Alien vertebrate risk assessment and invasion pathway modelling

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A thesis submitted in fulfilment of the requirements for the Degree of Doctor of Philosophy

June 2017
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The University of Adelaide, South Australia

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Abstract

Alien species are a key driver of the ongoing biodiversity crisis. Changing patterns in the number and identity of transported alien species, and recent changes in the importance of different pathways for transporting alien species (e.g., recent decline in the role of acclimatisation societies vs. the increase in importance of the pet trade), means that there is a novel pool of alien species available for introduction. There is a pressing need to evaluate the biosecurity risks posed by these emergent alien species and their pathways. In this thesis, I focussed on unravelling the patterns and processes driving the transport, introduction, and establishment of novel vertebrate taxa (e.g., alien amphibians, reptiles, and fishes) in Australia and the world. Complementarily, I have also developed approaches to support the implementation of early detection activities for emergent alien reptile species.

My results have highlighted the large number of new alien vertebrates being transported around the world, and particularly in Australia. The wildlife trade transports a substantial portion of all alien vertebrates, whereas unintentional pathways (i.e., stowaways) move fewer numbers of alien vertebrates (in terms of species transported). My research found that propagule number, the minimum number of release events of an alien species, is the main predictor of establishment success of self-sustaining reproductive alien populations. My global analysis of the relationship between the trade in Nearctic pet turtles and their establishment success revealed the complexities associated with managing novel pathways. The probability of introduction of a turtle species in a country (release or escape into the recipient environment) relates to the number of turtles imported, whereas the probability of establishment was associated with propagule numbers (number of releases) but not the number of individuals imported. My research on the establishment of alien fishes in Australia demonstrated substantial modern changes in the importance of transport pathways, with the recent rise of the ornamental fish trade as the key source of new alien species. These shifts in the importance of pathways for alien fish transport have also altered the processes governing the establishment success of alien fishes in Australia.

The prevention of the establishment of new alien species is the best course for managing their potential impacts. However, even the best of prevention strategies cannot realistically aspire to be perfect. In order to be successful at preventing new alien species, it is important to implement early detection systems. I have developed and evaluated a quantitative approach for the early detection of alien reptiles on Christmas Island. The results

indicate that large surveying efforts have to be conducted to ensure the absence of new alien reptiles with confidence.

Drawing from the results of my research, I conclude with some suggestions to improve preventive management strategies for alien species. Particularly, I argue in favour of incorporating economic considerations in prevention strategies (e.g., the benefits of early detection activities vs. delayed intervention and eradication), conducting further research into the importance and drivers of different transport pathways, and examining potential management alternatives to species-based risk assessments.

Thesis Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint award of this degree.

I give consent to this copy of my thesis when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968.

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I acknowledge the support I have received for my research through the provision of an Australian Government Research Training Program Scholarship (International Postgraduate Research Scholarship /Australian Postgraduate Award).

Pablo García Díaz
Christchurch, June 2017

Acknowledgements

Thus, if my intellectual creativity and mental instability were logically linked
as reflecting the upside and downside of the same genetic and developmental trajectory,
then I best see them together
Robert Trivers, an introductory comment to the chapter *Parent-offspring conflict* in his book
Natural selection and social theory

Aw, you can come up with statistics to prove anything, Kent.
Forty percent of all people know that
Homer Simpson in *Homer the Vigilante*

If we believe there's even a one percent chance that he is our enemy,
we have to take it as an absolute certainty
Bruce Wayne conducts a risk assessment on Superman in
Batman v Superman: Dawn of Justice

I am sucker for rare, threatened, and cryptic vertebrates, and I used to think that studying those species was the most complicated and challenging task in conservation biology. I was wrong. Working on preventing alien species for almost four years has proven to be way more complex than any other thing I have done so far. Amongst other factors, I will highlight two particularly challenging: the pervasive presence of uncertainties (which, I have always been taught are a bad thing but now I understand they are not necessarily so); and the need for using advanced quantitative methods for extracting information from all the noise in the data (you don't learn about this in your undergraduate years). The research presented in this thesis is the result of a process that, overall and in hindsight, has been really rewarding. Especially, my current grasp of how to construct and fit my own models for ecological systems was the main goal that I was pursuing when I decided to move to Adelaide. It took a hell lot of effort to learn new quantitative approaches, but it was worthwhile (or so I choose to think). I have to admit that I'm slightly disappointed in the

Australian fauna, not nearly as dangerous as they like to boast – four years co-habiting with venomous spiders, and chasing highly dangerous elapids and yet I'm still alive.

My PhD candidature has been sometimes tedious and I won't be able to submit my thesis if not for the support, help, and interest of a number of amazing people. I want to thank the support and help of my family, Dolores Diaz, Porfirio Garcia and Jorge Garcia. This work would not have been possible without the support, guidance and mentorship of my supervisors, who often went well beyond the call of duty. Thank you very much, Phill Cassey, Josh Ross, and Andrew Woolnough - it's been fun and I hope you have enjoyed as much as I have. I am very aware of my stubbornness and perhaps even strong character, I acknowledge your efforts in supervising me. J. Virtue was an excellent supervisor during my industry placement with Biosecurity South Australia.

The nature of my research implied compiling and curating data from a range of sources. A lot of people have collaborated providing data for my research, the list would be very long, but I do remember all of you. Nonetheless, I would like to make a special mention to M. Hutchinson, P. Bird, T. Wittmann, E. Smee, T. Prowse, the Office of Law Enforcement (United States Fish and Wildlife Service), and the Department of Agriculture and Water Resources (Australian Government) for their important contribution supporting my data-collection and curation efforts.

