANOVA. We used the package *vegan* to conduct both the homogeneity and PERMANOVA tests (Oksanen et al. 2019).

Model validation

Due to the large possibilities allowed by IBMs, it is important to quantify how valid the model is in terms of producing realistic patterns and behaviours. Model validation ideally follows the same bottom-up approach as the model, checking how valid are the agents and then how valid are the patterns that emerged from individuals' behaviour (Grimm and Railsback 2005). Therefore, we checked how valid our model is at two levels. First, we checked if our simulated individuals represent real world possibilities by contrasting simulated individuals' life-history traits against those traits' values for real herbivore mammal species, retrieved from the PanTHERIA Database (https://figshare.com/collections/PanTHERIA_a_species-level_database_of_life_history_ecology_and_geography_of_extant_and_recently_extinct_mammals/3301274) (Jones et al. 2009). We evaluated seven traits (Neonate body size, Litter size, Gestation period, Interval between reproduction seasons, Age of first reproduction (AFR), Weaning mass and longevity). Second, we checked if the distribution of body size in our native community, which is an emergence from the model, resembles the distribution of body size in real world mammals.

Results

Model validation

Apart from longevity, which had higher values for simulated species, simulated individuals had life-history traits that resembled the characteristics of real-world species (Fig.3). Nevertheless, even for longevity the allometric scaling of longevity was similar to the one for real-world species, only differing due to higher values overall. Neonate body mass and Weaning mass had the higher resemblance to the real pattern with simulated values that accurately captured not only the allometric scaling but also the real values for both traits, with real-world species having a slightly higher overdispersion. Litter size in our model was rounded, due to this value representing the actual number of offspring produced by and individual, not an average for the whole species. Nevertheless, it was possible to observe the overall pattern that larger litter sizes were more frequent in smaller individuals. Gestation period, interval between reproductive seasons and AFR had similar patterns, with a higher variation due to those traits being affected by species' life-history strategy. Despite failing to represent the whole trait variation, we were successful in representing the higher variation in those traits (when compared to Neonate body mass and Weaning mass) and all our simulated values fall within real-world possibilities. Nevertheless, our species were biased towards larger body size individuals, which makes it hard to makes assumptions about this behaviour on species below 100g, but there is an apparent higher overdispersion on smaller species.

The distribution of body size in the native community was not similar to the distribution of body size of real mammals (Fig.4), with our model underestimating the relative number of small individuals (<10kg), and overestimating the relative number of individuals within the 10-50kg interval. Body size distribution in our model approached a left-skewed normal distribution, while real body size distribution is closer to a Poisson distribution. Distribution of body size was an emergent pattern in our model, being a result of individuals with different life-history strategies competing for resources and allocating the obtained energy to processes with different priority.

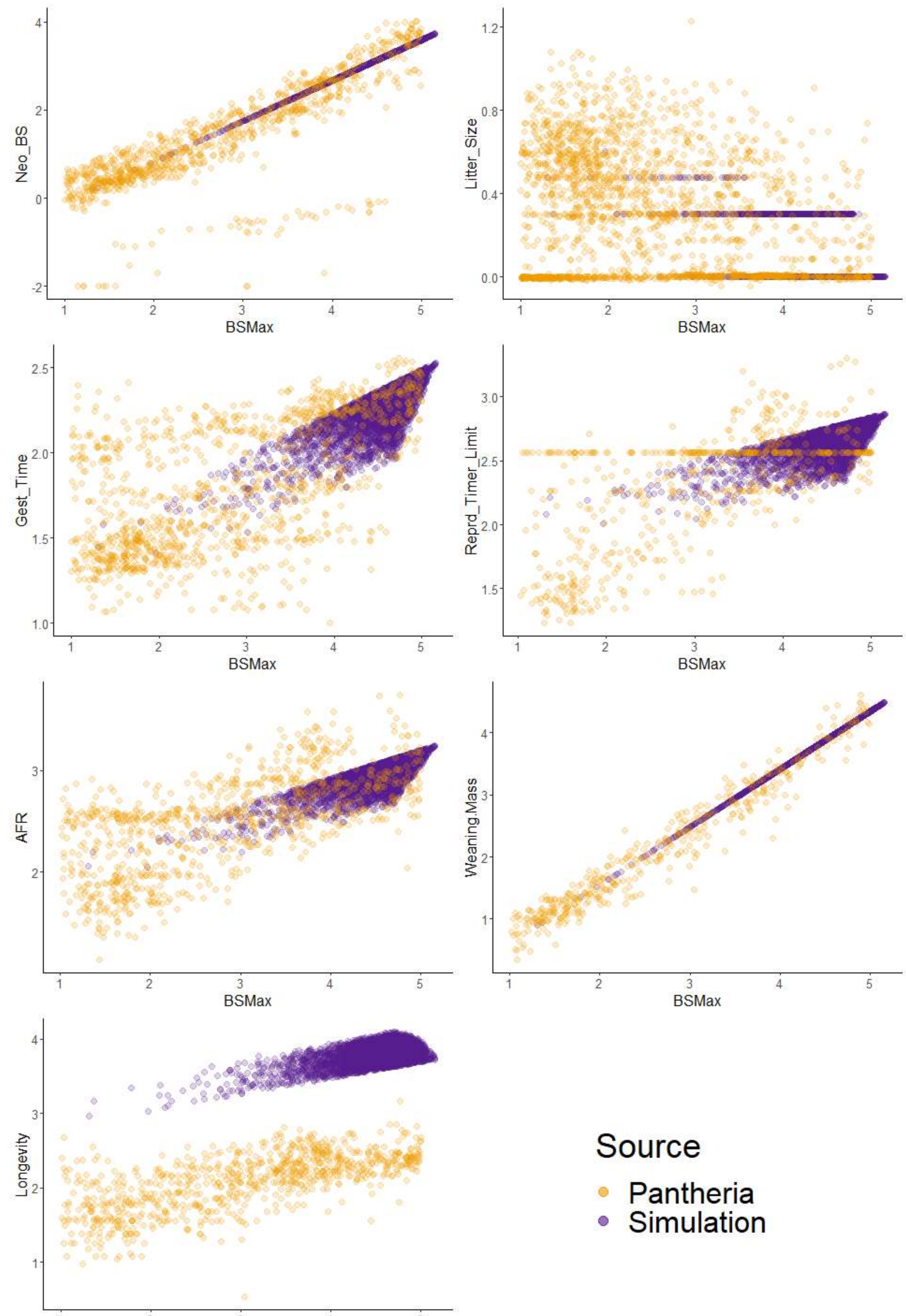

Figure 3: Simulated species life-history traits (this study) in comparison against real species life-history traits (from Pantheria database)

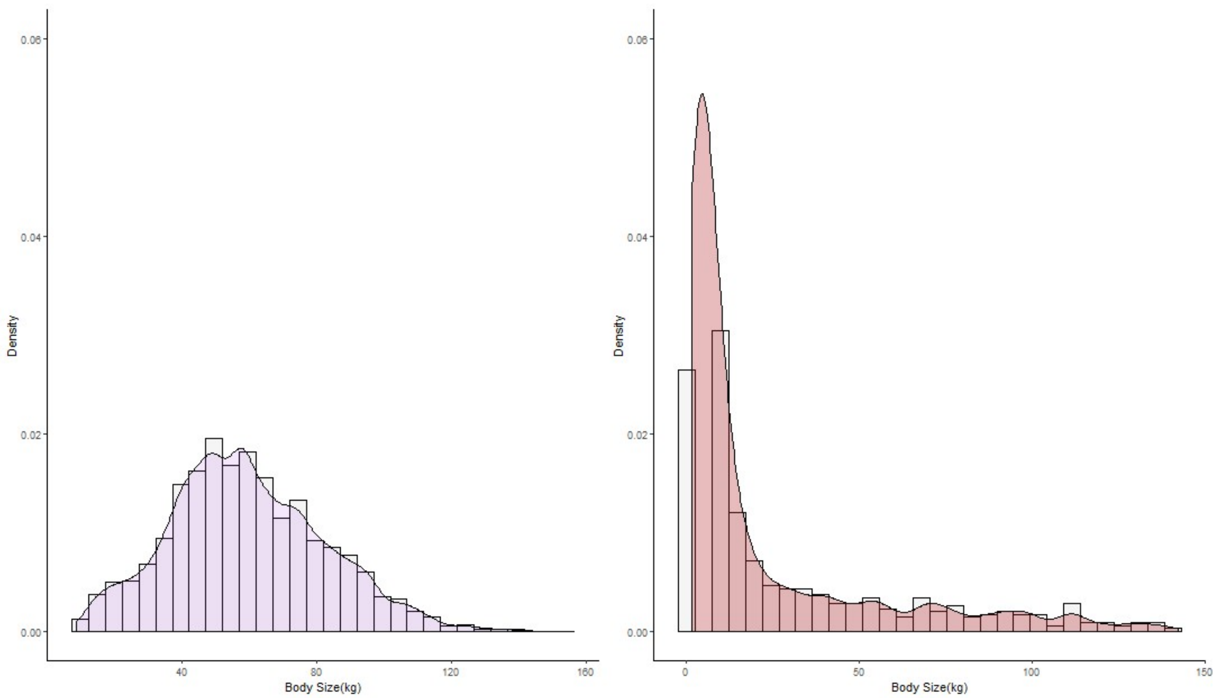

Figure 4: Comparison of native community body size distribution after 10 years of model (prior to invasion; left) and body size derived from real mammal data (Pantheria Database; right)

Invasion success and invader life-history strategy

Invasion success was affected by both life-history strategy and invader body size. In general, body size was determinant for all three aspects of invasion success (presence, abundance and proportion of invaded communities), being that larger individuals had a higher probability of surviving for the whole ten-year period. Nevertheless, invader abundance was also affected by its life-history strategy, being that even for large invaders there were some strategies that disfavored invasion success.

Invader presence in the system after the 10-year period was strongly determined by body size, being that large invaders had a higher likelihood of occupying the community after the 10-year period and remaining in the system for the full period when compared to small individuals. Nevertheless, only being large is not a guarantee for success and life-history strategies have an important role in determining invader presence in the system for the full period (Fig. 5a, Table 1). While the effect of life-history strategies seem more relevant for determining the success of individuals within an average body size range (30~60kg), being that investing in survival was essential for those individuals to remain in the system, with a positive interaction with growth and negative interaction with reproduction (Fig.5b, Table 1). For large individuals (80kg) there is a change in this pattern, as investment in reproduction makes possible for large individuals that do not prioritize survival to remain in the system. Radical investments in growth, on the other hand, reduce the likelihood for an invasive species to remain in the system (Fig. 5b). Notwithstanding, investing in survival seems to be the major driver for invaders' presence in the system. Invaders with very low investment in both growth and survival and high investment in reproduction were the ones with the fewer reports of invasion success, especially if those invaders had a small body size (Fig. 5a). The profile for a species to establish in the system, regardless of their abundance, is of a large species with large reserves, short gestation period and early sexual maturity. Investment in reproduction does not change the number of offspring for large species due to allometric restrictions, therefore, success is caused by a larger number of offspring but rather because of the earlier reproductive start and higher number of reproductive seasons.

Table 1: Results for the Binomial GLMM of invader presence in the system after the 10-year period against its body size, E_{REPR} and E_{SURV} and possible interactions that may arise from those variables.

Fixed Effects

Parameter	Estimate	CI	χ^2	df	R^2	p-value
Intercept	-4.185	±2.065	-			-
Body Size	0.040	±2.379	53.373	1	0.001	<0.001
E_{SURV}	-4.570	±3.244	52.032	1	0.019	<0.001
E_{REPR}	-16.200	±5.821	4.092	1	0.014	<0.05
Body Size: E_{SURV}	33.163	±7.283	70.633	1	0.061	<0.001
Body Size: E_{REPR}	22.808	±8.811	25.739	1	0.003	<0.001

Random Effects

Parameter	Variance	Std.Dev
Replicate	0.001	<0.001
Origin:Replicate	0.968	0.984

Model Results

AIC	BIC	LogLik	Deviance	Df.Resid	R^2
384.1	423.4	-184.1	368.1	992	0.206

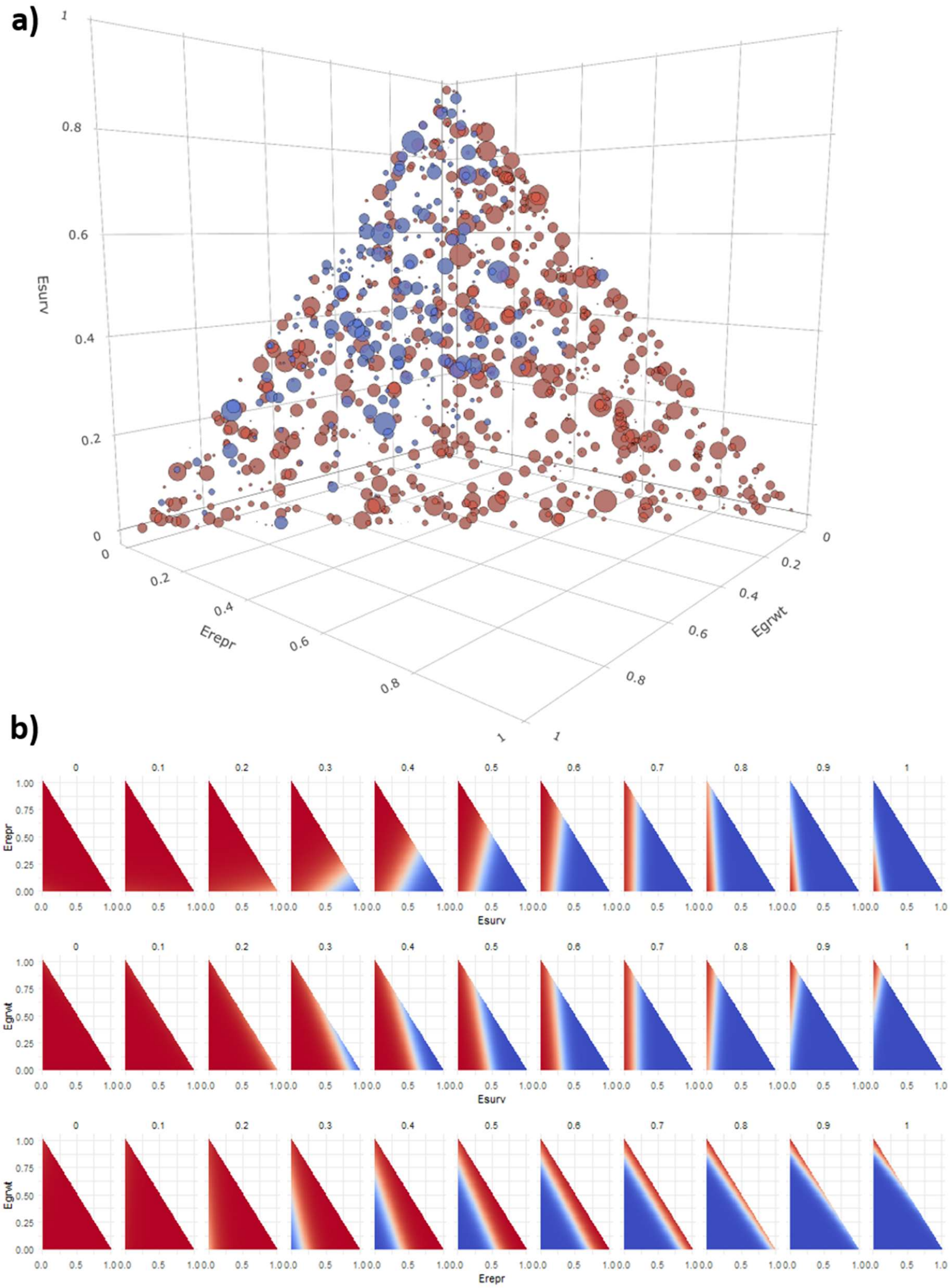

Figure 5: Invader life-history strategy and invasion outcome regarding invader presence in the system. (a) The three graphs axis represent the percentage of energy dedicated to each one of three allocation alternatives: growth, survival and reproduction, being that the combination of the three alternatives sum up to one. Blue circles indicate the invader was successful in remaining in the

community for the 10-year period after the invasion event, while red ones indicate the invader failed to establish itself in the community. Different circle size indicate the body size of the invader. (b) Graphical representation of regressions results between life-history strategies and body size and likelihood of invader remaining in the system. Each sub-plot represents a different body size class and how energy allocated to the different life-history strategies determine the outcome of the invasion for that class. Likelihood of establishment in represented in red to blue colours, in which red represents the lower likelihood of invader presence and blue represents the higher odds. In the upper panels invader presence is related to E_{REPR} and E_{SURV}, in the middle panels E_{GRWT} and E_{SURV} and in the lower panels E_{GRWT} and E_{REPR}.

Invaders' abundance in the system after the 10-year period was also determined by body size and its interaction with invaders' life-history strategy. Once more, larger individuals are more likely to have a higher final abundance in the system. The pattern for invader abundance was very similar to invader presence, but more restrict (Fig. 6a, Table 2). In addition, large invaders reach higher abundance when prioritizing investments for survival and reproduction. However, in order to reach the highest abundances, invaders must have a high degree of investment in both survival and reproduction (Fig. 6b). The profile for species with a high number of individuals in the system is of a large species with a short gestation period and early sexual maturity, with large reserves for survival during periods of food shortage and higher longevity, the same profile of presence in the system.

Table 2: Results for the Poisson GLMM of invader abundance in the system after the 10-year period against its body size, E_{REPR} and E_{SURV} and possible interactions that may arise from those variables.

Fixed Effects						
Parameter	**Estimate**	**CI**	χ^2	**df**	R^2	**p-value**
Intercept	-0.727	±0.974	-	1	-	-
Body Size	-3.280	±1.274	534.718	1	0.010	<0.001
E_{SURV}	-5.071	±2.859	1.810	1	0.042	<0.001
E_{REPR}	-14.842	±1.547	613.930	1	0.121	<0.001
Body Size: E_{SURV}	24.413	±4.241	104.564	1	0.142	<0.001
Body Size: E_{REPR}	22.129	±2.559	349.624	1	0.070	<0.001

Random Effects		
Parameter	**Variance**	**Std.Error**
Replicate	0.085	0.291
Origin:Replicate	1.100	1.049

Model Results

AIC	**BIC**	**LogLik**	**Deviance**	**Df.Resid**	R^2	**Overdispersion**
2249.2	2288.4	-1116.6	2233.2	992	0.451	0.294

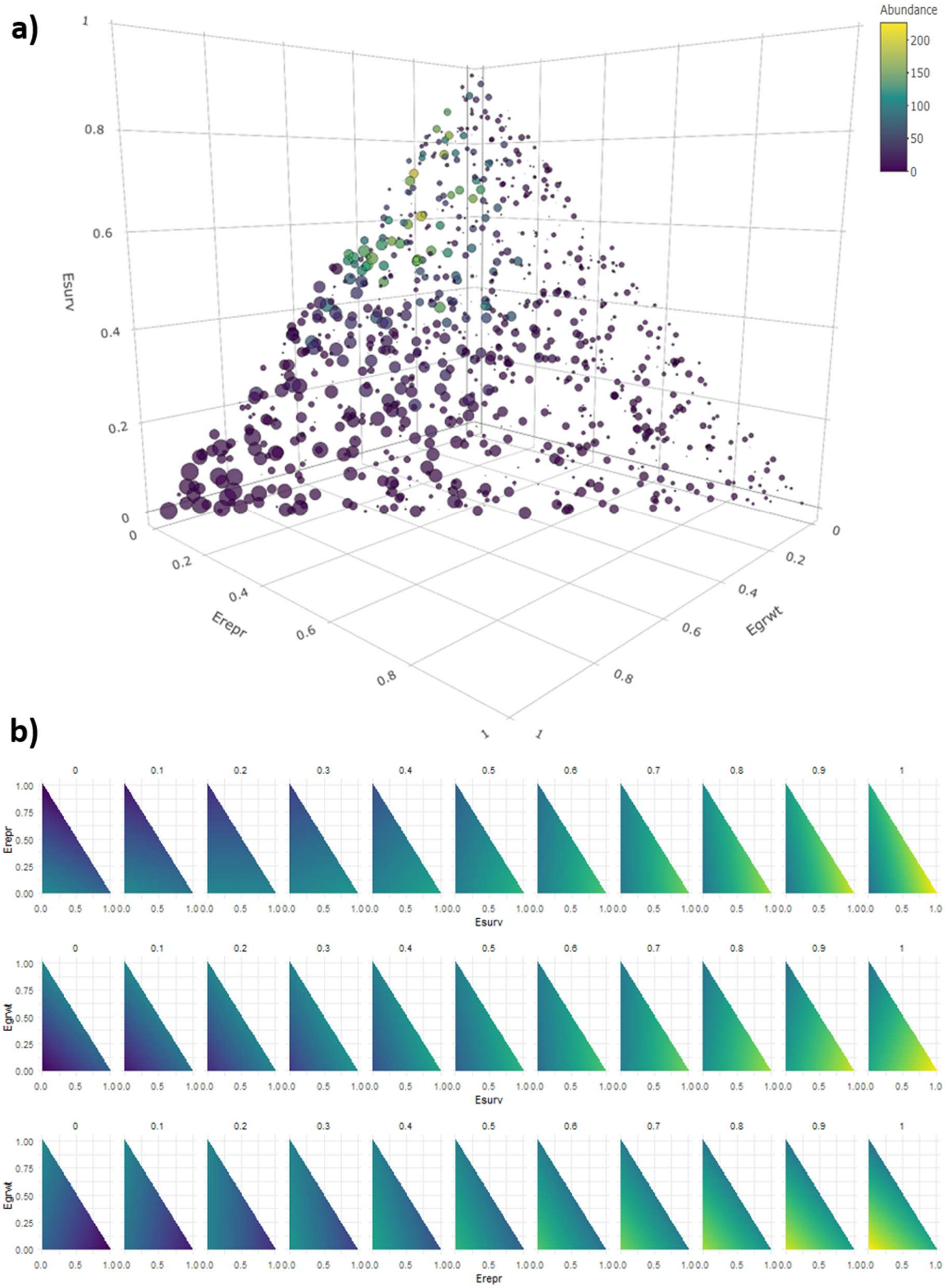

Figure 6: Invader life-history strategy and invasion outcome regarding invader abundance in the system. (a) The three graphs axis represent the percentage of energy dedicated to each one of three allocation alternatives: growth, survival and reproduction, being that the combination of the three alternatives sum up to one. Darker circles indicate lower levels of invader abundance in the

community after 10 years after the invasion event, while lighter ones indicate higher levels of abundance. Different circle size indicate the body size of the invader. (b) Graphical representation of regressions results between life-history strategies and body size and likelihood of invader abundance in the system. Each sub-plot represents a different body size class and how energy allocated to the different life-history strategies determine the outcome of the invasion for that class. Invader abundance is represented in purple to yellow colours, in which darker colours represents lower invader abundance and lighter tones represents higher abundance. In the upper panels invader abundance is related to E_{REPR} and E_{SURV}, in the middle panels E_{GRWT} and E_{SURV} and in the lower panels E_{GRWT} and E_{REPR}.

Finally, the proportion of invaded communities within the system was also directly related to body size and its interactions with investments for reproduction and survival (Fig. 7a, Table 3). Once more the pattern followed the ones for invader presence and abundance in the system, being that larger species had higher occupancy than smaller species and when prioritizing allocation for reproduction and survival. Once again E_{SURV} has the strongest effect, since even large species that give low priority for survival may fail to occupy any community within the system. E_{SURV} has a positive interaction with E_{REPR} and negative interaction with E_{GRWT} for the whole-body size spectrum. The profile for a widespread invader is once more of a large species with short gestation period and early sexual maturity, coupled with large reserves and high longevity.

Table 3: Results for the Binomial GLMM of proportion of communities occupied by the invader in the system after the 10-year period against its body size, E_{REPR} and E_{SURV} and possible interactions that may arise from those variables.

Fixed Effects						
Parameter	**Estimate**	**CI**	**χ^2**	**df**	**R^2**	**p-value**
Intercept	-5.503	±1.039	-	1	-	-
Body Size	-3.464	±1.348	536.661	1	0.010	<0.001
E_{SURV}	-5.233	±3.034	610.842	1	0.040	<0.001
E_{REPR}	-15.670	±1.629	1.545	1	0.113	<0.001
Body Size: E_{SURV}	26.048	±4.507	358.287	1	0.141	<0.001
Body Size: E_{REPR}	23.394	±2.697	103.474	1	0.066	<0.001

Random Effects		
Parameter	**Variance**	**Std.Error**
Replicate	0.109	0.331
Origin:Replicate	1.191	1.091

Model Results

AIC	**BIC**	**LogLik**	**Deviance**	**Df.Resid**	**R^2**
2085.9	2125.2	-1035.0	2069.9	992	0.441

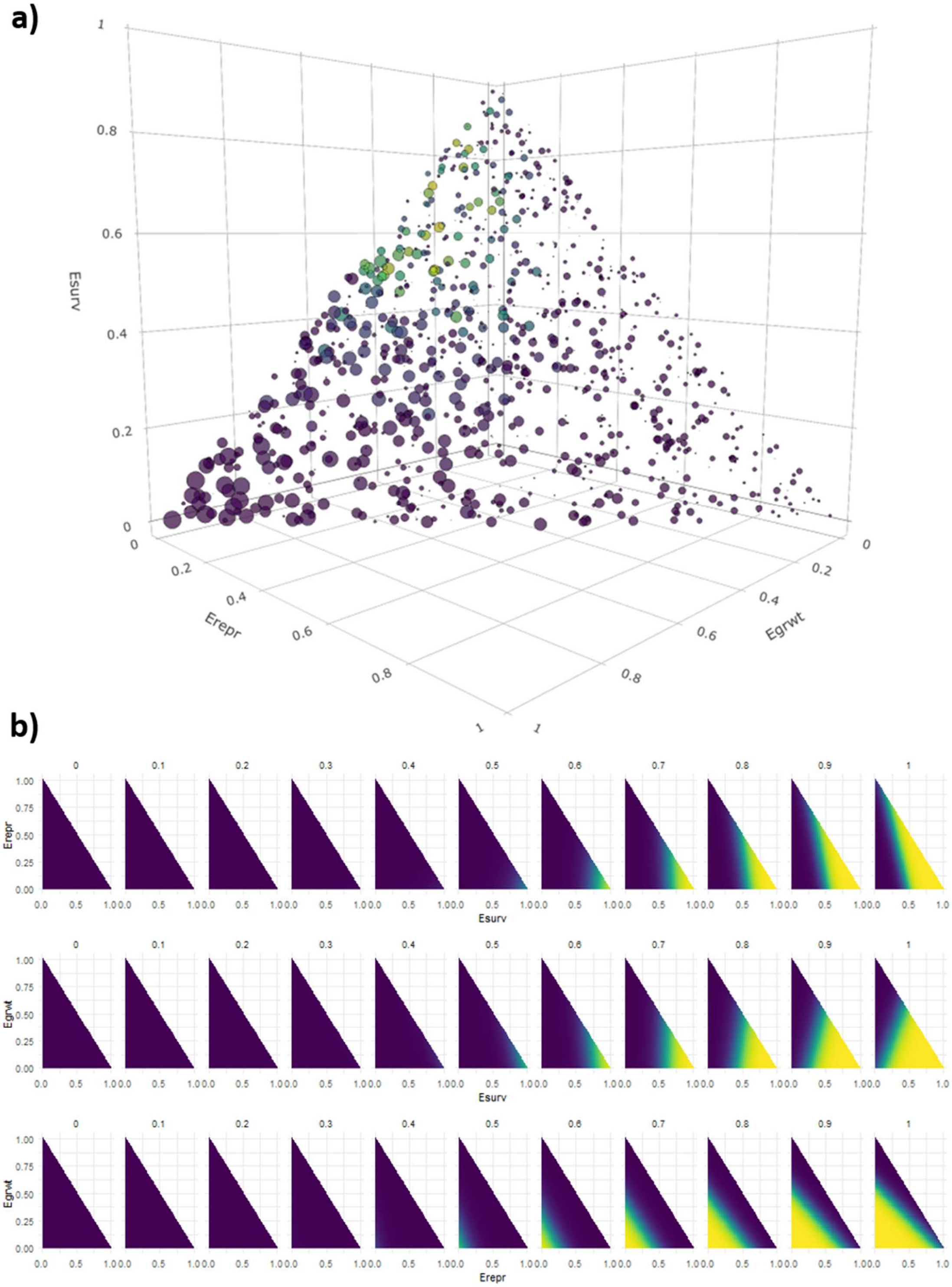

Figure 7: Invader life-history strategy and invasion outcome regarding the number of invaded communities. (a) The three graphs axis represent the percentage of energy dedicated to each one of three allocation alternatives: growth, survival and reproduction, being that the combination of the three alternatives sum up to one. Darker circles indicate lower number of occupied cellsof the

system after 10 years after the invasion event, while lighter ones indicate higher levels of occupancy. Different circle sizes indicate the body size of the invader. (b) Graphical representation of regressions results between life-history strategies and body size and proportion of occupied communities in the system. Each sub-plot represents a different body size class and how energy allocated to the different life-history strategies determine the outcome of the invasion for that class. System occupancy is represented in purple to yellow colours, in which darker colours represents lower occupancuy and lighter tones represents higher occupancy. In the upper panels invader abundance is related to E_{REPR} and E_{SURV}, in the middle panels E_{GRWT} and E_{SURV} and in the lower panels E_{GRWT} and E_{REPR}.

Invader life-history similarity to native community

Successful invaders were similar to the individuals of the native community (PERMANOVA: $F_{1,1823}$=1.5029, R^2=0.001, p>0.05), with survival (E_{SURV}) as the main priority for energy allocation and directing less resources for reproduction (E_{REPR}). On the other side, failed invaders had the exact opposite strategy (PERMANOVA: $F_{1,2297}$=209.08, R^2=0.08, p<0.001), with reproduction being the major priority and survival being outlooked. There were similar levels of investment to growth (E_{GRWT}) for individuals at the native community and both successful and unsuccessful invaders (Fig. 8).

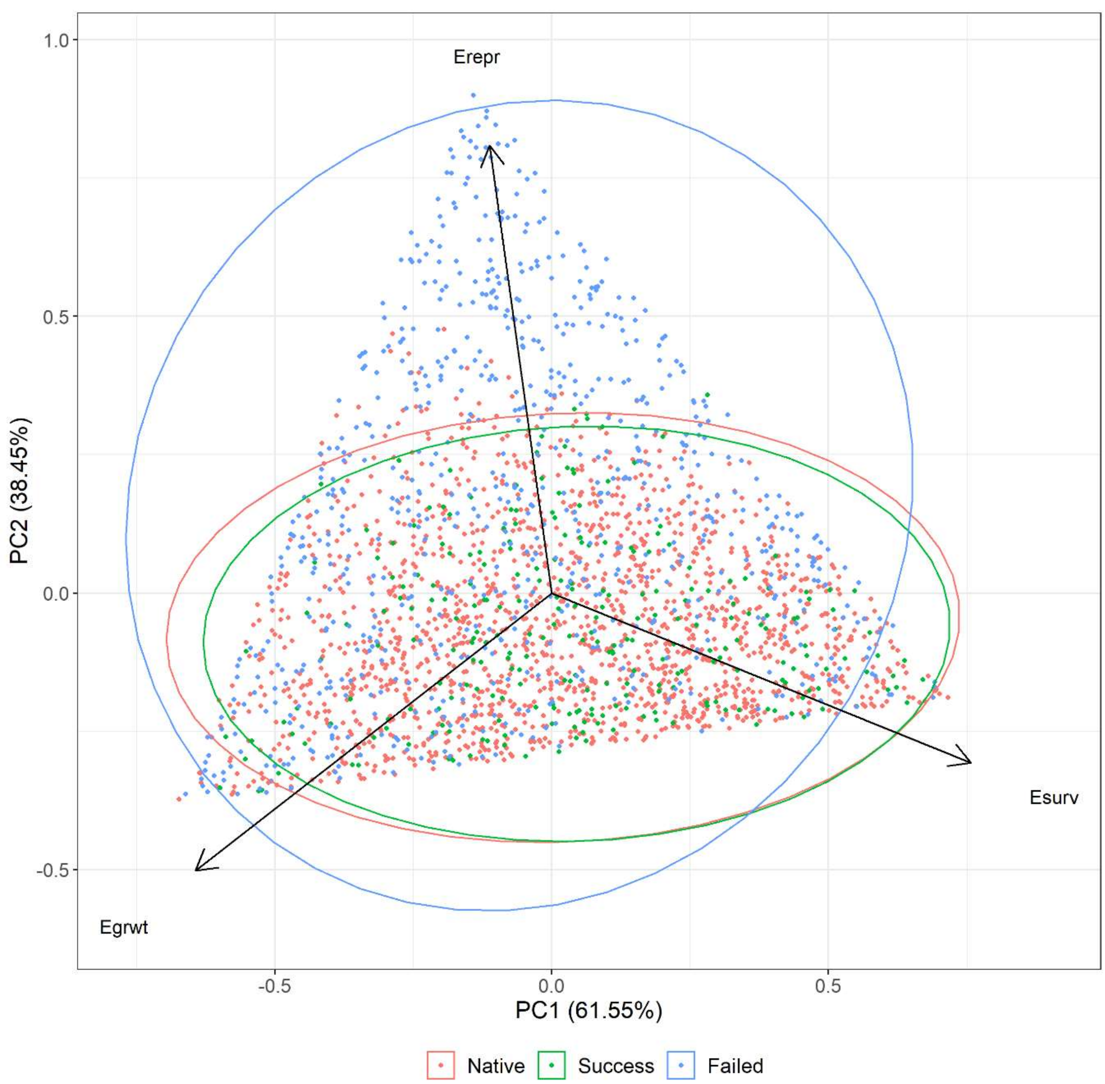

Figure 8: Average strategy comparison between individuals in the native community (prior to invasion; red), the successful invaders (green) and failed invaders (blue). The arrows represent the correlation between the energy allocation strategy and the principal components.

Discussion

Biological invasions were raised to the spotlight in the Anthropocene due to the increasing globalization, climate change and landscape changes which increased the reach and colonising opportunity for invaders (Early et al. 2016). Nevertheless, due to the wide variety and complexity of invasion processes, it is still not easy to predict the outcome of an introduction or the characteristics that turn a species into a successful invader. We identified that life-history strategies play a determinant role in the invasion success of mammals with average body size (30~80kg), but also are relevant for individuals with a large body size (>80kg). Small mammals had a low chance to establish and occupy the system, possibly due to the strong competition and small reserves to buffer the effects of demographic stochasticity. Differently, large mammalian herbivores have more than one energy allocation strategy they can rely on to remain in the system. Large invaders permanence, abundance and spread in the system is favoured by having larger energetic reserves and higher longevity, being that a high reproductive output may compensate for low investments in survival, which is not true for a high growth rate.

In mammals, there is a slow-fast continuum in which fast living species are the ones with shorter gestation periods, early maturity and large litter size (Promislow and Harvey 1990). For invasion biology there was the development of a classic belief that this kind of fast living species, that prioritize investments in reproduction, should be the most successful invaders, as the large litter size, short gestation period and early sexual maturity allow those individuals to rapidly increase the population number and reduce the period in which the population is exposed to demographic stochasticity (Pimm 1989, 1991). Nevertheless, an alternate theoretical model proposed that slow living species experience to a lesser extent the effects of demographic and environmental stochasticity, which may be a deciding factor for an invader permanence in the system (Sæther et al. 2004; Morris et al. 2008). We support the idea that the world is not so black and white, as different life-history strategies are favoured in different stages of the invasion and the final outcome is an interplay between how the invasive species invest the acquired energy and the native community individuals. Our results support both theoretical models, as the optimal invader was the one with short gestation period, early sexual maturity, large litter size, long lifespan and large reserves, which is a combination of both theoretical models.

The role of life-history strategies in invasion success is controversial, with support for both theoretical models and different characteristics (Kolar and Lodge 2001). Studies for birds goes against the classical theory, and found support for traits related to species' longevity and the number of broods per season, which is similar to the results we found for large species in our model (Kolar and Lodge 2001; Sol et al. 2012). Bird species with a higher longevity and higher number of broods per year have a lower brood value, which reduces the importance of a reproductive failure and may allow for invasive species to endure strong competition or environmental fluctuations (Sol et al. 2012). Nevertheless, there are evidences for mammals that invasion success is not so straightforward or binary, being that both reproductive and timing traits (litter size and reproductive lifespan) are relevant for the establishment and spread of alien mammals (Capellini et al. 2015). Our model partially supports those results; however, as we treated life-history strategies as syndromes, investing in reproduction causes changes to litter size, gestation period and age of first reproduction, being that the last two were not related to alien establish. Furthermore, we had a strong effect of body size upon invasive success (Capellini et al. 2015).