C. Ayres, M. Vall-llosera, M. Lurgi, K. Wells, D. Ramsey, V. Arevalo, T. Prowse, T. Buckmaster, S. Delean, M. Christy, and J. Virtue also deserve a special shoot out for their genuine interest in my work (including discussing my research with me), which has improved my work quite a lot. Also, thanks for your friendship and interest in going birdwatching and 'snaking' with me. The research presented in Chapter 6 (surveillance for detecting alien reptiles in Christmas Island), was a bit complex in several dimensions - it would not have been possible without the collaboration and support provided by the all the staff of the Christmas Island National Park, the Christmas Island Natural Resource Management Board, and the Department of Agriculture and Water Resources (Indian Ocean). The research on Christmas Island was conducted under permit number '*CIN_2015_5'* (Christmas Island National Park, Director of National Parks, Australian Government) and a '*Licence to undertake research activities on regulated crown land*'. The research was approved by the University of Adelaide Animal Ethics Committee (approval number '*S-2014-155*'). I want to acknowledge all my co-authors, listed in each chapter, the research presented here has been possible thanks to your collaboration. Thanks to all my colleagues and friends in Australia and Spain for making the process of a PhD candidature a bit less painful.

My PhD is part of the Invasive Animals CRC Project (1L4) in the 'National incursions response system' Theme of the 'Land pests' Program. The IA CRC funded my research through a PhD scholarship, funding to attend the workshop 'Bayesian Modelling using R' (School of Mathematics and Physics, Uni. Queensland), and the 2014 IA CRC Student Grant. I have benefited a lot from the annual workshops ran by the IA CRC as part of its 'Balanced Research Program', and I want to thank T. Buckmaster for his continuous support.

In preparing this final version of my PhD thesis, I want to acknowledge the revisions of the two examiners, Dr Robert Reed and an anonymous examiner. Their comments and suggestions helped me improve this thesis.

Repeating the words in the Thesis Declaration, just in case, I acknowledge the support I have received for my research through the provision of an Australian Government Research Training Program Scholarship (International Postgraduate Research Scholarship /Australian Postgraduate Award). Part of the research presented here used computing services provided by eRSA to the Invasion Ecology Group (University of Adelaide).

Concluding this section - to cold, nice Aussie beer! Outstanding mention to Coopers Pale Ale, Little Creatures, and Fat Yak Pacific Ale, for their role in inspiring me, my ideas, and my writing. (This statement is not, by any means, an admission of alcoholism)

Chapter 1. General Introduction

Introductory Background

Global biodiversity is experiencing an ongoing extinction crisis due to the detrimental effects of human activities on the environment (Pereira et al. 2012; Pimm et al. 2014; Ceballos et al. 2015; Magurran 2016). The adverse impacts of alien vertebrates have contributed substantially to this biodiversity crisis, being considered the second most important cause of current biodiversity loss and the leading cause of plant and animal extinctions since the 16th century (Clavero et al. 2009; Murphy and Romanuk 2014; Bellard et al. 2016; Maxwell et al. 2016). The impacts of alien vertebrates also produce substantial economic and social impacts (Pimentel et al. 2005; Vilà et al. 2010; Russell et al. 2015; Hoffmann and Broadhurst 2016). For example, it is estimated that alien vertebrates cost at least £ 409 million annually to Great Britain and at least AUD 720 million annually in Australia (McLeod 2004; Hulme et al. 2009; Williams et al. 2010; Hoffmann and Broadhurst 2016). In the social dimension, co-existing human values have resulted in some alien species being simultaneously considered as both beneficial and harmful, leading to conflicts over their proper management (White et al. 2008; Marshall et al. 2011; Marchetti and Engstrom 2016; Russell and Blackburn 2017).

The continuing development of human society and associated accelerating globalisation are changing the nature of the pathways that transport alien vertebrates, resulting in an increase in the number of species transported worldwide through emergent pathways (García-Berthou et al. 2005; Pyšek et al. 2011; Hulme 2015; Early et al. 2016; Saul et al. 2016; Turbelin et al. 2016). Moreover, these new pathways are enabling the transport of a novel pool of alien vertebrates, which are different from those transported on pathways dominant in the past. The intentional release of alien vertebrates by acclimatisation societies (especially fishes, mammals, and birds) during the European colonisation and settlement in areas around the globe has given way to much more subtle pathways, particularly the wildlife and the unintentional transport of species hitchhiking alongside people and commodities (Lever 1992; Jeschke and Strayer 2005; Hulme et al. 2015; Su et al. 2016; Dyer et al. 2017). Additionally, some of the novel pathways such as the aquaculture production and ornamental fish trade, have been growing for the last three decades (Fig. 1.1), posing an increasing threat as a source of new alien fish species. In summary, globalisation and evolution of human societies has shaped and modified the rates and composition of alien species' introductions worldwide, leading to the emergence of novel pathways and new alien vertebrates.

Unfortunately, the emergence of transport pathways and the increasing numbers of alien vertebrates are not matched by the management capabilities and capacities of the countries in the world (Early et al. 2016), suggesting an impending growth in the magnitude of impacts produced by alien vertebrates.