Body size has mixed results when considered as an explanation for invasive success, with some support for smaller species occupying larger geographical ranges (Duncan et al. 2001), but an number of studies that indicate the non-significance of body size in invasion success (Sol et al. 2012; Capellini et al. 2015; Duncan 2016). Our results go against all those evidences as it supports that body size positively affects invasion success. The reason for that disparity might be in the composition of our native community and in how individuals compete for resources. We created a stable community in which all individuals compete for the resources, regardless of their body size. Theory predicts that on stable environments K-selection prevails, favouring individuals with late maturity, multiple broods, long-living and with small reproductive effort (Stearns 1976). Our model is in accordance with this, as the dominant life-history strategy in the system was of long-living individuals with large reserves. Other that, under K-selection individuals are under a strong competition for resources. Small individuals have small reserves, restricted allometrically, and are more vulnerable against periods of starvation. On the other side, large individuals have larger reserves that allow those individuals to survive a few days without eating and replenish the reserves when they manage to acquire resources. It is possible that individuals with large body size will not have such strong advantage under a fluctuating environment scenario or with more than one source of energy.

There is an underlying difficulty in defining the life-history strategy of successful invaders, most of the studies rely on empirical observations and, as such, suffer from a strong confirmation bias (Simberloff and Gibbons 2004; Zenni and Nuñez 2013). Despite some noteworthy revisions that explored in depth failed invasions and multiple reasons associated with them (e.g. Zenni & Nuñez, 2013; Capellini et al., 2015), most studies that discuss species traits related to invasion success usually establish comparisons between invasive and non-invasive or native species (e.g. Roy et al., 2002; Hayes & Barry, 2008; Kempel et al., 2013; Schultheis & MacGuigan, 2018). Invasions success is a complex processes, that relies on the interaction of the alien species with the native community and the environment, in a way that an alien species might become invasive in one location and fail to establish in another (Shea and Chesson 2002; Simberloff et al. 2002). Moreover, the absence of detailed information about failed invasions might lead to misleading conclusions, in which the importance of a given trait might be overlooked or overestimated (Rejmanek and Richardson 1996; Zenni and Nuñez 2013). Therefore, the ideal design for a study that investigate traits related to invasive success should be closer to an experimental design, with multiple introductions under controlled conditions, but also taking in account different locations, environmental seasonality, seasonal variation of the native community and the number/frequency of propagules (Nentwig 2007). For most vertebrates, this experimental approach is simply out of reach, as one can easily imagine the logistic and time effort to apply this approach for a small toad in a continent scale, such as the cane toad invasion in Australia, even more for a large mammal worldwide, such as the feral pig. Therefore, realistic mechanistic simulation models like the one we introduced here rise as a suitable replacement for experimental studies, as they allow control over the activation of the multiple factors that may be determinant for invasive success, while also allowing to simulate multiple introductions of different invaders under the same conditions. The limitation is that such models rely on a huge amount of data, what is now being overcome due to the wider availability of traits databases (Ernest 2003; Frimpong and Angermeier 2009; Jones et al. 2009; Kattge et al. 2011; Faulwetter et al. 2014). Another limitation is that such models must be accurate, a feature which is not always the main objective of mechanistic models, as those models are usually focused on accurately representing a processes, which does not always translates in predictive accuracy or transferability (Levins 1966; Guisan and Zimmermann 2000; Yates et al. 2018). Alternatives to deal with this limitation is to anchor parameter estimation in a pattern (pattern-oriented modelling; Grimm et al., 1996; DeAngelis et al., 2005), or to validate the model predictions against multiple empirical patterns, usually not the ones model prediction is directed towards, such as we did while contrasting our individuals and community against real patterns (Grimm and Railsback 2005).

Finally, an important aspect of mechanistic modelling is acknowledging the model weaknesses and work on improvements. While our model was successful in creating realistic herbivore mammals, we underestimated trait variation, especially for large mammals. Consequently, we fail to encompass the full spectrum of possibilities for large mammals, some of which could result in successful invaders. A rather extreme example would be the feral pig (*Sus scrofa* Linnaeus 1758). According to our model, a species with the body size of a feral pig (average of 85kg) that prioritizes reproduction is limited to one offspring, has a gestation period of 6.5 months, reaches sexual maturity at 33 months and has a lifespan of 26 years. The real estimates for the feral pig are of 5.84 offspring at average, 3.5 months of gestation and sexual maturity at 9.39 months, with an average lifespan of 9 years (Jones et al. 2009). Therefore, it is possible that our model still does not encompass mammal herbivores with such extreme life-history strategies that makes life-history characteristics deviate by a considerable extent from what would be expected from allometry. Another point of debate is the resulting native community, which had a different body size frequency when compared to the PanTHERIA database. While the PanTHERIA database contains body size information for a substantial number of known mammal species (65.39%), it does not represent a community with interacting species, therefore contrasting our model with the database might not be adequate. As a matter of fact, when compared to studies that restrict mammal body size frequency to a given region, while there is not a single pattern, our results are much closer to some of the observed patterns (Bakker and Kelt 2000; Kelt and Meyer 2009).

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Appendix 1 – Overview, design concepts and details (ODD) protocol

Purpose

This model intends to evaluate how different life-history strategies plays a role in the invasion success of species. We start a native community from a large species pool with different strategies and test for different invaders covering a wide range of life-history strategies. As we grounded our models on metabolic allometric equations for herbivorous mammals, this model is best suited for testing competition among herbivorous mammals of different sizes.

Entities, state variables and scale

The biological entities of the model are herbivorous mammals which can be situated in one of the following stages: adults, juveniles and offspring. Adults are characterised by the following state variables: species identification, energy levels (required energy per day, daily ingested energy, daily consumed energy, actual reserve, maximum reserve), physical status (body size, age), reproduction status (pregnancy status, days until next reproduction) and geographical status (global -cell position- and regional -position within the cell- positions). Other than that, adult individuals are restricted by their respective species state variables: energetic restrains (basal metabolic rate), physical restrains (maximum body size, longevity), energy allocation priorities (life-history strategies), geographical origin (global -cell position- and regional -position within the cell- positions) and reproduction restrains (maximum neonate body size, litter size, age of first reproduction, weaning mass, gestation period and interval between reproductive seasons). Juvenile are younglings that rely on mother milk as the only source of energy, they are characterised by its species and mother identification, physical status (body size and age), energy levels (required energy per day, actual reserve and maximum reserve). Offspring are embryos, therefore rely entirely on the mother, they are characterised by its species and mother identification, physical status (body size and age) and embryonic growth rate. The spatial entities of the model are square cells of 1000x1000m in a matrix of 10x10 cells. Each cell is characterised by the amount of one resource, measured as energetic quantity, that are completely restored at the end of the iteration. Edge effects are avoided by assuming cyclic boundaries on all four sides. The temporal resolution is one day, so all state variables are parametrised by their daily values.

Process overview and scheduling

The core of the model is a resource consumption and allocation module that simulates how individuals compete for the available resource and make decisions based on their life-history strategies.

The model starts with a large species pool, higher than the total carrying capacity. Each species has a random centre of origin, and species' individuals are allocated around this centre based on their dispersal capacity, which is dependent on their body size. Species life-history strategies and degree of resource specialisation are randomly sampled from the all the possibilities and vary between 0-1. Individuals will compete for the resources within cells in a hierarchical way, being that species priority is defined at random. Individual then follow this priority order to move semi-consciously along the landscape according to their maximum daily movement. Individuals move in a pattern similar to the concept of home range and with some information of their surroundings, individuals identify from a Moore Neighbourhood the four cells with more energy and move randomly to one of them. After expending half of their maximum daily movement individuals will always move towards their original position. This process continues until all individuals had a chance to forage. Individuals that ate more than their basal metabolic rate (BMR) will have excess energy, which they will allocate based on their species' life-history strategy. Energy can be allocated to three processes: i) Growth, ii) Survival and iii) Reproduction, being that energy allocated to one of the process is made unavailable. Individuals that ate exactly the required their BMR will have the energy to maintain themselves but will not go through the process of energy allocation, as all consumed energy has already been used for maintenance. The remaining individuals that did not eat, or ate less than the required for maintenance, will undergo dispersion to other cells giving preference to more energetic locations, in a way similar to the foraging process. Individual will then proceed to try to forage in this new cell, if there is no available resources the individual will extract the amount of energy required for its maintenance, BMR, from its reserves. If the individual does not have enough reserves, it dies.

To avoid increasing model complexity, all females individuals are able to produce offspring. After an individual reaches maturity, it will have a reproduction timer. When this timer reaches zero it means it is reproductive season and this individual is now pregnant. Pregnant individuals expand their maximum reserves and have to allocate energy for offspring growth. After a gestation period, every individual will add new younglings to the system, limited by the maximum amount of offspring its species can produce and influenced by the total amount of energy invested for the offspring. Younglings rely on their mother`s milk until they reach a weaning mass, which means individuals with younglings will need to allocate resources to milk production. Mammal herbivores increase their ingested energy to supply the demands of milk production, in our model this is translated as an increase of 50% in the maximum daily ingestion. After reaching the weaning mass younglings are now considered adults and have to undergo the foraging process as any other individual in the system.

Those processes are kept running for 3650 days (10 years) without interference to create the native community. After this period the invasion is simulated by adding a 50 individuals from a species to the community. This new species follows the same processes as all the others, with its degree of resource specialization and life-history strategy also being randomly sampled from all the possibilities. In short, there is no practical difference between an invader and a native species.

By the end of the day, adult individuals update their actual and maximum reserve levels, grow, age, become pregnant, produce offspring and update their position. Offspring become younglings if the gestation period is over and youngling become adults when they reach the target weaning mass. Finally, energy levels within the cells are also restored to their maximum amount and a new cycle begins.

Design concepts

Basic principles

The whole model is based on allometric equations, being that every ratio is determined by individual species and current body size. As for the BMR, the model follows the $3/4$ exponent proposed by the Metabolic Theory of Ecology (MTE; Brown et al., 2004). However, as there is no effect of temperature in the model, we simplified our metabolic theory to the allometric scaling as originally proposed by Kleiber (1932). Intercept and inclination parameters for the metabolic scaling of mammals came from White & Seymour (2005). Data for the allometric scaling of the reproduction timer and growth curves came from De Marco (1999). Allometric scaling of litter size, neonate body size and gestation period came from Blueweiss *et al.* (1978) and built from the data available at Ernest *et al.* (2003), which was also used as source for the construction of the allometric scaling of the age of first reproduction and weaning mass (R^2>0.9). Scaling for parameters K and I of the Gompertz growth equation and species longevity came from Zullinger *et al.* (1984). Individuals` maximum reserve levels came from Lindstedt & Schaeffer (2002). Allometric scaling of parameters related to the consumption of resource were gathered from different sources: maximum ingestion rate (IGMax; Nagy, 2001), daily movement distance and incremental cost of locomotion (DMD and ICL; Garland, 1983), maximum food processing rate, maximum foraging velocity, time required to crop a bite and maximum bite size (R_{max}, V_{max}, h_{max}, S_{max}; Shipley et al., 1994, 1996). Resource intake model is regulated by bite mass and takes into account the time spent foraging in each cell, following the model developed by Spalinger & Hobbs (1992).

Aside from the allometric equations, another principle of the model is that energy consumed is allocated to three targets (growth, survival or reproduction) with its priority being determined according to species' life-history strategy. The different allocation strategies create a deviation from what would be the expected value considering only the allometric scaling, i.e. species with the same body size would have the same gestation period, however this period would be lower in the species that prioritizes energy allocation for reproduction. Aside from gestation period, energy allocated for reproduction increases litter size and decreases the age of sexual maturity. Energy allocated for growth increases the maximum body size a species can reach, increases dispersal distance and would result in a small priority while competing for food resources. Finally, energy invested in survival results in larger maximum reserves and greater lifespan.

We expect to test some classic invasion theories. We also will evaluate the effect of propagule pressure on invasion success, a highly debated hypothesis (Lockwood et al. 2005; Simberloff 2009; Kempel et al. 2013; Blackburn et al. 2015; Gallien and Carboni 2016). Finally, we will also evaluate how body size may have an effect on invasion success, an hypothesis already discussed by other studies (Roy et al. 2002). Most of all, our main focus is to evaluate the effect of different life-history strategies on invasion success and how those strategies interact with other species' traits, one of the major difficulties in invasion biology (Stearns 2000; Ricklefs and WIlkelski 2002; Sol et al. 2012).

Emergence

The whole community structure and invasion success result emerges from the model. Resource consumption priority among species is also determined at random, being that the result of this interaction and the optimal strategy is an emergent property. The interaction between species' traits and their influence on species' success is also an emergence. Therefore, our main result, invasion success, is *per se* an emergence in the model, as it relies on individuals' traits interactions.

Adaptation and objectives

The whole resource consumption and energy allocation could be considered an adaptive process in our model. Individuals have a limit they can allocate for growth, which follows a Gompertz Growth Model (De Marco Jr. 1999; Tjørve and Tjørve 2017), that means that there is a limit an individual can grow in each time step. While different species have different growth rates, the existence of this limitation means that even if an individual has a priority for growth it will allocate energy for other strategies if it reached this cap. The other processes also have caps, the amount of energy allocated for survival is limited by the maximum amount of reserve in an individual and for reproduction there is a limitation of energy that can be allocated for offspring and youngling nutrition. The existence of those caps means that energy allocation is adaptive to some extent, even with the existence of species life-history strategies.

Another adaptive aspect in our model is the resource consumption and dispersal process. While an unfed individual does not seek to maximise its efficiency while looking for resources in other cells, it will leave its cell and look for sources of energy in other communities if it could not reach its minimum requirements in its original community.

Prediction and Sensing

Individual prediction and sensing are based on their daily experience. Individuals that ate at least the resources required for their maintenance on one day have the expectation that this will continue to happen on the next day, therefore will not leave their original location. Individuals that did not reach this maintenance amount will leave the cell, as they expect that this will continue to happen on the next day if they stay on the same community.

Individuals have some information about resource levels on surrounding communities, they move at random to one of the four most energetic communities, but do not have information about the community structure of the target cell and whether they will be successful in outperforming those individuals in the foraging process.

Interaction

Individuals interact indirectly through resource consumption and depletion on a daily basis. Other than that, individual's with offspring or younglings interact with their spawn by allocating resources to feed them.

Stochasticity

Stochasticity is included in our model in several ways. First, while generating the species pool, species and individuals are created from a random sample of all the possible combinations of body size, degree of resource specialization and energy allocation strategies, which means that every community is unique. Other than that, the centre of origin for species is also determined by random, which means that even if the original species pool was always the same, the resulting interactions among individuals would change. Finally, resources are distributed at random in the world, which causes different patterns of individuals' interactions and is responsible for differences in the processes of dispersion and extinction. Individuals' daily order of resource consumption is also determined at random. There is also stochasticity in the foraging and dispersion step, as individuals have some information about their surroundings but choose their next destination randomly from the four most energetic neighbours.

Observation

From our model we observed the following characteristics from the invader: total abundance in the system, the number of invaded communities, life-history strategy, body size, degree of specialism for both resources and the community that acted as the origin for the invasion. We measure those observations at the end of the modelling process, after 10 years of invasion. If the invader has been extinguished from the world before the 10 year period, the model is interrupted and those measures are recorded at that time, together with the time it took for the invader to be extinguished.

Initialisation

The simulation starts with the creation of the species pool, with 300 different species of herbivore mammals being allocated throughout the world at random. Each species has information about their BMR, maximum body size, life-history strategy (species allocate acquired energy for growth, survival and reproduction in a complementary way, i.e. if a species allocates 0.6 for growth and 0.2 for survival, it allocates the remaining 0.2 for reproduction; those numbers are chosen at random, but the sum of all three strategies always sum up to 1), species centre of origin (1-10) and the spatial position within this cell (0-1000 for two axis), neonate body size, litter size, gestation period, interval between reproductive seasons, age of first reproduction, weaning mass, longevity and respective values for Gompertz I and K. Each species starts with up to 10 individuals. Individuals begin with an age that is 70% of the longevity of the species, a body size that is predicted based on its age-related value of the Gompertz equation, actual level of reserve (50% of the maximum reserve) and maximum reserve and spatial position the individual (grid and within cell). Individuals are initialised not pregnant, not fed, at the beginning of a reproductive season and without any ingested energy. There are only adults at the model initialisation.

After species populate the world the model is run by 10 years and the world composition at that moment is saved. Invasion process will happen at this point, so that invasive species will always meet the same initial status. Invaders are created in the same way of the initial individuals and are inserted in the system with different propagule pressures (50 and 200 individuals) and with different introduction scenarios (a single or multiple events of introduction).

Submodels

Resource consumption

Individuals acquire resources following a model in which intake is regulated by bite mass (Eq.1; Spalinger & Hobbs, 1992). In this model intake rate (I, g/min) is regulated by the rate of processing food (R_{max}, g/min), the time required to crop a bite (h, min) and maximum bite size (S, g).

$$I = \frac{R_{max}S}{R_{max}h+S} \qquad \text{(Eq.1)}$$

All the necessary variables to calculate the intake rate (R_{max},h,S) also scale allometrically (Eq.2,3,4; Shipley et al., 1994). W represents individuals' weight in kilograms.

$$R_{max} = 0.748 * W^{0.69} \quad \text{(Eq.2)}$$

$$h = 0.011 * W^{0.03} \quad \text{(Eq.3)}$$

$$S = 0.096 * W^{0.71} \quad \text{(Eq.4)}$$

To calculate individuals' total intake within a day we multiplied the intake rate (I) by the tiem individuals' spent foraging within each cell (T_{cell}; Eq.5). We calculated T_{cell} by multiplying individuals' foraging velocity (V_{max}; m/min) by the distance it travelled within this cell (d_{cell}; m). V_{max} also scales allometrically (Eq.6; Shipley et al., 1996).

$$T_{cell} = V_{max} * d_{cell} \quad \text{(Eq.5)}$$

$$V_{max} = 52.160 * W^{0.04} \quad \text{(Eq.6)}$$

Finally, the energy ingested by an individual within a day (E_{day}; KJ) is a sum of the the intake rate within the cell(I_{cell};g/min) times the time spent foraging in each cell visited by the individual during that foraging step (T_{cell}; min). To calculate the energy acquired from the ingested resources we followed the conversion factor indicated by Nagy (2001), which considers that non-fermenters herbivores absorb 10kJ/g dry mass (Eq.7).

$$E_{day} = \sum(T_{cell} * I_{cell}) * 10 \quad \text{(Eq.7)}$$

Resource consumption has two limitation: the maximum amount of resources and individual can ingest within a day (IGMax; kJ; Nagy, 2001) and the maximum daily distance it can travel (DMD; m; Garland, 1983). Both measures scales allometrically and interrupt the foraging process if their levels are reached (Eqs. 8,9). The scaling of IG_{max} considers individual's weight in grams (*w*) and is also multiplied by the conversion factor of 10kJ/g. DMD scaling is measured in quilometers, so we converted it to meters in the end to match our model's spatial units.

$$IG_{max} = (0.859 * w^{0.628}) * 10 \quad \text{(Eq.8)}$$

$$DMD = (0.875 * W^{0.22}) * 1000 \quad \text{(Eq.9)}$$

Other than that, individuals also waste energy while forging, which we incorporated by subtracting the incremental cost of locomotion (ICL; kJ/m; Garland *et al.* 1983) from the energy ingested in the day (E_{day}). The ICL also scales allometrically and was originally measured in J/km, we then made conversions to match our model's units (Eq.10).

$$ICL = (10{,}678 * W^{0.70})/1000000 \qquad \text{(Eq.10)}$$

Dispersion

In our model we assume all individuals are active dispersers, therefore the body size plays a major role in their dispersal capacity (Jenkins et al. 2007). For mammals, we used the relation established by Santini *et al*.(2013) for herbivores and omnivores between body size in kilograms (W_t) and mean distance in km (DS_{MAX}) to create the dispersal ceiling (Eq. 11). We then created a uniform dispersal kernel and sampled a random number from that distribution to determine the new individual location.

$$DS_{MAX} = 1.070 * {W_t}^{0.68} \qquad \text{(Eq.11)}$$

Dispersal happens in three moments. The first one is when individuals are created, as they disperse around species' center of origin in a random direction. The second is when individuals do not meet their resources demands and need to establish a new home range. In this step individuals disperse toward more energetic cells, in the same semi-conscious way present in the foraging step. The third moment dispersal is present is when younglings wean and need to establish their new home range. Those new adults also look for more energetic cells in a semi-conscious way.

Growth

Individuals growth follows Gompertz Growth Equation (Eq.12):

$$W_t = W_\infty e^{-e^{k(t-I)}} \qquad \text{(Eq.12)}$$

According to the equation the body size of an individual (W_t; g) in a specific time (t; day) is given by its maximum body weight (W_∞; g), its upper asymptote (I) and its growth rate (K). While values for W_∞ are established in the process of species' creation, values for K and I are calculated considering the allometric scaling of those metrics (Eqs. 13,14).

$$K = 0.125 * w^{-0.302} \qquad \text{(Eq.13)}$$

$$I = 3.343 * w^{0.354} \qquad \text{(Eq.14)}$$

Energy allocated for growth and reproduction (E_{GRWT} and $E_{SURV.}$) alters species' W_∞, K and I. According to the amount of energy allocated for growth (E_{GRWTH}) individuals will increase or reduce their W_∞ (Eq. 15). Similarly, according to the energy allocate for reproduction (E_{GRWTH}), individuals will have higher or lower values for K, reaching sexual maturity earlier (Eq. 16). Similarly, investment in survival (E_{SURV}) results in individuals reaching Gompertz asymptote later in life (Eq. 17).

$$W_\infty = W_\infty + (W_\infty * (-0.5 + E_{GRWTH}) \quad \text{(Eq.15)}$$

$$K = 0.125 * w^{-0.302} + (0.125 * w^{-0.302} * (-0.5 + E_{GRWTH})) \quad \text{(Eq.16)}$$

$$I = \left(3.343 * w^{0.354} + \left(3.343 * w^{0.354} * (-0.5 + E_{SURV})\right)\right) \quad \text{(Eq.17)}$$

From the Gompertz equation we predict the weight of the individual in a given time (W_t) and the value it could reach on the next day (W_{t+1}). This difference is how many grams an individual is able to grow in a day. We convert from grams to kJ considering the energy contained in 1g of tissue. Each gram of wet flesh contains about 7kJ (Peters 1983), added to that, there is also the cost of synthesizing new tissue, which is around 6kJ for mammal (embryos and adults) (Moses et al. 2008),which results in an energy of 13kJ/g of tissue produced in the growth step.

Longevity

Specie's longevity also scales allometrically. We used the data from Ernest (2003) for mammals' maximum lifespan and fitted a power function in the form $Y = aM^b$, in which M is the weight of the individual in grams, to calculate individuals' maximum lifespan in days (R^2=0.687; df=590; p<0.001). From the data we extracted values for the *a* and *b* coefficients (Eq. 18). Energy invested for survival ($E_{SURV.}$) affects maximum longevity, being that the amount of energy allocated for survival (E_{SURV}) may increase or decrease its value for longevity when only allometry is considered (Eq. 19).

$$Longevity = round(795.478 * {W_\infty}^{0.219}) \quad \text{(Eq.18)}$$

$$Longevity = round\left(795.478 * {W_\infty}^{0.219} + \left(795.478 * {W_\infty}^{0.219} * (-0.5 + E_{SURV})\right)\right) \quad \text{(Eq.19)}$$

Energetic Reserves

The amount of energy allocated to survival (E_{SURV}) also affects the maximum amount of reserves an individual can storage. We consider species allocate energy as fat, which contains (39.3kJ/g;Schmidt-Nielsen, 1997) and assume that fat storage, in grams, increases with body size, in kilograms, according to Lindstedt & Schaeffer (2002; Eq. 20).

$$Fat\ Storage = 39.3 * (75 * {W_t}^{1.19}) \quad \text{(Eq.20)}$$

Energy allocation for survival ($E_{SURV.}$) has an effect on the total amount of fat storage an individual can have (Eq. 21), being that individuals might have larger or smaller reserves that what would be expected only by allometry.

$$Fat\ Storage = 39.3 * \left(75 * W_t^{1.19} + \left(75 * W_t^{1.19} * (-0.5 + E_{SURV})\right)\right) \qquad \text{(Eq.21)}$$

Reproduction

There are several sub models within the reproduction sub model, we will briefly describe each of them. The priority of energy to reproduction affects the age of sexual maturity, litter size and gestation time. The size of offspring and weaning mass area affected only by individuals' body size.

Neonate Body Size

We found several models for neonate body size (NBS; grams) scaling allometrically (Blueweiss et al. 1978; Millar 1981; Martin and MacLarnon 1985; Lee et al. 1991; De Marco Jr. 1999), with some variation among them. Of the 6 models, 4 converged to similar values, we contrasted those models to empirical values from Ernest (2003) and chose the equation from Blueweiss *et al.* (1978; Eq. 22).

$$NBS = 0.097 * W_\infty{}^{0.92} \qquad \text{(Eq.22)}$$

Gestation Time

We also found several models for gestation time (GT; Blueweiss et al., 1978; Millar, 1981; Martin & MacLarnon, 1985; De Marco Jr., 1999), but unlike the neonate body size there was little variation among them (140~190 days of gestation for an individual with 30kg). As two of the four models converged to very similar results, we chose Blueweiss *et al.* (1978; Eq. 23) due to its good fit when compared to empirical values (Ernest 2003).

$$GT = round(11.659 * W_\infty{}^{0.249}) \qquad \text{(Eq.23)}$$

Energy invested for reproduction (E_{REPR}) affects species' gestation time in a way that species that allocate more than half of its energy to E_{REPR} have reduced gestation periods than what would be expected by allometry (Eq. 24).

$$GT = round\left(11.659 * W_t^{0.249} + \left(11.659 * W_\infty{}^{0.249} * (0.5 - E_{REPR})\right)\right) \qquad \text{(Eq.24)}$$

Litter Size

Individual maximum litter size ($LS_{MAX;}$ Eq. 25) comes from Blueweiss *et al*.(1978), and was also contrasted with empirical values (Ernest 2003).

$$LS_{MAX} = 5.997 * W_\infty{}^{-0.142} \qquad \text{(Eq.25)}$$

Energy allocated for reproduction ($E_{REPR.}$) affects litter size. Offspring would still have the same neonate body size (NBS), but an individual that invest little to reproduction will produce less offspring than what would be expected by allometry (Eq. 26).

$$LS_{MAX} = round\left(5.997 * W_{\infty}{}^{-0.142} + \left(5.997 * W_{\infty}{}^{-0.142} * (-0.5 + E_{REPR})\right)\right) \quad \text{(Eq.26)}$$

Sexual Maturity

Individual's age of first reproduction (AFR) is also determined by their body size and affected by E_{REPR}. The power function was built using data from Ernest (2003), for individuals body weight in grams and age of first reproduction in days (Eq.27; R^2=0.594; df=815; p<0.001).

$$AFR = round\left(44.470 * W_{\infty}{}^{-0.276} + \left(44.470 * W_{\infty}{}^{-0.276} * (0.5 - E_{REPR})\right)\right) \quad \text{(Eq.27)}$$

Weaning Mass

We also built the power function for weaning mass using data from Ernest (2003). Weaning mass for younglings is given in grams and is based only on specie's maximum body size (Eq. 28; R^2=0.970; df=394; p<0.001). Weaning mass is not affected by life-history strategies, being determined only by allometry. In practice it means that two younglings of species with the same body size will undergo weaning in the same mass, however the species with a higher E_{GRWTH} will reach this mass earlier due E_{GRWTH} effects over Gompertz's K (Eq.16).

$$WeaningMass = 0.485 * W_{\infty}{}^{0.931} \quad \text{(Eq.28)}$$

Offspring Growth

Offspring daily growth is a result of the interaction between individuals' gestation period (Gestation Time; Eq. 24) and neonate body mass (NBS; Eq. 22). We chose not to establish power functions in this step and promote a linear growth to avoid overcomplicating the model and, as already demonstrated, gestation period is an effective way to estimate embryo growth (Ricklefs 2010). The result is that when considered species with the same body size, the one with the lowest gestation period will invest a higher amount of daily energy for offspring grow (Eq. 29).

$$OffspringGrowth = {}^{NBS}\!/_{GestationTime} \quad \text{(Eq.29)}$$

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Chapter 3: Invading success in real world: how life-history traits and land-use patterns separates winners from losers in realistic simulated communities

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Abstract

Biological invasions are the result of a complex interplay between invaders, the native community and the landscape throughout space and time. Accurately representing the processes that arise from these interactions is essential to understand the key factors responsible for invasion success. Community co-occurrence theory states that variable environments play a major role in species co-occurrence, which might be a decisive factor for invaders' permanence in the system. The outcome between resource fluctuation at different habitats within a landscape and how species are able to efficiently make use of those resources in relation to other species in the community is the key to understand why invaders succeed in some environments and fail at others. In this study we created a system to represent this complexity. We evaluate how invasion success is determined by the competition for resources between the native community and invaders reaching a real landscape at the agriculture expansion frontier at Brazil. We simulate invasion events at three time periods, in which the system goes from a highly conserved landscape (95%) up to a loss of 25% of forest cover and agriculture expansion in a period of 18 years. We analyze how different herbivore mammals' invaders life-history strategy (reproduction, survival and growth) succeed in the different invasion periods and how those strategies interact with the degree of specialization and invaders' body size. Invasion success, measured as invader's presence, abundance and system occupation, was highly variable throughout the years, with a higher invasive success when the agriculture expanded more within the system. There was also a variation among invasion periods of how life-history strategies, degree of specialization and degree of agriculture use were determinant for invasion success. We demonstrate that the different factors intertwine to determine invasion success, in a way that at different time periods or landscapes the same invader might succeed or fail to establish itself in the system. Therefore, accurate predictions of biological invasions require more complex models that more closely represent the processes that occur in the system.

Introduction

Albert Einstein once said "*Everything should be made as simple as possible, but not simpler*". This means that we should always try to make things as easy as possible but take precautions to not make them so simple in a way that they no longer accurately represent the phenomena they intend to describe. In Ecology, in order to understand the behavior of environmental systems, there was a strong development of mathematical models, with the goal of creating relatively simple explanations for complex phenomena (Harte 1988; Connor et al. 2007). Powered by the recent advance of both computational capacity and data availability, ecological models reached a high degree of complexity, advancing in terms of accuracy and realism as they are built based on individual behavior (DeAngelis and Mooij 2005). Nevertheless, due to a high level of details and a large amount of information, such models have potential to become intangible and stalled by the execution of the numerous number of processes (DeAngelis et al. 2005; Grimm and Railsback 2005). A concept which resembles the ideas of Einstein is the Medawar Zone (Loehle C. 1990), which establishes a relation between model complexity and payoff. Very simple models have low payoff due to their extreme simplicity. It means their capability to explain real phenomena is very low. On the other side, if a model is extremely complex its payoff is also low, as it is extremely likely to get tangled in its details in a way that it becomes hard to keep track of the overall situation. Therefore, the solution is to seek for the Medawar Zone: a zone in which models are as simples as possible, but not simpler. However, there are no solid boundaries that ease the identification of this region and most of the time it its delimited by trial and error or by using a pattern as guidance (DeAngelis et al. 2005). Individual-based models are usually aimed at making a precise description of the system agents, for example accurately describing its behavior and producing real population dynamics (Grimm and Railsback 2005), while they often simplify the system in which those individuals are inserted. It is obvious that the earth is not flat, but we often ignore that it is not static. Temporal and spatial environmental variations are responsible for favoring a different set of attributes and, consequently, a different set of species (Stearns 1976), while also being essential for species coexistence (Chesson 2000a).

Community assembling processes are an important arena where the complexity and model properties are under continuing tests seeking for the development of a well-grounded general theory. Based on a community-oriented point of view, species diversity is maintained by both fluctuation-dependent and fluctuation-independent mechanisms (Chesson 2000b). Fluctuation-independent are mechanisms that exist regardless of environmental variability such as resource partitioning and frequency-dependent predation. Notwithstanding, stable coexistence of species is critically reliable on the fluctuation of resources, as coexistence might depend on species having different responses to fluctuating resources, e.g. different growth rates, or by an interplay between intra- and interspecific competition and the environmental fluctuations, also called storage effect (Chesson 1994, 2000b). Storage effect can be resumed by three steps: species respond differently to the environment, which combined to the existing covariance between competition and environmental variability means that a species might be regulated by intra-or interspecific competition at a given time period/location. When a species is favored by the environmental conditions, intraspecific competition is strongest, when conditions are unfavorable interspecific competition is stronger. Which leads to the final step, buffered population growth, which limits the negative effects of interspecific competition and allows it to survive until conditions are once again favorable. This buffer might arise in the form of seed banks, resting eggs or, as is more common in mammals, long-lived adults with large reserves (Chesson 1994, 2000a, b). Other than that, spatially structured habitat makes it able for species to reduce competitive effects and avoid unfavorable sites at specific time periods and temporarily move to other favorable locations (Tilman 1994). Therefore, environmental variability has a major role in allowing species coexistence, which has a major benefit of increasing diversity (McCann 2000; Ives and Carpenter 2007), but might also have drawbacks, such as enabling the establishment of alien species (Shea and Chesson 2002).

Invasion is an important ecological real-time experiment to understand community assembling processes. Invasion success is a result of several interacting factors. In general, the invasion process can be divided in four stages the alien species must undergo to become an invader: transport, colonization, establishment and dispersal (Theoharides and Dukes 2007; Blackburn et al. 2011). Each stage has a dominant factor, or barrier, the alien species must transpose, being that invasive species are only those species that surpassed all four barriers. Environmental variability can be determinant for the establishment of the alien species, as in this stage biotic resistance is the major barrier and variability might allow for different species to coexist due to resource fluctuation or environmental heterogeneity (Davis et al. 2000; Shea and Chesson 2002; Cleland et al. 2004; Melbourne et al. 2007). Resource can be a limiting factor in a community and be a major driver for invasion success, therefore any new species in the system will invariably compete with the already established individuals in the system (Davis and Pelsor 2001). Consequently, alien species must seek niche opportunities that allow them to overcome this competition and persist in the system. Niche opportunities may arise from one three sources: resource opportunities, enemies escape opportunities and how the physical space interacts with the other two sources (Shea and Chesson 2002). Resource opportunities may arrive when an invader is more efficient than residents at using resources but might also occur when invaders are less efficient by providing windows of opportunity that arise from temporal resource fluctuation. Less efficient invaders can persist in the community by the mechanisms of the storage effect, which translates to fluctuating environments being more susceptible to alien species establishment (Chesson 2000b; Shea and Chesson 2002; Melbourne et al. 2007). Other than taking advantage of temporal fluctuations, alien species might also find advantages within the different features of the landscape. Homogeneous environments offer few opportunities for alien species establishment, as alien and natives compete for the same type of resource, the only successful alien species would be the ones that outcompete the natives. Heterogeneous landscapes, on the other hand, offer a wide variety of resources and increase the likelihood that invaders will have the upper hand in any given type of resource, while allowing native species to avoid extinction in the system due to the high diversity of resources (Tilman 1994; Chesson 2000a; Melbourne et al. 2007). Therefore, alien species establishment is an interplay between how natives and alien species interact throughout the landscape over the time.

Several hypothesis for invasion success consider the interaction between the alien species and the native community or the landscape, some noteworthy ones are the biotic resistance hypothesis (Elton 1958), the empty niche hypothesis (Elton 1958), niche breadth-invasion hypothesis (Mayr 1965; Ehrlich 1989; Vazquez 2006) and stochastic niche theory (Tilman 2004). Biotic resistance hypothesis is probably one of the most studied invasion-related hypotheses and is focused on how the different native communities resist the establishment of the alien species. The most classical approach relates richness in the native community to invasion success, being that communities with more species pose a greater barrier for alien establishment (e.g. Cleland et al. 2004; Beaury et al. 2019). However, there is no predominance either for or against the hypothesis, with mixed results and the possible existence of the effect being scale-dependent (Cleland et al. 2004; Melbourne et al. 2007; Jeschke et al. 2012). Empty niche hypothesis suggests that alien species are able to use resources not used by native species, or even use the existing resources more efficiently. This hypothesis can be easily linked to the biotic resistance, as with a higher diversity it is also less likely that there are non-exploited resources in the system (Herbold and Moyle 1986; Simberloff 1995; Levine and D'Antonio 1999). Niche-breadth hypothesis supports that generalist species are more likely to become invaders, since they can exploit a large variety of resources (Cassey et al. 2004; Vazquez 2006; Crowder and Snyder 2010). Finally, stochastic niche theory links alien species establishment to the availability of resources and stochastic processes. Stochastic niche theory states that community assembly is a result of success and failure of aliens' propagules, that due to their low density, are more susceptible to demographic stochasticity. After this stage, successful propagules must grow and thrive under a scenario of resource limitation, in which most of the resources are consumed by native individuals. As a result, probability of invasion success depends on invader's resource requirement in relation to those individuals within the native community. Therefore, any slight decrease in resources results in a large decrease in likelihood of establishment, and the low invasibility of diverse communities is cause not by diversity itself, but due to the low availability of the existent resources in that community (Tilman 2004). There are several common points between the hypothesis of biotic resistance, empty niche, niche breadth-invasibility and stochastic niche theory, being that the relation between those hypothesis and community theory for co-existence of species is easily observable. In its root, all the previous hypothesis proposes an explanation to how invaders can co-exist with individuals of the native community, and as proposed by Chesson *et al.* (2000b), the natural fluctuation and spatial heterogeneity of resources might play a determinant role. Given the relevance and support for invasibility being related to resource availability (Davis and Pelsor 2001) and how invader traits interact with native community traits while competing for resources (Mata et al. 2013), analyzing invasion processes from an energetic viewpoint is a good strategy to evaluate invasion success.