Target 9 of the Aichi Biodiversity Targets (Convention on Biological Diversity Strategic Plan for Biodiversity, 2011-2020; https://www.cbd.int/sp/targets/rationale/target-9) and, recently, the International Union for Conservation of Nature Honolulu Challenge on Invasive Species (https://www.iucn.org/theme/species/our-work/invasive-species/honolulu-challenge-invasive-alien-species) have recognised the central importance of tackling the mounting problem of alien species. Prevention has been demonstrated to be the best approach to managing alien vertebrates, especially considering the forecasted increase in the numbers of potential alien species transported around the world (Leung et al. 2002; Lodge et al. 2006; Keller and Springborn 2013; Early et al. 2016). Alien vertebrates cannot cause ecological impacts if they are never released into the new environments, although economic and social impacts may arise even without the alien species being present at large (e.g., the economic benefits produced by the pet trade). Strategies focussing on preventing new species establishing (see Fig. 1.2) are also the most sensible in economic terms (Fig. 1.3) (Keller et al. 2007; Springborn et al. 2011; Keller and Springborn 2013; Lodge et al. 2016).

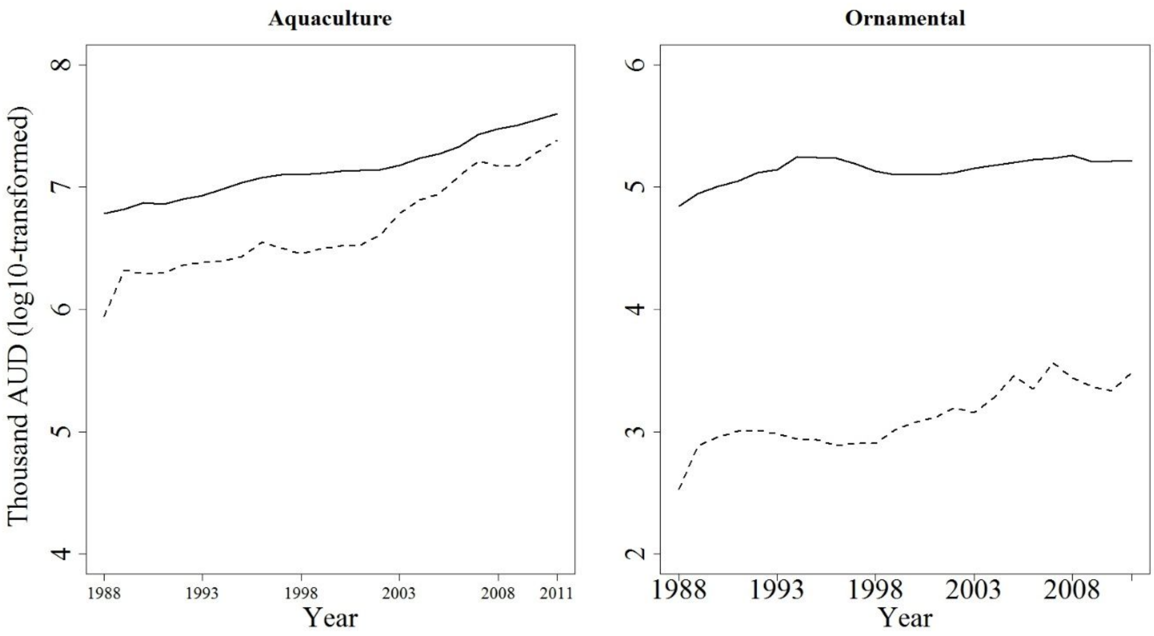
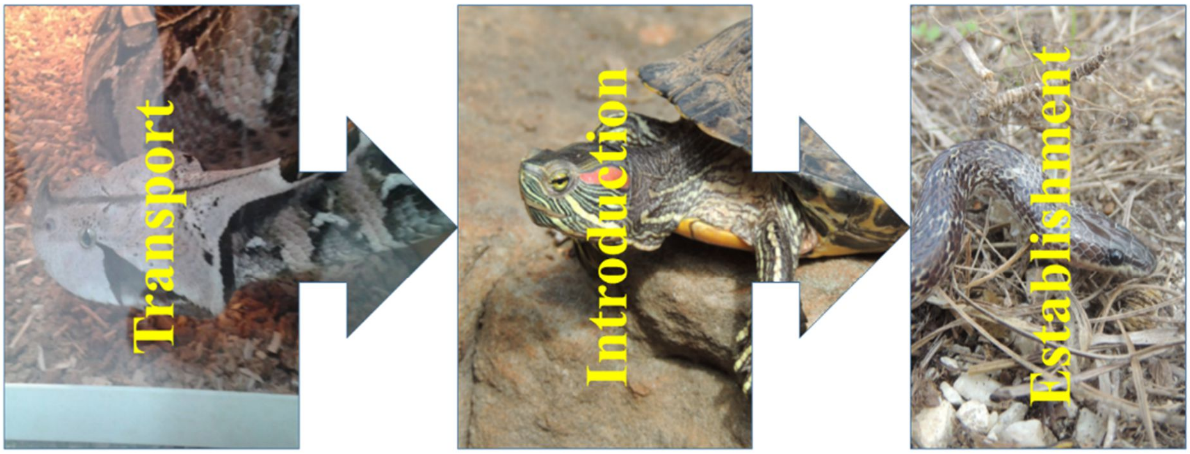


Fig. 1.1. Trends in the value of aquaculture and ornamental fishes in the world (solid line) and in Australia (dashed line). Graph constructed using official FAO Fisheries & Aquaculture data obtained using the FishStat Plus software (http://www.fao.org/fishery/statistics/software/fishstat/en).