In this study we created a simulation model to explore invasion success in a real landscape, with temporal and spatial variability. We simulated invasions in a landscape that went through a rapid land-conversion process in the last 20 years, with seasonal resource fluctuation and spatial heterogeneity. We've created three invasion events, one at the first year of the simulation, in which the landscape was almost entirely composed by natural vegetation and two other events further in time, when the land-conversion was already in progress. We are interested in how different invaders' life-history strategies will interact with the native community in a scenario of real temporal and spatial variability and how this interaction will be determinant for invasion success. We use our model to explore theories and hypothesis regarding biological invasions. According to the community ecology, co-existence is more likely in heterogeneous and fluctuating environments, therefore we expect invaders to have a higher invasive success in more heterogeneous landscapes (Fig. 1a). Furthermore, efficiency on using resources is determinant for persistence in homogeneous landscapes, while in heterogeneous landscapes species might co-exist regardless of their specialization, which opens the possibility for generalists to occupy the system. Therefore, we expect highly specialized invasive species to succeed when the landscape is predominantly composed by natural vegetation and as the land-conversion moves forward generalists' species will be able to persist (Fig. 1b). Additionally, life-history strategies favored by fluctuating environments are different from the ones in stable environments, therefore we expect the predominant life-history strategy for invasive success to change as the landscape undergoes land-conversion (Fig. 1c). Finally, empty-niche and niche-breadth hypothesis predictions state that invaders might find an empty-niche in agricultural areas and exploit resources unused by natives. Therefore, we expect a higher invasive success by invaders with a higher efficiency at agricultural areas (Fig. 1d). In the end, we hope to untangle the multiple causes of variation in the invasive process and clarify some of the key aspects that determine invasive success.

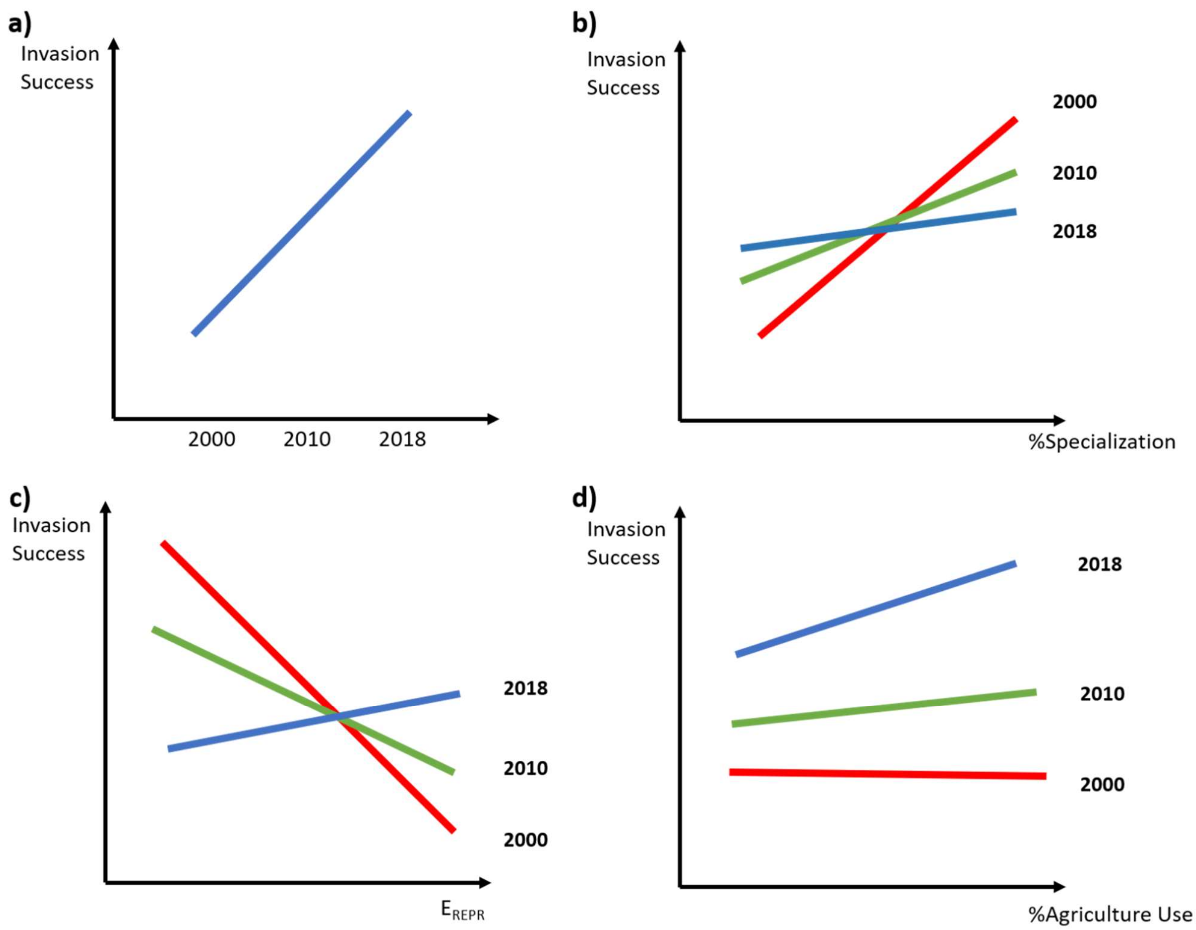

Figure 1: Invasion process predictions and how success of invasion varies according to each hypothesis. Co-occurrence theory states that species co-occurrence increases with environment heterogeneity. As in our system landscape heterogeneity increases as time advances, invasion success at 2018 should be higher than at 2000 (a). Also according to co-occurrence theory, under stable, homogeneous conditions only highly specialized invaders should be able to establish in the system, while resource fluctuation and heterogeneity allows for generalists to also persist in the system. Therefore, invasion success at 2000 should be dependent on invaders' degree of specialization, while this effect should be much weaker at 2018 (b). According to life-history theory, stable environments favor K-strategist species, while heterogeneous environments favor r-strategists. Therefore, we expect that species that prioritize reproduction to be disfavored at the year of 2000, when the landscape is highly homogeneous, while species that prioritize survival will have an advantage. On the opposite, in the year of 2018, within a more heterogeneous landscape, investing in reproduction should be advantageous, while investing in survival should be harmful (c). Finally, according to niche-breadth and empty niche hypothesis, as agriculture becomes more common in the landscape, invaders that are more efficient at acquiring resources from agriculture

should have a higher invasive success. Therefore, we expect the degree of agriculture efficiency to be determinant for invaders' persistence at the year of 2018, while having no effect at the year 2000 (d).

Methods

Experimental overview

We evaluated the invasion success of species being introduced at a landscape (123,5 x 202,5 km) at the northern region of the Cerrado biome, within a region known as MATOPIBA (due to the border between the provinces of MAranhão, TOcantins, PIauí and BAhia). This region is the current Brazilian agriculture frontier and is undergoing a fast process of land conversion, with deforestation rates increasing by 61.6% in the last years and cropland areas increasing up to 41~328% in those four provinces during the 2002-2013 period (Sano et al. 2019). The MATOPIBA region is also relevant if we consider those four provinces comprise four of the five States with the higher percentage of Cerrado natural vegetation, and soybean demand is expected to increase even further in the next decade, which probably will increase the pressure over natural remnants on the regions (Strassburg et al. 2017).

We applied the same model developed at Chapter 2 at the MATOPIBA region, with minor modifications to consider species use of the different land-use classes. We used the MapBiomas data for land-use, with a resolution of 30m and measured at a yearly interval, with the land-use being classified in six different classes, four of which occur in our landscape: forest, non-forest natural vegetation (which we named grasslands), agriculture and barren areas (MapBiomas 2019). We applied the model between the years of 2000 and 2018, a period of high rates of land conversion in the region (Fig. 2). During this period the landscape underwent a strong process of land-conversion, with the loss of 22.8% of forest cover and 1.1% of grasslands, and a consequent increase of 23.3% of croplands and 0.6% of barren areas. Energetic conditions for the region were obtained from the MODIS/Terra Project and downloaded via AρρEEARS (AppEEARS Team 2019), from which we gathered data for Net Photosynthesis (MOD17A2Hv006) and net annual productivity (MOD17A3Hv006), both measured from 2000 to 2018 on a 8-day interval with a resolution of 1km². We rescaled both MapBiomas and energetic conditions to 1km, in order to reduce processing time and match the same cell size used for chapter two.

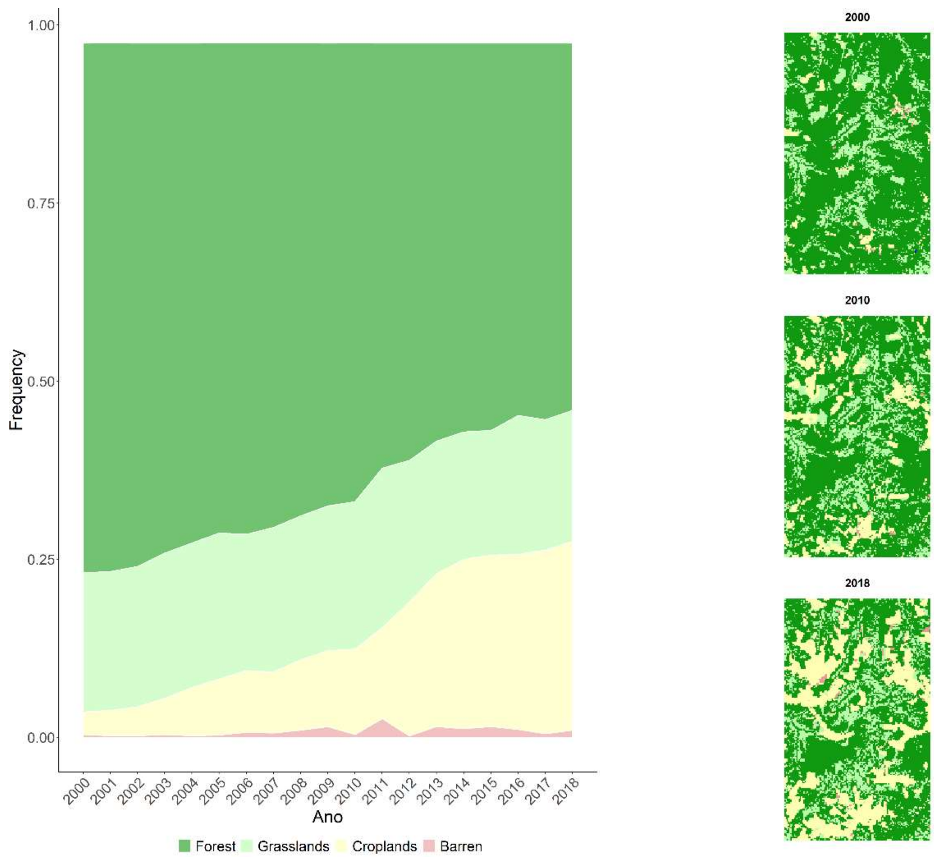

Figure 2: Land-use in the a landscape inserted within the MATOPIBA region, at the northern boundary of the Brazilian Cerradio biome between the years of 2000 and 2018.

We started our simulation in the year 2000 and used the land-use and energetic conditions of this year to create the baseline community for our model. We created a species pool of 100 species with different levels of habitat specialization for the four classes. For native species we allowed for specialization in natural areas to vary between 0 and 0.8 and non-natural areas between 0 and 0.2. For invasive species the variation of those rates were the same for natural areas (0-0.8) and a bit higher for non-natural (0-0.5), in that way we avoid creating invaders that are highly specialized in anthropogenic environments to an extent that they will rarely interact with natives. We randomly allocated species along the landscape, but always defining as center of origin a cell class in which the species have higher specialization. We then started the same model based in energetic budgets, allometric relations and life-history theories used in chapter 2, but with minor changes in which habitat specialization modifies individuals' resource consumption efficiency and decision-making in the foraging process. We once more ran the model for a 20-years period in order to reach a stable native community, but at this first step we fixed land-use and energetic data to the year 2000 in order to create a stable native community considering only those conditions, in which almost the totality of the landscape was composed of natural vegetation (93.8%). This community will be used as a basal community for models for the year 2010. After the 10-year period we introduced 50 different exotic species, created with random attributes for life-history strategies, body size and degree of habitat specificity. Once again, we introduced those invasive species one at a time, making sure that different invaders always meet the same native community (Fig. 3).

For the invasion scenario considering landscape configuration at the year 2010 we used the basal community from 2000 as our starting point. We allowed this community to continue its dynamic without the introduction of invaders simulating the land-use changes and energetic dynamics that occur between 2000 and 2010. Land-use changes on a yearly base, following the MapBiomas database, while the energetic amount is updated daily following the Net Photosynthesis for the last eight days. When the model reaches the year of 2010, we once again establish this as a second basal community, which will be used as input for the year 2018. At this step we perform a second invasion event, in which we introduce 50 different exotic species one at a time. At last, we use the basal community produced in the 2010 step and repeat this process for the 2010-2018 variation for land-use and energetic conditions. When the simulation reaches 2018, we introduce the final 50 invaders (Fig. 3).

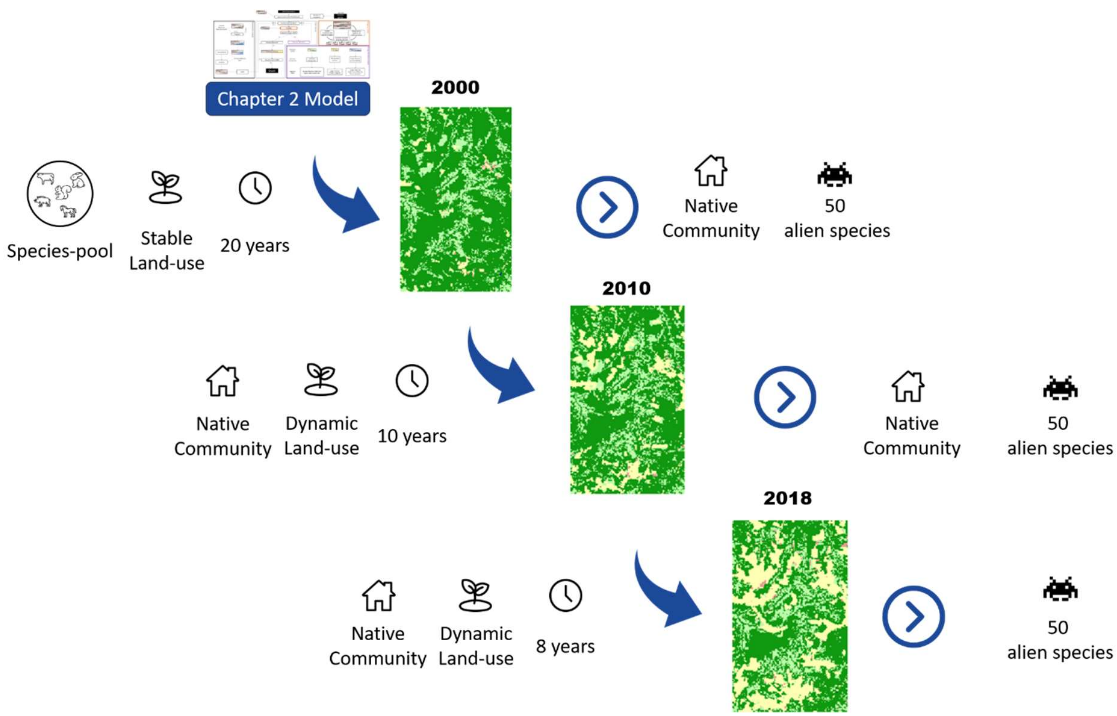

Figure 3: Overview of the experimental design. We apply the same model used in chapter 2 to a real landscape at the MATOPIBA region, Brazilian Cerrado biome. The model runs for 18 years and follows the land-use changes that occurred in that landscape for that period. The starting point is the year 2000, when the natural vegetation within the landscape is over 95% of the total area. We

create a species pool of 100 species, each with 10 individuals and run the model for 20 years under stable land-use conditions. This first step is performed to generate an initial stable native community. At the end of the 20 years we store the native community to be used in the following steps and begin the first invasion event, in which 50 different invaders are inserted into the community, one at a time. In a next step, not related to the changes produced by the invaders, we submit the native community stored prior to the invasion event to the land-use changes that occurred in that landscape over 10 years. At the end of the ten years, we once again store the resulting native community and perform another invasion event, again with 50 different invaders. At the final step, we submit the native community to the last 8 years of land-use change, a period which the landscape underwent rapid land-conversion, and at the end of that period perform the final introduction event of 50 invaders. This framework is replicated 20 times, in order to generate different species pools and native communities.

Invasion success

We used the same three metrics used in chapter 2 to measure invasion success: invaders' presence (Eq.1) and abundance (Eq.2) in the system after 10 years of the species' introduction and the number of communities(cells) occupied by the invader (Eq.3). We used Generalized Linear Mixed Models (GLMMs) to evaluate the effect of different life-history strategies ($E_{REPR.}$, $E_{GRWT.}$, $E_{SURV.}$) and their interactions with maximum body size (BS), but this time also considered the effects of invader's degree of natural habitat specificity (N_{SPE}) and anthropogenic habitat specificity (A_{SPE}). We consider as N_{ESP} the maximum level of specificity an invader has for a natural land-use classes (forest or grasslands) and A_{SPE} the maximum level of specificity an invader has for anthropogenic classes (agriculture or barren). We consider invader's center of origin (ORI), which is nested within replicates, a random effect as the composition of the native community in the center of origin also affects the invasion success. We also consider failed invasions in our analysis, as they represent life-history strategies that were not successful.

Furthermore, we use all three aspects of invasive success to test our model results against the four theoretical predictions of theories and hypothesis related to biological invasions (Fig. 1).

$$\boldsymbol{Presence} \sim (\boldsymbol{BS} * \boldsymbol{Erepr} * \boldsymbol{Year}) + (\boldsymbol{BS} * \boldsymbol{Esurv} * \boldsymbol{Year}) + (\boldsymbol{N_{ESP}} * \boldsymbol{BS} * \boldsymbol{Year}) + (\boldsymbol{A_{ESP}} * \boldsymbol{BS} * \boldsymbol{Year}) + (\boldsymbol{1}|\boldsymbol{Replicate}/\boldsymbol{ORI}) \qquad \textit{\textbf{(Eq.1)}}$$

$$\boldsymbol{Abundance \sim (BS * Erepr * Year) + (BS * Esurv * Year) + (N_{ESP} * BS * Year) + (A_{ESP} * BS * Year) + (1|Replicate/ORI)} \quad \textbf{\textit{(Eq.2)}}$$

$$\%_{\boldsymbol{INVADED\ COMMUNITIES}} \boldsymbol{\sim (BS * Erepr * Year) + (BS * Esurv * Year) + (N_{ESP} * BS * Year) + (A_{ESP} * BS * Year) + (1|Replicate/ORI)} \quad \textbf{\textit{(Eq.3)}}$$

Similarity to native community

We once more evaluated successful invaders had similar life-history strategies when compared to the native community. We established comparisons for the 3 periods of invasion (2000, 2010, 2018) by a PERMANOVA with Euclidian distance and 9999 repetitions to contrast each one of the native communities' individuals for a given period and successful and unsuccessful invaders at this community. We tested for homogeneity of multivariate dispersions prior to conducting the PERMANOVA. We used the package *vegan* to conduct both the homogeneity of multivariate dispersion and PERMANOVA tests (Oksanen et al. 2019).

Results

Invasion success

Invader presence in the system was determined by all six factors (BS, E_{SURV}, E_{REPR}, N_{ESP}, A_{ESP} and Year), but with very different relevance, and only once there was an interaction between invasion period and agriculture utilization (Table 1, χ^2 values). Body size was the most determinant of all factors, in which small invaders have a higher likelihood of establishing in the system (Table 1, Figs. 5-8). Next, the period of invasion was highly determinant by invasion outcome, being that in the year of 2018 invaders had a higher chance of remaining in the system (Table 1, Figs. 5-8). As for life-history strategies, invaders that allocated energy for reproduction had a great disadvantage, while investing at survival had a small, but positive, effect (Table 1, Figs. 6-7). Finally, specialists had a slightly higher chance of remaining in the system than generalists, both for natural and anthropogenic habitat, being that in the year of 2018 species with a higher utilization of agriculture had a much higher success in remaining in the system than species with a poor utilization (Table 1, Figs. 5,8).

Table 1: Factors affecting invader presence in the system for all three periods ($Year_{2000,2010,2018}$). Acronyms: E_{SURV}: energy allocated for survival; E_{REPR}: energy allocated for reproduction; *BS*: Invader body size; N_{ESP}: degree of specialization for natural habitats; A_{ESP}: degree of specialization for anthropogenic habitats. Value marked with a * stand for significative results.

Fixed Effects

Parameter	Estimate	CI	χ^2	df	p-value
(Intercept)	1.901	±0.666	-	-	-
E_{SURV}	0.664	±0.808	30.559*	1	<0.001*
E_{REPR}	-3.947	±0.861	119.587*	1	<0.001*
BS	-4.246	±1.283	328.314*	1	<0.001*
N_{ESP}	1.037	±0.561	50.079*	1	<0.001*
A_{ESP}	0.908	±0.529	55.470*	1	<0.001*
$Year_{2010}$	-0.586	±1.007	222.172*	2	<0.001*
$Year_{2018}$	-0.675	±0.994	-	-	-
E_{SURV}:BS	0.864	±1.785	0.171	1	0.679
BS:$Year_{2010}$	-1.324	±1.985	0.491	2	0.781
BS:$Year_{2018}$	2.554	±1.698	-	-	-
E_{SURV}:$Year_{2010}$	0.528	±1.227	5.179	2	0.075
E_{SURV}:$Year_{2018}$	1.817	±1.494	-	-	-
E_{REPR}:BS	-0.090	±1.716	0.940	1	0.332
E_{REPR}:$Year_{2010}$	2.359	±1.163	9.198*	2	<0.05*
E_{REPR}:$Year_{2018}$	2.054	±1.246	-	-	0.115
N_{ESP}:$Year_{2010}$	-0.311	±0.803	1.357	2	0.507
N_{ESP}:$Year_{2018}$	0.337	±0.926	-	-	-
BS:N_{ESP}	0.059	±1.200	0.128	1	0.719
A_{ESP}:$Year_{2010}$	0.132	±0.832	16.981*	2	<0.001*
A_{ESP}:$Year_{2018}$	3.163	±0.922	-	-	-
BS:A_{ESP}	-0.876	±1.097	3.426	1	0.064
E_{SURV}:BS:$Year_{2010}$	1.599	±2.543	3.435	2	0.182
E_{SURV}:BS:$Year_{2018}$	-3.805	±2.806	-	-	-
E_{REPR}:BS:$Year_{2010}$	-1.176	±2.416	0.390	2	0.825
E_{REPR}:BS:$Year_{2018}$	-1.484	±2.385	-	-	-
BS:N_{ESP}:$Year_{2010}$	1.322	±1.657	1.625	2	0.445
BS:N_{ESP}:$Year_{2018}$	-0.887	±1.710	-	-	-
BS:A_{ESP}:$Year_{2010}$	1.372	±1.676	5.180	2	0.075
BS:A_{ESP}:$Year_{2018}$	-2.723	±1.642	-	-	-

Random Effects

Parameter	Variance	Std.Dev
Replicate	<0.001	<0.2934
Origin:Replicate	<0.001	<0.001

Model Results

AIC	BIC	LogLik	Deviance	Df	R^2m	R^2c
2993.9	3186.1	-1464.9	2929.9	2968	0.477	0.490

Invader abundance in the system is a much more complex factor of invasive success, which is affected differently by the several variables in all three periods (Table 2). First, body size is highly determinant of final invader abundance, being that small species reach much higher number of individuals in the system than large individuals (Table 2, Figs. 5-8). Hereupon, the way in which the abundance of small and large species responds to the different life-history strategies and degree of specialization vary at the different invasion periods. Beginning by life-history strategies, prioritizing reproduction has a negative effect for all body sizes and all periods. Nevertheless, the strength of this negative effect is weaker for small species invading the system at the year 2018 and reaches its maximum for large species reaching the system at the year 2000 (Table 2, Fig. 6). Species that prioritize survival, on the other hand, had a little to none gains in abundance, with the exception of medium and large species that reached the system in 2010, for which investing in survival greatly increased the total number of individuals in the landscape (Table 2, Fig. 7). Next, being a specialist was beneficial for small species, even more if they were reaching the system at the year of 2000 but was not so determinant for medium and large mammals, having almost no effect for determining the abundance of large mammals reaching the system at 2018. Nevertheless, medium and large species reaching the system at 2010 were an exception, in which specialists were able to achieve a higher number of individuals in the system (Table 2, Fig. 5). Finally, a higher utilization of the resources available at agriculture areas was relevant for the abundance of mammals of all sizes in the year 2018; had no effect for small mammals and positive effects for medium and large mammals for the year of 2010 and at the year of 2000 varied from a positive effect upon the abundance of small mammals, to a small positive effect upon medium mammals and a negative effect for the abundance of large mammals (Table 2, Fig. 8).

Invader number of occupied cells in the system had a pattern similar to invader abundance (Table 3). Once more body size was highly determinant for invasive success, being that small species occupied a higher number of cells. As for invader abundance, the multiple variables had different effects upon small, medium, and large species. The way in which system occupancy was affected by the different could be explained by the correlation of 0.99 between the two metrics. Due to that we avoid repeating the detailed explanation as we did for invader abundance, as all the effects described for abundance were also valid for system occupation.

Table 2: Factors affecting invader abundance in the system for all three periods ($Year_{2000,2010,2018}$). Acronyms: E_{SURV}: energy allocated for survival; E_{REPR}: energy allocated for reproduction; *BS*: Invader body size; N_{ESP}: degree of specialization for natural habitats; A_{ESP}: degree of specialization for anthropogenic habitats. Value marked with a * stand for significative results.

Fixed Effects

Parameter	Estimate	CI	χ^2	df	p-value
(Intercept)	-0.142	±0.549	-	-	-
E_{SURV}	1.747	±0.743	22.995*	1	<0.001*
E_{REPR}	-0.243	±0.682	119.426*	1	<0.001*
BS	-1.474	±1.169	1159.125*	1	<0.001*
N_{ESP}	4.016	±0.535	164.328*	1	<0.001*
A_{ESP}	2.377	±0.491	134.263*	1	<0.001*
$Year_{2010}$	4.262	±0.875	273.038*	2	<0.001*
$Year_{2018}$	2.797	±0.745	-	-	-
E_{SURV}:BS	-1.167	±1.657	1.077	1	0.299
BS:$Year_{2010}$	-10.024	±1.868	3.565	2	0.168
BS:$Year_{2018}$	-2.745	±1.492	-	-	-
E_{SURV}:$Year_{2010}$	-2.025	±1.045	4.357	2	0.113
E_{SURV}:$Year_{2018}$	-1.152	±0.954	-	-	-
E_{REPR}:BS	-8.607	±1.772	17.510*	1	<0.001*
E_{REPR}:$Year_{2010}$	-2.274	±0.992	7.545*	2	<0.05*
E_{REPR}:$Year_{2018}$	0.075	±0.941	-	-	-
N_{ESP}:$Year_{2010}$	-4.328	±1.245	26.045*	2	<0.001*
N_{ESP}:$Year_{2018}$	-2.245	±0.745	-	-	-
BS:N_{ESP}	-2.327	±0.679	4.864*	1	<0.05*
A_{ESP}:$Year_{2010}$	-2.739	±0.749	15.955*	2	<0.001*
A_{ESP}:$Year_{2018}$	0.346	±0.631	-	-	-
BS:A_{ESP}	-3.365	±1.147	1.661	1	0.197
E_{SURV}:BS:$Year_{2010}$	6.117	±2.300	7.746*	2	<0.05*
E_{SURV}:BS:$Year_{2018}$	1.009	±2.112	-	-	-
E_{REPR}:BS:$Year_{2010}$	8.575	±2.400	11.530*	2	<0.01*
E_{REPR}:BS:$Year_{2018}$	4.360	±2.267	-	-	-
BS:N_{ESP}:$Year_{2010}$	5.926	±1.687	11.394*	2	<0.01*
BS:N_{ESP}:$Year_{2018}$	2.499	±1.529	-	-	-
BS:A_{ESP}:$Year_{2010}$	6.744	±1.672	15.579*	2	<0.001*
BS:A_{ESP}:$Year_{2018}$	1.960	±1.432	-	-	-

Random Effects

Parameter	Variance	Std.Dev
Replicate	0.062	0.249
Origin:Replicate	4.510	2.123

Model Results

AIC	BIC	LogLik	Deviance	Df	R^2m	R^2c
20020.4	20212.7	-9978.2	19956.4	2968	0.512	0.958

Table 3: Factors affecting invader number of occupied cells in the system for all three periods (Year$_{2000,2010,2018}$). Acronyms: E_{SURV}: energy allocated for survival; E_{REPR}: energy allocated for reproduction; *BS*: Invader body size; N_{ESP}: degree of specialization for natural habitats; A_{ESP}: degree of specialization for anthropogenic habitats. Value marked with a * stand for significative results.

Fixed Effects

Parameter	Estimate	CI	χ^2	df	p-value
(Intercept)	0.092	±0.555	-	-	-
E_{SURV}	1.736	±0.742	23.009*	1	<0.001*
E_{REPR}	-0.543	±0.688	124.730*	1	<0.001*
BS	-1.792	±1.187	1162.785*	1	<0.001*
N_{ESP}	3.869	±0.538	161.776*	1	<0.001*
A_{ESP}	2.236	±0.496	131.082*	1	<0.001*
Year$_{2010}$	4.018	±0.886	273.939*	2	<0.001*
Year$_{2018}$	2.568	±0.749	-	-	-
E_{SURV}:BS	-1.143	±1.656	1.108	1	0.292
BS:Year$_{2010}$	-9.672	±1.900	3.877	2	0.143
BS:Year$_{2018}$	-2.433	±1.507	-	-	-
E_{SURV}:Year$_{2010}$	-2.025	±1.054	4.402	2	0.110
E_{SURV}:Year$_{2018}$	-1.149	±0.950	-	-	-
E_{REPR}:BS	-8.176	±1.785	16.078*	1	<0.001*
E_{REPR}:Year$_{2010}$	-1.961	±0.995	9.197*	2	<0.05*
E_{REPR}:Year$_{2018}$	0.349	±0.945	-	-	-
N_{ESP}:Year$_{2010}$	-4.082	±1.255	25.425*	2	<0.001*
N_{ESP}:Year$_{2018}$	-2.105	±0.746	-	-	-
BS:N_{ESP}	-2.193	±0.682	4.383*	1	<0.05*
A_{ESP}:Year$_{2010}$	-2.591	±0.755	17.223*	2	<0.001*
A_{ESP}:Year$_{2018}$	0.486	±0.637	-	-	-
BS:A_{ESP}	-3.191	±1.159	1.486	1	0.222
E_{SURV}:BS:Year$_{2010}$	6.105	±2.327	7.521*	2	<0.05*
E_{SURV}:BS:Year$_{2018}$	0.994	±2.100	-	-	-
E_{REPR}:BS:Year$_{2010}$	8.127	±2.397	10.400*	2	<0.01*
E_{REPR}:BS:Year$_{2018}$	3.992	±2.276	-	-	-
BS:N_{ESP}:Year$_{2010}$	5.678	±1.694	10.509*	2	<0.01*
BS:N_{ESP}:Year$_{2018}$	2.274	±1.540	-	-	-
BS:A_{ESP}:Year$_{2010}$	6.553	±1.690	14.677*	2	<0.001*
BS:A_{ESP}:Year$_{2018}$	1.783	±1.446	-	-	-

Random Effects

Parameter	Variance	Std.Dev
Replicate	0.061	0.248
Origin:Replicate	4.471	2.114

Model Results

AIC	BIC	LogLik	Deviance	Df	R^2m	R^2c
19979.9	20172.1	-9957.9	19915.9	2968	0.512	0.958

Invasion hypothesis

Invasion success over the years increased, both in the number of successful invaders as in the average number of invaders at the system at the end of the ten-year period. On the other side, the native community just before the invasion event suffered from a progressive decrease from the year 2000 up to the year 2018, both for native richness and abundance (Fig. 4). Those predictions are, to some extent, in accordance with community theory of higher co-occurrence in heterogeneous environments, as there is an increase in invader presence and abundance in the system in more heterogeneous environments (Fig. 1a). This is supported by evaluating native community richness and abundance before and after successful invasion events (Fig. 5). Native community suffered a sharp decrease after the ten-year period for invasions in the year of 2000, with only 11% of the remaining species remaining after the ten-year period on average. Nevertheless, this native richness loss was not accompanied by a loss of abundance, as native abundance remained at the same levels before and after the invasion process. At the year of 2018, there was a reduced extinction of the remaining native extinction, with approximately 30% of natives remaining in the system, accompanied by a slight increase in native abundance. The combination of those results is in accordance with the predictions for both the higher co-occurrence between the native community and the invaders in more heterogeneous environments and the higher invasion success due to an empty niche created by the extinction of natives.

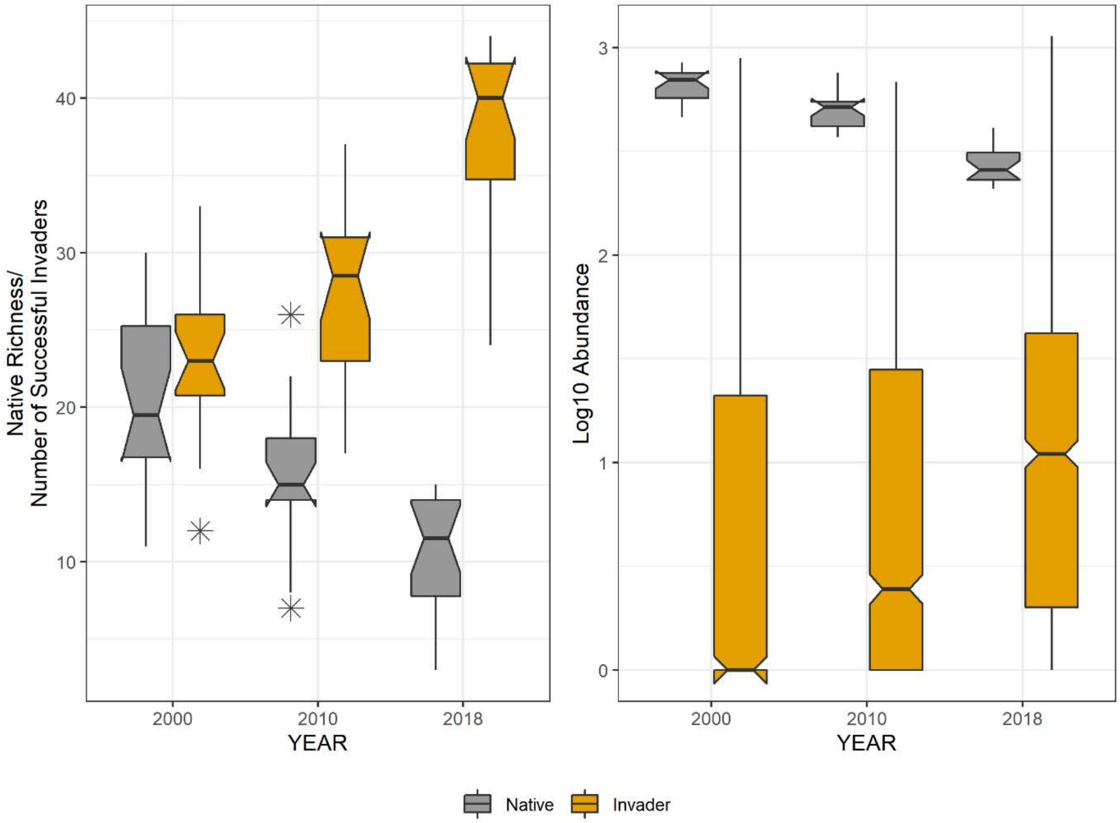

Figure 4: Invader and native richness and abundance in the system. The left panel represents the number of native species existent right before each invasion event (grey) and the number of invaders that successfully established in the system (yellow). Right panels represent the average abundance of all natives in the system right before the invasion events (grey) and the average abundance of invaders at the end of invasion events (yellow). Invaders that failed to establish in the system are also included in the abundance analysis, with its abundance considered to be zero.