Movement of species outside their native range

Release or escape into the wild

Formation of self-sustaining, reproductive, populations

Fig. 1.2. The three first stages of the invasion pathway representing the focus of the research presented in this thesis. Preventive management actions tackle these three stages and aim to avoid the establishment of new alien species. Note that impacts can occur at any stage of the invasion pathway. Modified from Blackburn et al. (2011) and Lockwood et al. (2013). Photos represent alien reptiles reported in Australia and studied during the course of the research presented in this thesis. From left to the right: Gaboon viper (*Bitis gabonica*) kept in captivity (transport; see Chapter 4); a Red-eared slider turtle (*Trachemys scripta elegans*) found in Adelaide, South Australia (introduction; see Chapters 3 and 4); and a Wolf snake (*Lycodon capucinus*), an alien snake widespread on Christmas Island (establishment; see Chapters 4 and 6). All photos by Pablo García Díaz.

In particular, the crucial need for identifying, understanding, prioritising and managing transport pathways is well recognised for successfully preventing the introduction and impacts of new alien species (McGeoch et al. 2015; Latombe et al. 2016; Woodford et al. 2016). Although more information does not always equates to better management in conservation (Canessa et al. 2015), it is clear that a gap in our knowledge regarding the potential risks posed by emergent pathways and alien vertebrates hinders the range and efficacy of management strategies, including regulatory interventions, that can be deployed. Insights into the determinants and dynamics of these pathways and groups of alien vertebrates are essential for developing pro-active strategies to avoid their potential impacts (Clout and Williams 2009).

Alien species affect each and every country in the world and this requires specific evidence-informed management strategies and policies. In this thesis there is a focus on case studies of emergent alien vertebrates in Australia, building on the long and accredited tradition of managing alien vertebrates in this country (Wilson and Weber 2002; Clout and

Williams 2009). This culture provided me with a unique opportunity to research, in detail, questions of high relevance to the global management of alien emergent vertebrates. In particular, there are three features of the Australian system that are worth highlighting here: (i) a variety of management strategies and regulatory frameworks are already existing for dealing with alien vertebrates (Turbelin et al. 2016), which implies that I can examine their efficacy and recommend potential improvements; (ii) federal and state biosecurity agencies report on alien species detected in their jurisdictions, a sound basis for investigating and understanding transport pathways and management strategies; and (iii) there is a willingness to incorporate scientific knowledge into the planning and implementation of alien vertebrate management strategies, which in turn means an interest for collaboration between scientists and managers. Ideally, the conclusions drawn from the case studies presented here can be used to inform the ongoing efforts in developing and delivering good policies in other regions of the world (Hulme et al. 2009; Gray et al. 2015; Tollington et al. 2015; Early et al. 2016; US Department of the Interior 2016), to form a best practice in evidence-based policy-making (Barber 2015).

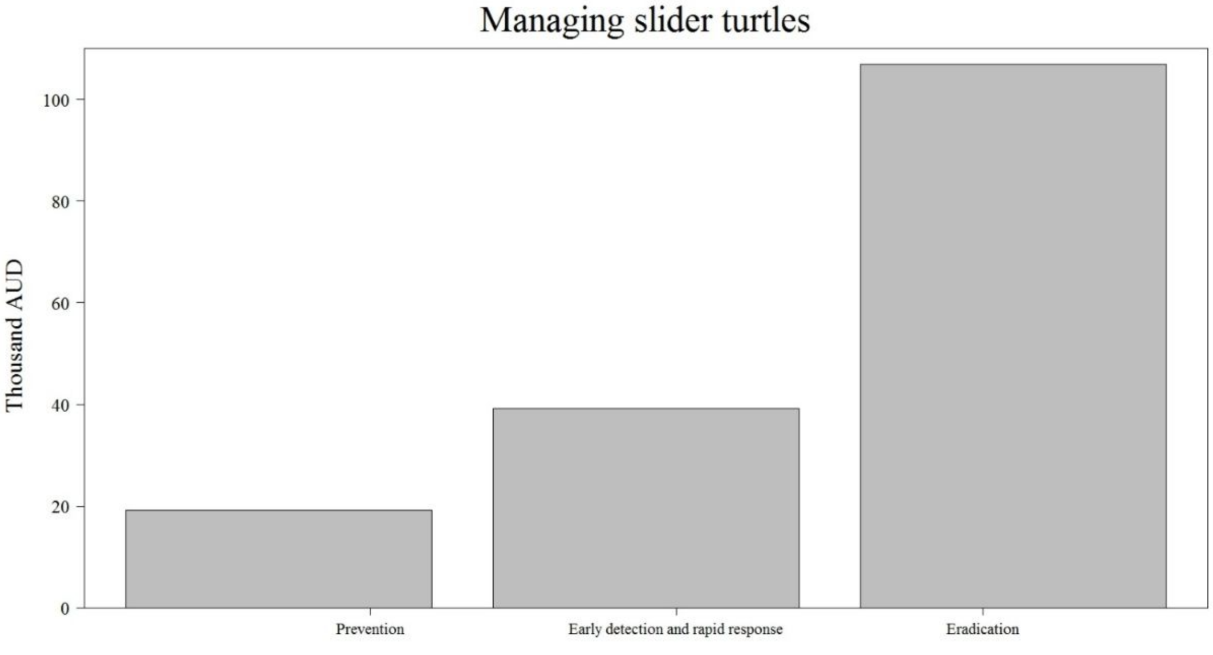


Fig. 1.3. The estimated annual economic costs of three management strategies for alien Red-eared slider turtles (*Trachemys scripta elegans*). Estimates are for the Australian states of Victoria (prevention and early detection, 2011-2016; A. Kay, Department of Economic Development, Jobs, Transport and Resources, comm. pers.) and Queensland, 2004-2013 (Biosecurity Queensland 2016). The combined annual cost was AU$ 121157.