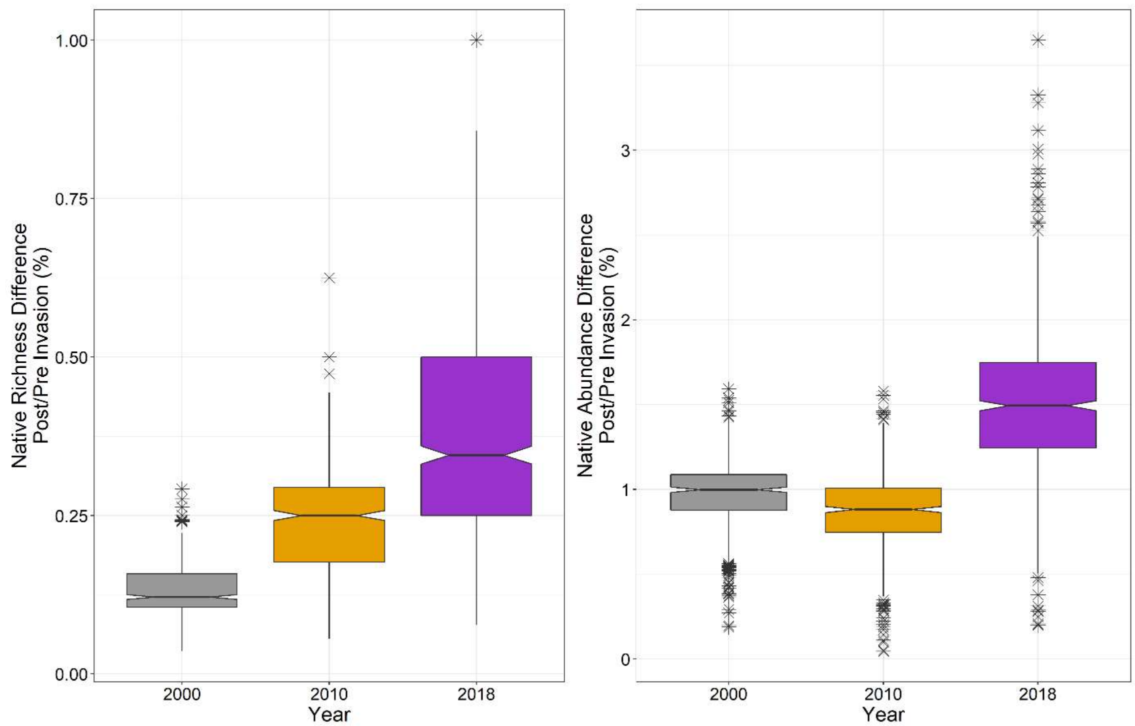

Figure 5: Native richness and abundance difference within native community after and before the ten-year period of successful invasion events among the three time periods. Values in the Y-axis represent the proportion of species in the native community that remained after the ten years of invasion (left) and the proportional of those species compared to the abundance of natives before the invasion event took place (right).

Invasion success response to natural habitat specialization varied among the three metrics, especially between invaders' presence in the system when compared to both abundance and number of occupied communities (Fig. 6). Overall, specialists had a higher likelihood of remaining in the system. Nevertheless, the difference between the likelihood of establishment for specialists and generalists was higher for the years of 2000 and 2010 and for larger mammals. For the year of 2018, small specialists and generalists invading the system had almost the same likelihood of remaining in the system, while medium and large specialists had a slight advantage. This pattern was inverted for both abundance and system occupation. For small species, specialist species had a higher abundance and system occupation at all three periods. The same pattern was observed for medium and large invaders at the years 2000 and 2010. Nevertheless, for the year of 2018, being a specialist did not increase invaders' abundance and system occupation for medium and large mammals. Those results are in accordance with the predictions of the co-occurrence theory (Fig. 1b), as specialists invaders succeed when the landscape is predominantly composed by natural vegetation and as the land-conversion moves forward generalists' species achieve a higher invasive success, reaching the same levels of abundance and system occupation as specialists.

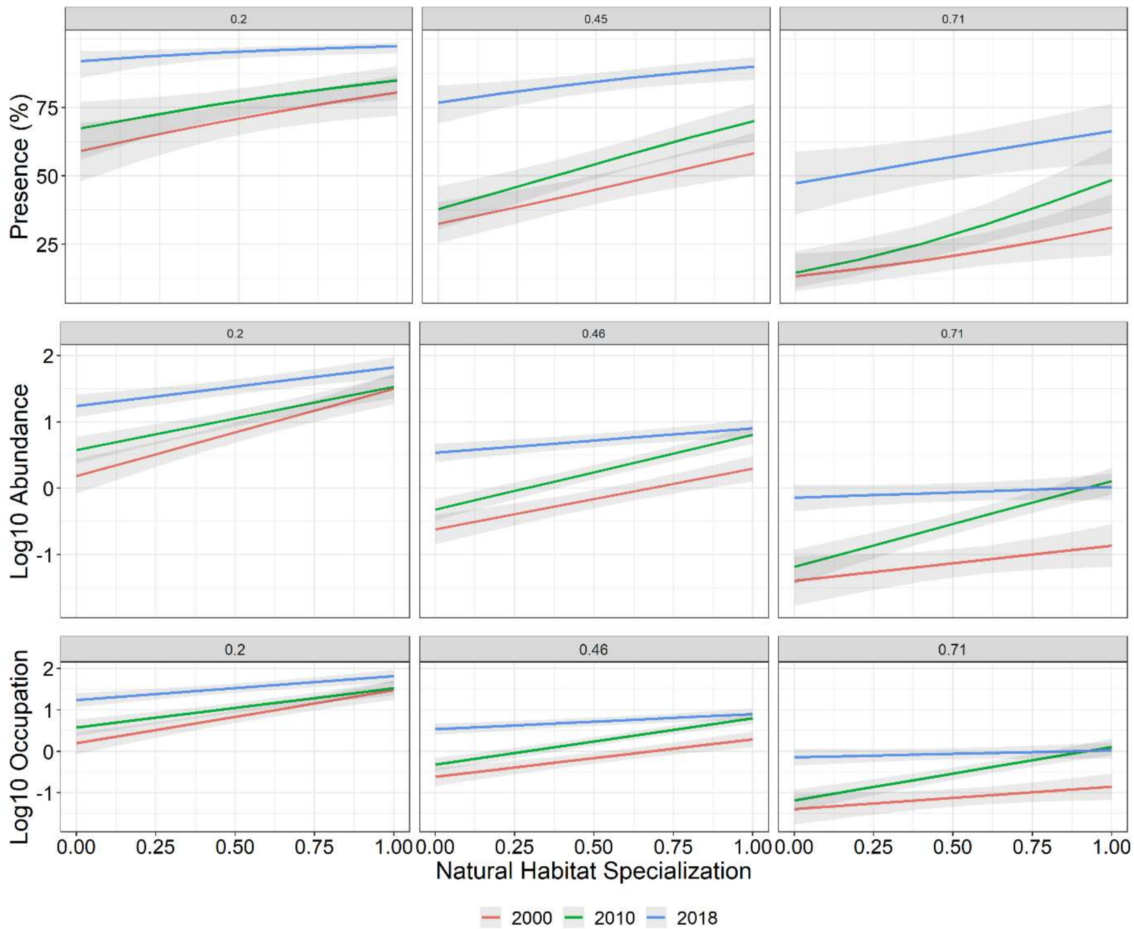

Figure 6: Invasion success based on invaders' degree of natural habitat specialization. Different colors represent the different periods of invasion: 2000(red), 2010(green) and 2018(blue). The different columns represent invaders of different body size. Left panels represent invasion success of small mammals (10-30kg), center panels represent medium mammals (30-60kg) and right panels represent large mammal (60-100kg). Different rows represent the three different aspects of invasion success. The upper row represents the likelihood of invaders being present in the system after the ten-year period. Middle row stands for invader abundance in the system and the bottom row represents the system occupation.

Invasion success response to life-history strategies also varied according to invader body size and period of invasion (Fig. 7). Nevertheless, there was a common overall effect for the three invasion success metrics when considered the degree of prioritization for both reproduction and survival. In general, investing in reproduction had a negative effect, but the strength of the consequences differed among species of different body sizes that reach the system at different time periods. Small, medium and large species that prioritize reproduction were much less successful in remaining in the system, but this effect was weaker for small invaders reaching the system at 2010 and even more if those invaders reach the system at 2018. The negative effects of reproduction upon all aspects of invasive success were highest for invaders reaching the system at 2000, especially if those invaders have a large body size. Prioritizing investments in survival, on the other hand, had positive effects for invasion success. Nevertheless, the strength of this positive effect varied according to the aspect of invasion success, the body size of the invader and the invasion period (Fig. 8). Prioritizing survival was a key strategy for medium and large invaders reaching the system at the year of 2010, as the higher the priority the higher the likelihood of the invaders remaining in the system, reach higher abundances and occupying a larger portion of the system. This same positive effect was also observable for all three aspects of invasion success for small invaders reaching the system at the same year, but to a much weaker extent. Species reaching the system at 2000 also benefited from investments toward survival. Nevertheless, the positive effect was restricted only to invader presence in the system, only being observable for the components of abundance and system occupation for small species and, even so, to a small extent. Investment in survival had the smallest effects at the year of 2018, with small to zero positive effects for invaders of all body sizes and for all three aspects of invasion success. Those results are partially in accordance to the predictions of life-history theory (Fig. 1c), as stable environments are expected to disfavor species that prioritize investments in reproduction, which agrees to the stronger negative effects we found for invaders in the year of 2000. Nevertheless, investing in survival did not have strong positive effects in the same year, which would be expected. On the opposite side, investing in reproduction did have lesser detriments in the year of 2018, but not to an extent in which it became beneficial for invaders.

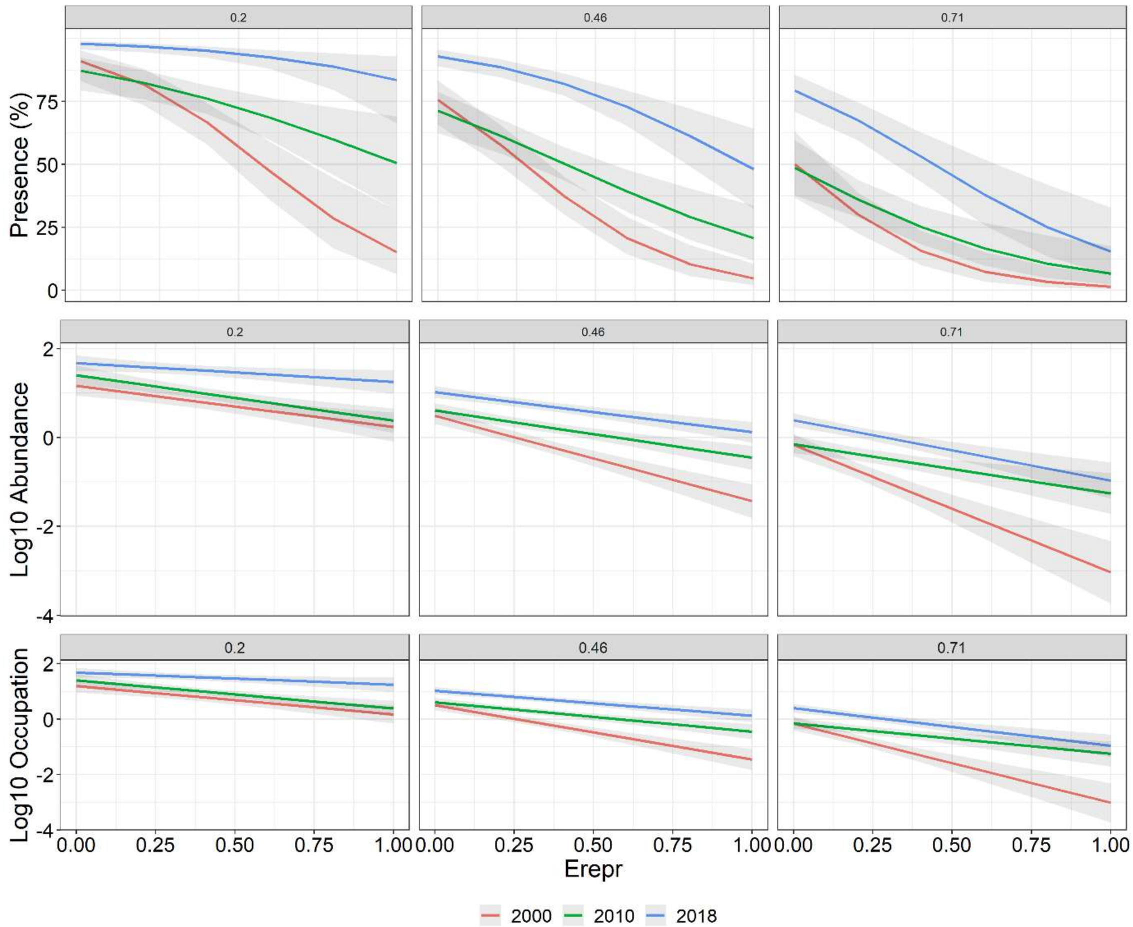

Figure 7: Invasion success based on invaders' degree of energy allocated for reproduction. Different colors represent the different periods of invasion: 2000(red), 2010(green) and 2018(blue). The different columns represent invaders of different body size. Left panels represent invasion success of small mammals (10-30kg), center panels represent medium mammals (30-60kg) and right panels represent large mammal (60-100kg). Different rows represent the three different aspects of invasion success. The upper row represents the likelihood of invaders being present in the system after the ten-year period. Middle row stands for invader abundance in the system and the bottom row represents the system occupation.

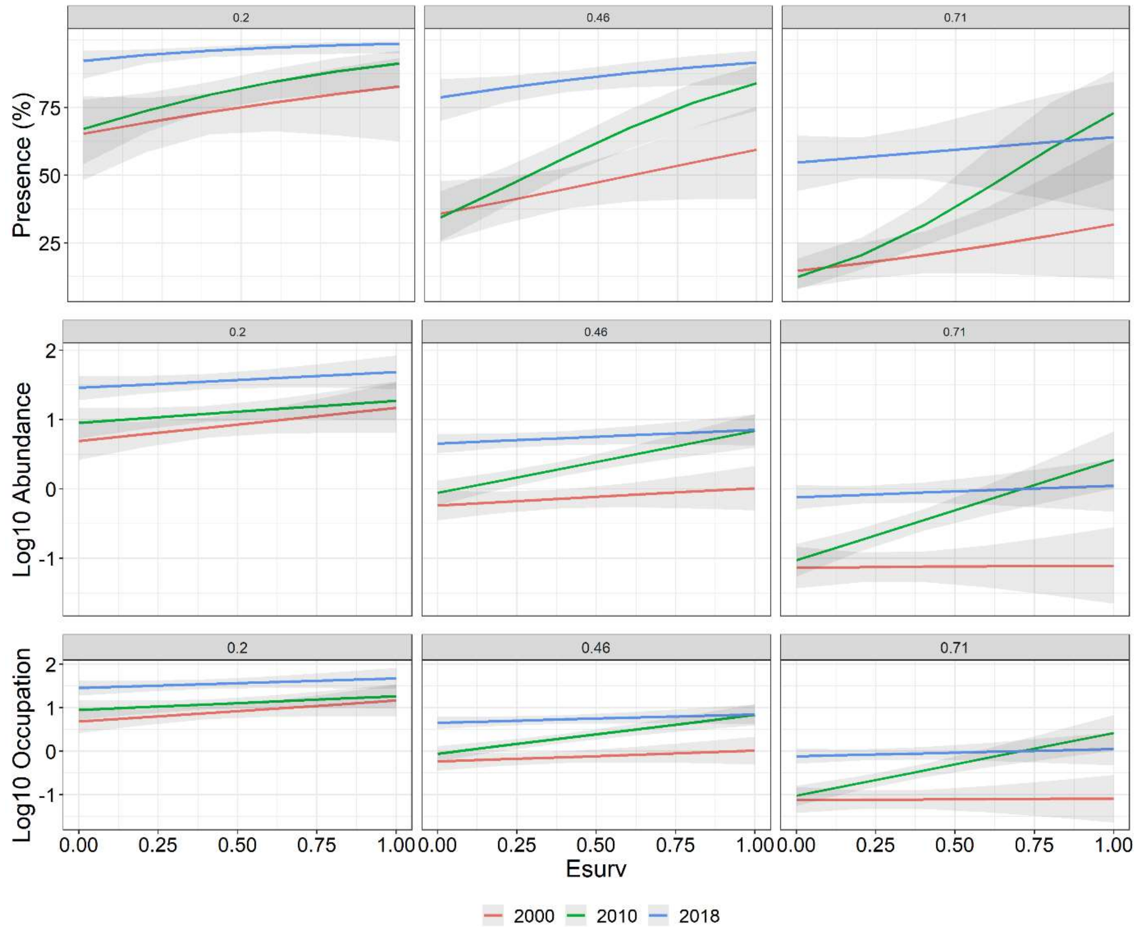

Figure 8: Invasion success based on invaders' degree energy allocated for survival. Different colors represent the different periods of invasion: 2000(red), 2010(green) and 2018(blue). The different columns represent invaders of different body size. Left panels represent invasion success of small mammals (10-30kg), center panels represent medium mammals (30-60kg) and right panels represent large mammal (60-100kg). Different rows represent the three different aspects of invasion success. The upper row represents the likelihood of invaders being present in the system after the ten-year period. Middle row stands for invader abundance in the system and the bottom row represents the system occupation.

Finally, invasion success related to agriculture use by invaders was highly related to the period of invasion and to a lesser extent to invader body size (Fig. 9). Invaders reaching the system at the year of 2018 had an overall higher invasion success, regardless of agriculture use. In addition, invaders that were able to better utilize agricultural resources had a higher likelihood of remaining in the system, being that the benefits were even stronger for large mammals, accompanied by larger levels of abundance and system occupation. Positive effects were also observable for the year of 2010, but dependent on body size. The presence of small invasive species were slightly benefited by a better use of agriculture, but the abundance and system occupation of those species was not affected. Medium and large mammals, on the other hand, had a higher invasive success in all three aspects when the individuals had a better utilization of agriculture resources. Finally, invaders reaching the system at the year of 2000 had the smallest benefits from a better utilization of agriculture. While small species had a higher invasive success in all three aspects, medium mammals had only small to neutral benefits, which was even worse for large species, in which a better utilization of agriculture resulted in a lower invasive success. Despite the higher invasive success of small mammals in the year of 2000, our results are in accordance with the empty-niche and niche-breadth hypothesis (Fig. 1d), since invaders with a higher agriculture utilization had a higher invasive success, especially for the year of 2018, when agriculture in the landscape reaches its highest proportion.