Research Framework: The Invasion Pathway and Risk Assessments

The invasion pathway (Fig. 1.2) provides the conceptual framework for studying and managing biological invasions (Lodge et al. 2006; Blackburn et al. 2011; Leung et al. 2012). The invasion pathway proposes a series of successive stages that an alien species overcomes to become an invasive species, and is commonly conceptualised as being composed of four stages (the three stages in Fig. 1.2 plus spread, not studied in this thesis). Importantly, preventive and early response management activities tackle all of these first three stages.

The invasion pathway and the different transport vectors for alien vertebrates provide the conceptual background for the research presented here. Throughout this thesis, the common approach employed was to compile information on three groups of emerging alien vertebrates in Australia and the world (Henderson et al. 2011; Hulme 2015), amphibians, reptiles, and fishes, and develop statistical models for understanding the dynamics and characteristics of different transport pathways and the factors that determine the successful transit of alien species through the first three stages of the invasion pathway.

The results and conclusions obtained from the analyses can be used to develop and construct risk assessments, which in turn are fundamental to the process of prioritising and managing alien vertebrates and transport pathways (Keller and Springborn 2013; McGeoch et al. 2015; Lodge et al. 2016). Risk assessments are a key tool in environmental management (Burgman 2005; Linkov et al. 2006; Covello and Merkhoher 2013), and are increasingly used in alien species management (a search in Google Scholar, 17/01/2017, with the terms *risk assessment alien species* returned over 100k results). In its broadest form, risk assessments attempt to estimate the likelihood of a given event and the consequences of such an event should it happen (Burgman 2005; Covello and Merkhoher 2013).

Translated into alien species management, a risk assessment would frequently attempt to evaluate the likelihood of transitioning through any stage of the invasion pathway and the resulting impact. Lodge et al. (2016) have recently provided an extensive review of risk assessment methods for alien species management. More frequently, however, it is only the risk of establishment that is evaluated in alien vertebrate management (Keller and Springborn 2013; Faulkner et al. 2016). This is because impacts are exceedingly difficult to predict, chiefly due to the limited generalisations that can be drawn from alien species impact research (Ricciardi and Simberloff 2009; Ricciardi et al. 2013; Jeschke et al. 2014). Recent research promises new advances in the area of assessing and predicting alien species' ecological impacts, notably the possibility of achieving a consensual and semi-objective methodology to evaluate impacts (Kumschick et al. 2012; Kumschick and Richardson 2013;

Howeth et al. 2016; Latombe et al. 2016; Dick et al. 2017; Kumschick et al. 2017; Turbé et al. 2017). Establishment success serves as a proxy for impacts and for potential management costs, given that established populations of alien amphibians, reptiles, and fishes are difficult to eradicate and will always produce long-running impacts requiring a serious commitment to long-term control (Strayer 2010; Dorcas and Willson 2011; Ricciardi et al. 2013; Reed et al. 2016). The management and policing implications of risk assessments involve, for example, banning the trade in those alien species that are deemed to pose an untenable risk, and targeting quarantine inspection efforts on commodities potentially transporting risky species (Bacon et al. 2012; Keller and Springborn 2013; Heersink et al. 2015; Faulkner et al. 2016; Lodge et al. 2016). Nonetheless, the outcomes of risk assessments for alien species tend to be interpreted conservatively by risk-averse managers and decision-makers who apply the precautionary principle and forbid species for which current risk assessment may not be sufficiently sensitive to evaluate their risk realistically (Hone et al. 2015; Groves and Game 2016). Evidence-informed risk assessments are thus fundamental to good management and regulation practices.

Species-based risk assessments are routinely conducted in Australia for managing the importation of the three taxonomic groups analysed in this thesis (Bomford et al. 2005; Bomford 2008). The importation of alien amphibians and reptiles for private purposes (i.e., pet keeping) is prohibited under the *Environment Biodiversity Protection Act 1999* (https://www.environment.gov.au/epbc). Applying for a permit to import alien amphibians or reptiles for purposes such as public displays in zoos also requires conducting a risk assessment (Bomford et al. 2005; Cassey and Hogg 2015). The importation of alien fish for aquaculture is prohibited, whereas the importation of ornamental fish is regulated by the *EPBC Act 1999 List of Specimens Taken to be Suitable for Live Import* informed by species-based risk assessments (https://www.legislation.gov.au/Details/F2015C00959) (Bomford and Glover 2004; Whittington and Chong 2007; Deveney and Beyer 2014). Additionally, each state in Australia has implemented its own legislation, and produced lists of prohibited alien fish within its jurisdiction. Species-specific risk assessments are complemented by compulsory quarantining, where imported animals are maintained in quarantine facilities and screened to ensure that they are not acting as vectors for alien parasites and diseases (Whittington and Chong 2007; Becker et al. 2014; Rimmer et al. 2015).

Given that impacts of alien species may occur at any stage of the invasion pathway (Fig. 1.2), in my research I have evaluated the factors that influence the transit of alien amphibians, reptiles, and fishes through the three first stages as potential sources of risks.

Nonetheless, I have also emphasised research into establishment success of the three alien vertebrate groups. Risk assessments and the comparative study of the transit of alien vertebrates through the invasion pathway pose important analytical challenges, such as the inherent uncertainties due to natural variations, measurement error, and structural statistical model uncertainty (Regan et al. 2002; Sol et al. 2008; Leung et al. 2012; Kéry and Royle 2016). I have adopted a strong quantitative approach in this thesis in order to deliver reliable conclusions while properly accounting for potential sources of uncertainty and biases in my analyses.