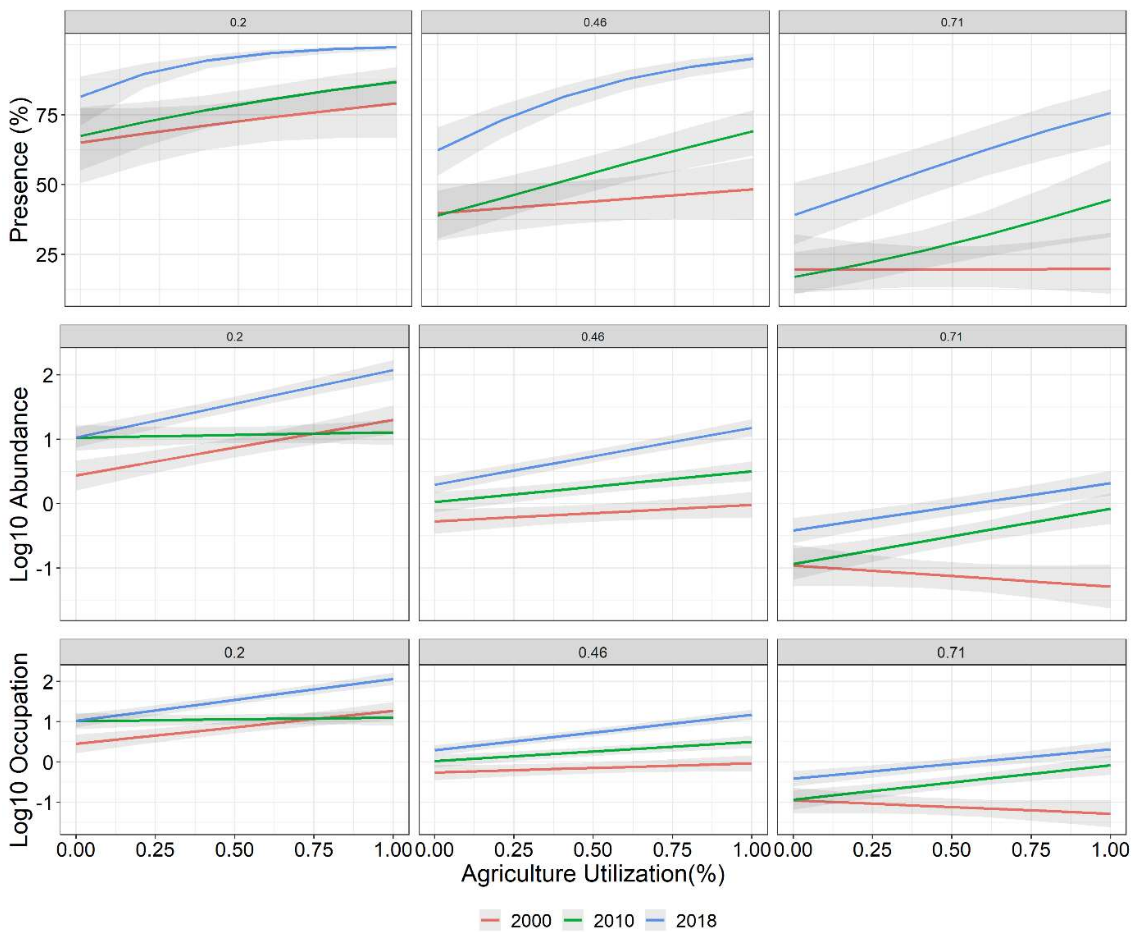

Figure 9: Invasion success based on invaders' degree of agriculture utilization. Different colors represent the different periods of invasion: 2000(red), 2010(green) and 2018(blue). The different columns represent invaders of different body size. Left panels represent invasion success of small

mammals (10-30kg), center panels represent medium mammals (30-60kg) and right panels represent large mammal (60-100kg). Different rows represent the three different aspects of invasion success. The upper row represents the likelihood of invaders being present in the system after the ten-year period. Middle row stands for invader abundance in the system and the bottom row represents the system occupation.

Similarity to native community

Invader similarity with the native community varied among the different invasion periods. Successful invaders among the ones reaching the community in the year 2000 were the ones with similar life-history strategies to the native community (PERMANOVA: $F_{1,1070}$=7.233, R^2=0.006), while invaders who failed to remain in the system were the ones with different life-history strategies (PERMANOVA: $F_{1,976}$=68.202, R^2=0.065). Both the native community and successful invaders in the year 2000 prioritize energy allocation for survival while failed invaders prioritize energy allocation for both reproduction and growth (Fig 6). For the year 2010, both successful (PERMANOVA: $F_{1,851}$=95.871, R^2=0.101)and unsuccessful (PERMANOVA: $F_{1,767}$=157.180, R^2=0.170) invaders were less similar to the native community , being that once more failed invaders differed more from native species. As the native community descends from the native community of the year 2000, the main allocation priority is for survival, while successful invaders prioritize both survival and growth and failed invaders prioritize reproduction and growth (Fig. 10). Finally, for the year 2018 once again the pattern was of successful invaders being more similar to natives (PERMANOVA: $F_{1,960}$=74.000, R^2=0.071) than unsuccessful invaders (PERMANOVA: $F_{1,448}$=105.070, R^2=0.189). Nevertheless, this was the period of the least difference between the native community and both successful and unsuccessful invaders life-history strategies. In this year most invaders were successful in establishing in the system (75.6%, against 54.2% in 2010 and 54.7% in 2000), which resulted in a wide variety of successful invaders life-history strategies. We avoid reporting p-values for all PERMANOVA analysis and instead focus on the F-metric, as the high number of degrees of freedom will almost always result in significant p-value (White et al. 2014).

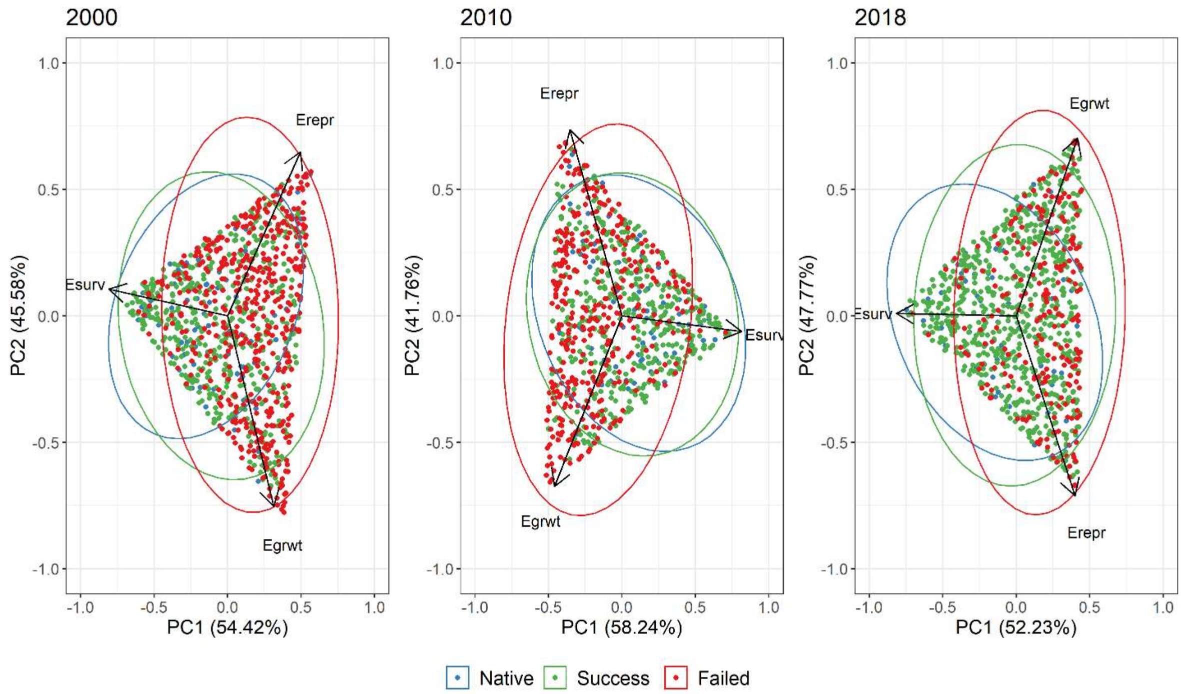

Figure 10: Life-history strategy similarity between the native community (blue) and successful (green) and failed invaders (red) over the different invasion periods. Each point in the graph represents the life-history strategy of a species and arrows represent how the strategies (reproduction, survival and growth) are related to the principal components.

Discussion

Invasion success increased over the years, being affected with different intensity by species' life-history strategies, body size, degree of resource specialization and use of agriculture. We were able to test our model against classic hypothesis and theories that can be applied to biological invasions and most of our results are in accordance with the patterns predicted by those theories. Finally, the predominant life-history strategies of invaders changed over the time, initially being closer to the prevailing strategy of the native community and at the final stage comprising a wider subset of all the available possibilities.

Invasion success was determined by a conjuncture of factors, one of which being the degree of habitat specialization of the invader. Chesson's theory of co-occurrence states that diversity is favored in more heterogeneous systems, which, henceforth, also increases the propensity for invasion success (Chesson 2000b; Shea and Chesson 2002; Melbourne et al. 2007). In our system, the initial landscape configuration was close to one of spatial homogeneity but with a temporal fluctuation of resources and as the time progresses land-use changes increase even further this heterogeneity, as the natural vegetation cover decreases, and the number of agriculture patches increases. As expected, this led to a higher invasion success, with a smaller difference between the invasion success of habitat generalists and specialists species. Several population models reinforce those results and indicate that generalists persistence in the system is only possible in fluctuating and heterogeneous resources (e.g. Wilson and Yoshimura 1994; Nagelkerke and Menken 2013). While those models are focused towards discussing the evolutionary rise of generalists and specialists, their results fit in our discussion as we are also interested in how environment conditions allow the permanence of generalists and specialists in the system. We did not find a complete failure to occupy the system by generalists, as concluded by those population models, but this may be due to our system never being completely homogeneous. Moreover, as Chesson (2000b) predictions for species co-occurrence state, when our landscape had higher land-use heterogeneity there was a higher co-occurrence rate between the native community and the invaders. This pattern might reflect the changes we are actually seeing in the world, of a decline in specialists and a higher introduction of generalist species (Clavel et al. 2011). Although we created highly habitat specialized invaders, it is unlikely that invaders will match or even surpass the degree of specialization of natives, as specialization is an evolutionary event and, as a consequence, native have evolved over time to maximize the gains obtained from a specific resource (Futuyma and Moreno 1988; Kassen 2002). Introduced species are unlikely to have higher gains when compared to specialized natives, which is an explanation of why most invasive species are generalists (Fisher and Owens 2004) and why areas with a higher degree of conservation are less vulnerable to biological invasions (Shawn Smallwood 1994). Therefore, land-use changes cause the extinction of specialists and create conditions for the establishment of generalist invaders and the co-occurrence with the native species.

Nevertheless, it is likely that co-occurrence alone does not explain the magnitude of increase in invasive success. As the native cover loss advances, the native community suffered from the extinction of several species, with an average reduction in species richness of approximately 50% and a reduction in native abundance of 58%. This harsh reduction in the native community opens the possibility for a higher number of invaders to succeed in the system, as the resources previously occupied by natives are now vacant, especially those in agricultural areas. Resource availability has been demonstrated as one key determinant for invasion success (Davis and Pelsor 2001; Mata et al. 2013), factors that are favored by both the extinction of multiple species and individuals of the native community and the expansion of new resources poorly explored by natives. In our system, invaders had a minor advantage for utilizing the resources available at agriculture when compared to natives (maximum assimilation efficiency of 0.4 for invaders against 0.2 for natives), in a way that no invader could be considered an agriculture specialist species, so much that invaders still had higher efficiency from natural resources when compared to agriculture. Nevertheless, this minor difference was determinant for invaders to occupy agriculture areas, which were more likely to be avoided by natives while making decisions in the foraging step. The higher diet generalism was proposed as an explanation for invasive success in several studies (i.e. Cassey et al. 2004; Vazquez 2006; Crowder and Snyder 2010), a process which is even more determinant if the invaders are able to explore resources not utilized by the native community.

In the end invader success is also dependent on how invaders use resources, which has different benefits according to the landscape configuration (Gatto et al. 1989). According to our results, investing heavily in reproduction, which results in more offspring, shorter gestation period and earlier sexual maturity, has stronger negative consequences in a more homogeneous landscape and smaller, but still negative, effects at a more heterogeneous landscape. On the other hand, investment in survival had a slightly positive effect at more homogenous landscapes, and a neutral to positive effect at more heterogeneous landscapes. However, the optimal moment for investing in survival was at a transition point, in which the landscape still had a large natural cover, but agriculture was expanding in the system. This pattern is predicted to happen according to life-history theory, in which k-strategists are favored in more homogenous and stable environments and r-strategists are favored in more heterogeneous and variables systems (Stearns 1976). Life-history traits associated with k-strategists are delayed reproduction, iteroparity, small clutches, parental care, smaller reproduction effort, few offspring; while traits for r-strategists are the opposite. Several studies indicate that investing in reproduction is advantageous for invaders because it allows them to reduce the period in which the populations are more susceptible to negative demographic stochastic processes (Allee effect), common at the initial stages of the invasion in which abundance of invaders in the system is still low (Legendre et al. 1999; Sæther et al. 2004). As we did not include male individuals in the model, our system may fail to capture the full complexity of demographic stochasticity, such as difficulties in finding a mate, which could result in overestimation of the invasion success (Taylor and Hastings 2005). Therefore, it is possible that we are overestimating the effects of investing in reproduction, as this would allow small populations of invaders to more rapidly increase its numbers in the system, which would in turn increase the chances of reproducing and reduce the effects of demographic stochasticity. Nevertheless, it is likely that the overall pattern of reproduction having stronger negative effects in a more homogeneous landscape is unlikely to be altered by those modifications. Investing in reproduction demands a lot of effort and energy directed towards generating and sustaining the offspring (Speakman 2008b). Therefore, more heterogeneous landscapes may decrease the competitive effect between natives and invaders due to resource fluctuation and different degree of efficiency for the several resources. Under those conditions, invaders are more likely to mitigate the negative effects of reproduction, as there is a higher resource availability, and a rapid population growth would be optimal to avoid demographic stochasticity (Tilman 2004).

The existence of an optimal life-history strategy, in its turn, is also dependent on how species are interacting with the landscape. At the first moment, both native community and successful invaders converged towards a life-history strategy in which prioritizing survival was vital for species' persistence in the system. As time moves forward and the landscape begins to change in structure, species had to deal with a new source of variability that disrupts the previously established equilibrium. At this new stage, several species that were successful at the more homogeneous system fail to remain in the system and become extinct. This process by itself, gave space for new species to establish in the system. Nevertheless, those newcomers will only remain in the system if their life-history strategy allows them to overcome the competition for resources against other life-history strategies. At the final moment, the native community is still restricted to the predominant survival strategy, which was the ancient optimal strategy. Nevertheless, this new variable system cannot support all those individuals with the same strategy, which lead to the extinction of some, but not all, native species. Successful invaders were a broader subset of all possible life-history strategies, which may happen because of one of two reasons: the new landscape configuration opens up the possibility for more than a single optimal life-history strategy to persist in the system, co-occurrence theory predicts that more heterogeneous environments make it possible for more species to co-exist (Chesson 2000a); or this is still a transitory state with little competition and given more time several successful invaders will fail to remain in the system.

Invasion success is an interplay of complex environmental, spatial, temporal and biotic factors that come together to determine the result of a biological invasion (Hastings et al. 2005). In that way, any given model will possibly fail to represent all key aspects of the system. Nevertheless, it is always essential to take a critical point of view in order to prevent models to become overly simple and fail to capture the main processes responsible for the invasion outcome. In this study we may have oversimplified our individuals by relying only on females and failed to capture important spatial-demographic processes which may be essential for the success rate of different life-history strategies. Other than that, by only creating individuals within a single trophic level we may have underestimated the effect of predation and parasitism in invasion success (Liu and Stiling 2006). We also used a single method of colonization and did not explore the effect of propagule pressure, another factor frequently cited as determinant for invasion success (Lockwood et al. 2005). Notwithstanding, we do believe our model brings a new method to explore the theoretical and practical aspects of an invasion process an opens a wide array of possibilities to explore in detail the process of biological invasion. Invasions will always be individual processes, but if we seek to improve our ability to respond to the arrival of alien species, mechanistic models based on solid theoretical basis seems like a way of doing so.

We demonstrate here that rapid agriculture expansion and a consequent land-use conversion, like the one occurring at the MATOPIBA region, is a determinant process for invasion success. Invasion success increased in all aspects as agriculture expanded upon the native vegetation. Besides, apart from the absolute increase in invasion success, there is also a modification in the type of invasions that were successful in establishing in the landscape. Higher agriculture cover within the landscapes increases the amount of resources available to invaders, as the native community is not able to efficiently use those areas. As a consequence, agriculture may be a relevant sour of supply for species that are highly efficient in obtaining resources from it, which may lead to a high density of invaders that will, inevitably, occupy agriculture areas and cause damage to crops, just as it is with the feral pig (*Sus scrofa* Linnaeus, 1758) (Thurfjell et al. 2009). In addition, our model also reinforced the abrupt native species loss during rapid land-use conversion process. The loss of species and decrease in abundance, by itself, increases the availability of resources in the landscape and increases the likelihood for invaders to establish in the system. Finally, from an evolutionary point of view, the native community comprises species that were adapted to the original configuration of the landscape, in which a given set of life-history strategies were advantageous. With the land-use conversion, it is also possible that those life-history strategies are now harmful and native species will have a reduced fitness when compared to invaders with different life-history strategies.

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Concluding Remarks

Invasion prediction is not an easy task as, how we demonstrated; invasion success is determined by several intertwingled complex factors. Nevertheless, there are some valuable lessons to be taken from this study.

First of all, using only niche models to predict invasion outcomes is definitely an error prone method. Niche models are adequate to identify areas for the second invasion stage (colonization) and, even so, there is a possibility that those areas will be under- or overestimated, as there is a mismatch between species existing and fundamental niche that may cause modelling algorithms to fail to capture the real relation between the species and the environmental predictors. Other than the mismatch between the existing niche and the realised niche, which cause species not to be in equilibrium and may lead to even more troublesome scenarios.

Second, predicting the outcome of an invasion process, which includes the third and fourth stage (establishment and dispersal) requires understanding how the invader interacts with the native community and the landscape. Invader life-history strategy is relevant for invasion success. Nevertheless, this is highly dependent on the spatial configuration of the landscape and temporal fluctuation of resources. Therefore, models that intend to predict invasion outcome must, to some extent, be case-specific. However, a general framework based on mechanistic resource competition and energy budgets and life-history theory seems like a promising framework to do so.

Finally, during this thesis we identified several key processes that may be relevant for the model outcome. Including other trophic levels, creating individuals with sexual differences and, for birds and mammals, including the cost of thermoregulation, may lead to different results and produce more realistic outcomes. This thesis was only the beginning, there is a wide range of possibilities to explore considering the framework we started to develop here, related or not to biological invasions.