Preventive management strategies need to be complemented with early detection and rapid response strategies (Fig. 1.3), because a fully protective preventive management system is unattainable in reality. In order to provide a comprehensive picture of the risks and management actions available for dealing with emergent alien vertebrates, I have developed and tested a framework for the early detection of new introductions of alien reptiles.

Objectives and Overview

The research presented in this thesis uses quantitative methods with the main goal of informing management activities aimed at preventing the establishment and potential impacts of alien amphibians, reptiles, and fishes. More specifically, my thesis addresses the following set of objectives:

1. Provide an integrative analysis across transport pathways of the taxonomic composition and determinants of alien amphibian transport and introduction in Australia;
2. Understand the role of the wildlife trade (legal and illegal) as a source of alien reptiles in Australia and the world, including examining the factors that link the trade in alien reptiles with the process of invasion;
3. Assess gaps in the knowledge of the distribution of alien turtles in the world, and summarise priority countries for improving the completeness of alien species' inventories;
4. Study how the temporal dynamics of transport pathways have shaped the biogeography of alien fishes in Australia;
5. Examine the factors influencing alien fish richness in Australian drainages in two periods, pre-1970 and post-1970;

6. Quantify the reliability of historical models to predict alien fish richness in modern times in Australia;
7. Develop a quantitative framework to serve as a basis for planning and implementing early detection activities for alien reptiles;
8. Estimate how detection probabilities vary across alien reptile species and environments, guiding the design of early detection activities; and,
9. Provide robust quantitative methods for supporting the management of alien species;

In achieving these objectives, the core of my thesis has focussed on the factors that influence the transit of alien amphibians (Chapter 2), reptiles (Chapter 3 and 4), and fishes (Chapter 5) through the invasion pathway. Chapter 6 presents a framework for detecting and rapidly responding to new introductions. The final chapter (Chapter 7) provides a general discussion of the topics and results. A brief appraisal of the main results and conclusions of the data chapters follows (Chapters 2-6) is provided here:

- **Chapter 2:** ***Patterns of transport and introduction of alien amphibians in Australia.*** I examine the composition of the pool of alien amphibians that have been transported and subsequently introduced in Australia. Transported amphibians represented a biased taxonomic sample of all the extant amphibians within the same taxonomic families as transported species, whereas introduced amphibians were a random sample of all the transported species. Most of the transported and introduced amphibians were domestic species, native to some parts of Australia but introduced elsewhere inside the country. The models of the probability of transport and introduction supported the explanation that the two stages were determined by the ease with which alien amphibians can potentially be captured (intentionally or unintentionally) and maintained in captivity (for species in the trade pathway).

- **Chapter 3.** ***Understanding the biological invasion risk posed by the global wildlife trade: propagule pressure drives the introduction and establishment of Nearctic turtles*.**
  The pet trade is a major source for new alien species. In this Chapter, I study the link between the dynamics of the global trade in pet Nearctic turtles and their risk of introduction and establishment in countries around the world. I used data on exports

of Nearctic turtles from the USA provided by United States Fish and Wildlife Service (the LEMIS database) coupled with a novel hierarchical model to infer the factors that influence the introduction and establishment of Nearctic turtles in the world. The probability of introduction in a country was related to the total number of turtles imported and the age at maturity of the species. In this Chapter, I researched the probability of establishment of slider turtles (*Trachemys scripta*) around the world. Establishment success was affected by the propagule number (minimum number of release events in a country) and the number of native turtle species in the country (interpreted as an indicator of habitat availability for turtles). Additionally, the results of the hierarchical models suggest that the presence of alien Nearctic turtles in some countries has been overlooked and not yet reported.

- **Chapter 4.** ***The illegal wildlife trade is a likely source of alien species.***
  Blanket bans on the trade of alien species may lead to perverse policy outcomes, potentially fostering the illegal trade in those species. This may create an incentive for the transport of risky alien species. In this Chapter, I used a comprehensive database of the identities of 28 illegally kept reptile species in the state of Victoria (Australia) to evaluate the potential risk, in terms of the probability of establishment, posed by this pathway. Firstly, I developed a model for predicting the establishment success of alien reptiles in Australia. Small reptiles (body length) that had been introduced more frequently in the wild (high propagule pressure) were more likely to become established relative to species that failed in establishing in Australia. Secondly, I used the previous predictive model to assess 28 alien reptile species. The screening process revealed substantial variability in the establishment risk across species, and a whole-pathway analysis indicated that five out of the 28 species may likely become established if ever released in Australia. Therefore, the illegal wildlife trade represents a potential reservoir of alien species.

- **Chapter 5.** ***Transport pathways shape the biogeography of alien freshwater fishes.***
  Human activities may change the number and taxonomic identity of species transported via different pathways, potentially leading to parallel shifts in the biogeography of alien species. In this Chapter, I explore the patterns and processes of alien freshwater fish richness in Australia in two periods (pre-1970 and post-1970).

The two periods were exclusively characterised by the distinctive dominance of the acclimatisation and ornamental fish pathways (pre-1970 and post-1970, respectively). Species richness models revealed that the changes in the number of species transported by the two pathways in the two periods altered the underlying processes influencing alien freshwater fish occurrence. Pre-1970, alien fishes were most likely to occur in inland drainages characterised by a high human influence, a higher altitude, and a flatter terrain than the average across drainages. Conversely, my results indicate that post-1970 alien fishes were most likely to occur in northern and south-western tropical and sub-tropical coastal drainages, characterised by being steeper and warmer (in summer) than the average across drainages. The findings presented in this Chapter demonstrate that changes in human uses for wildlife result in concomitant changes in transport pathways and, in turn, in shifts in the influence of different processes upon alien species' biogeography.

- **Chapter 6.** ***A framework for designing and implementing early detection surveys for alien reptiles.***

  Effective rapid responses for preventing the establishment of new alien species need early detection activities to be in place. In the final data chapter of my PhD thesis, I developed and tested a quantitative framework for the implementation of early detection activities. The framework is structured around a set of successive stages and draws elements from spatial and strategic environmental planning. I used the case study of early detection activities for detecting five alien reptile species in Christmas Island to demonstrate the application of the framework and test its reliability. Detection probabilities tend to increase with longer surveying times, and night surveys were better for detecting alien reptiles. I applied Bayes' rule to estimate the surveying effort required for attaining a high confidence in the absence of alien reptiles, given none were detected. The posterior estimates indicate that an extensive surveying effort had to be deployed to ensure the absence of alien reptiles confidently. Designing and conducting early detection activities for alien reptiles would be a challenging yet fundamental task. In this Chapter, I provide robust and tested tools for aiding and informing procedures for deploying early detection activities.

Statement of Authorship

Title of Paper	Patterns of transport and introduction of exotic amphibians in Australia
Publication Status	☑ Published ☐ Accepted for Publication ☐ Submitted for Publication ☐ Unpublished and Unsubmitted work written in manuscript style
Publication Details	García-Díaz, P. & Cassey, P. (2014). Patterns of transport and introduction of exotic amphibians in Australia. *Diversity and Distributions*, 21(4): 455-466. 10.1111/ddi.12176

Principal Author

Name of Principal Author (Candidate)	Pablo Garcia Diaz		
Contribution to the Paper	Planned and developed the research, compiled the data, developed the models and analysed the data, written the manuscript.		
Overall percentage (%)	80%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	15/02/2017

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Please cut and paste additional co-author panels here as required.

Name of Co-Author	Associate Professor Phillip Cassey		
Contribution to the Paper	Contributed ideas to the development of the research, revised and edited the manuscript		
Signature		Date	15/02/2017

Chapter 2. Patterns of Transport and Introduction of Alien Amphibians in Australia

Pablo García-Díaz · Phillip Cassey

Publication: García-Díaz, P. & Cassey, P. (2014). Patterns of transport and introduction of exotic amphibians in Australia. *Diversity and Distributions*, 20(4): 455-466. doi: 10.1111/ddi.12176.

Code accessibility: the annotated code for running the analyses in this Chapter is publically available at: https://github.com/pablogarciadiaz/PhD-thesis-code

Data accessibility: the updated database of transported and introduced amphibians in Australia will be publically available from FigShare after the embargo expires. For the purposes of marking, the updated database can be downloaded from the following link: https://figshare.com/s/0f71a94416dc9661f5a7.

Appendix: material accompanying this chapter can be found at Appendix 1 of this thesis.

Abstract

Research on amphibian invasions has largely focused on the likelihood of successful establishment, while analysis of the previous stages in the invasion pathway (transport and introduction) is scarce despite its critical importance. Here we investigate the patterns of taxonomic and geographic non-randomness as well as the factors affecting the transport and introduction of amphibians in Australia. We compiled and analysed a database on the identity of transported and introduced amphibians. First, we tested for taxonomic (family-level) and geographic non-randomness by comparing transported and introduced species with all extant caudates and anurans. Second, we constructed models to examine the influence of different factors upon the probability of transport and introduction of amphibians in Australia. Amphibians were transported via two main pathways: trade (71 species) and stowaway (38 species). In addition, several species were transported through both pathways. Transported species represented a taxonomic and geographic non-random sample of all extant amphibian species. Conversely, introduced species constituted a random sample of the transported amphibians. Regardless of the transport pathway, the probability of transport of amphibians increased with increasing extent of their native geographical range. A large number of native Australian species have been transported outside their naturally occurring ranges, representing over 65% of the introduced species. Introduction is strongly correlated to the transport pathway, i.e. species transported through two pathways were more likely to be released or escape from captivity. The probability of amphibians being transported and introduced to, or within, Australia is critically affected by their availability to be captured, bred and housed in captivity. Management strategies to prevent the future introduction and establishment of new amphibians need to include the people involved in species trade, as well as continued vigilance by biosecurity and custom agencies.

Keywords: Anura, Caudata, exotic species, invasion pathway, wildlife trade

Introduction

Recent human activities have transported (intentionally or accidentally) an increasing number of species across unprecedented large distances, which have otherwise been impossible to achieve by natural dispersal alone (Levine and D'Antonio 2003; Wilson et al. 2009; Wilson et al. 2016). The majority of transported species do not succeed in establishing alien populations in the environments they encounter, but those that do establish self-sustaining populations may eventually spread and colonize their recipient environment, becoming invasive pests (Blackburn et al. 2011; Leung et al. 2012; Lockwood et al. 2013). Invasive vertebrates can negatively impact native communities through a variety of interactions (Simberloff et al. 2012; Lockwood et al. 2013; Ricciardi et al. 2013). Predicting the establishment and risk (including the environmental, economic, and social costs) of new invasive species is an issue of considerable global concern (Clout and Williams 2009; Leung et al. 2012).

Invasions are shaped by the characteristics of the species which transit the invasion pathway (Blackburn et al. 2011). These taxa frequently represent a non-random subset of all extant species (Blackburn and Cassey 2007; Tingley et al. 2010; Van Wilgen et al. 2010). These patterns probably reflect the migratory and colonising movements of humans, the international trade network (McAusland and Costello 2004; Westphal et al. 2008), and the spatial distribution of vertebrate species richness in the world (Orme et al. 2005). In turn, the existence of these non-random patterns suggests that selected species are likely to share several characteristics (Blackburn and Duncan 2001a; Kolar and Lodge 2001; Sol et al. 2012).

Transportation is thought to be strongly affected by the degree to which species are available for, or subject to, human activities (Cassey et al. 2004b; Blackburn et al. 2009; Wilson et al. 2009; Van Wilgen et al. 2010). For example, pet traders usually prefer species with particular attributes, like large body size or conspicuous colours, which make them attractive to breeders and/or private keepers (Cassey et al. 2004b; Alacs and Georges 2008; Carrete and Tella 2008; Van Wilgen et al. 2010; Tapley et al. 2011; Masin et al. 2013). Introduction, establishment and spread are most likely driven by species- and location-specific characteristics as well as by the initial number of individuals released (Kolar and Lodge 2001; Duncan et al. 2003; Lockwood et al. 2005; Hayes and Barry 2008; Leung et al. 2012).

Alien amphibians are a serious, although understudied, threat to biodiversity (Kraus 2009, 2015; Measey et al. 2016). Examples include the devastating impact of the Cane toad, *Rhinella marina* (Linnaeus, 1758), on native biological communities of Australia (Shine 2010), and the introduction of the American bullfrog, *Lithobates catesbeianus* (Shaw, 1802), and the African clawed frog, *Xenopus laevis* (Daudin, 1802), globally (Kraus 2009). Cane toads are fatally toxic to many native Australian predators and have precipitated population declines of these predators (Shine, 2010), whereas the two latter species have spread chytridiomycosis (Weldon et al. 2004; Garner et al. 2006), an epizootic fungus responsible for the decline and extinction of several amphibian species (Kilpatrick et al. 2010). Alien amphibians are considered an emergent threat to Australian biosecurity (Bomford et al. 2005) and an increasing number of new incursions into the country have been detected during the last decade (Henderson et al. 2011). In other developed countries of the world, like the United Kingdom and the United States, there has been a concomitant increase in the live trade of amphibians during the last decade (Schlaepfer et al. 2005; Smith et al. 2009; Tapley et al. 2011), increasing the chances of introductions of alien species.

Recent research has revealed the importance of climate matching (between native and recipient environments), life-history traits (particularly attaining maturity at younger ages) and the transport pathways in explaining introduction and establishment success of amphibians (Bomford et al. 2009b; Kraus 2009; Van Wilgen et al. 2009; Tingley et al. 2010; Van Wilgen et al. 2010; Poessel et al. 2012; Rago et al. 2012; Van Wilgen and Richardson 2012; Allen et al. 2013; Allen et al. 2017). Many of these results are in concordance with other alien vertebrate studies; particularly birds (Blackburn and Duncan 2001b; Cassey et al. 2004b; Jeschke and Strayer 2006; Blackburn et al. 2009; Sol et al. 2012), mammals (Forsyth et al. 2004; Jeschke and Strayer 2006; Bomford et al. 2009a) and fish (Kolar and Lodge 2002; Jeschke and Strayer 2006; García-Berthou 2007; Bomford et al. 2010).

Until now, the vast majority of research on alien amphibians has focused on establishment success, missing the key roles of transport (movement of species beyond their native range) and introduction (release, or escape, of transported individuals into the wild) (Puth and Post 2005; Blackburn et al. 2011). To fill this knowledge gap we compiled and analysed a database on the identity of transported and introduced (versus non-introduced) amphibians in Australia. Our specific aims were to assess: (1) the patterns of geographic and taxonomic non-randomness in these first stages of the invasion pathway; (2) whether the observed patterns of introduction and transport correlate to specific characteristics of the amphibians (body size, threat status, native geographic range extension, and latitudinal and longitudinal distribution mid-points) previously shown as determinants of introduction and establishment success in vertebrates; (3) whether international imports to Australia and the international flight network of Australia affects the unintentional probability of amphibian transport; and (4) whether intentional and accidental transport influences the likelihood of introduction. To the best of our knowledge, this is the first time that the factors affecting the transport stage, including trade and stowaways, for alien amphibians has been quantitatively studied (see also the account of Christy *et al.*, 2007) and therefore represents a key step in understanding and predicting amphibian invasions.

Material and Methods

We defined a transported amphibian species as one that has been moved outside its native range (Blackburn et al. 2011; Lockwood et al. 2013). We note that this definition also includes the transport of native Australian species to localities outside their naturally occurring distribution (i.e., domestic exotics; *sensu* Guo & Ricklefs, 2010). An introduced species was defined as one that has been released, or has escaped, into the wild (Blackburn et al. 2011; Lockwood et al. 2013). We compiled the first database for amphibians transported and introduced in Australia. We collated the data on transported amphibians from 26 sources (see data accessibility statement) including scientific works, published legislation of Commonwealth and state governments of Australia, the CITES database (Convention on International Trade in Endangered Species of Wild Fauna and Flora), and classified advertisement web pages in Australia. Data on introduced species were obtained from Kraus (2009) and Henderson *et al.* (2011). A total of 19 species were considered to be introduced in Australia. Taxonomy follows that of Frost *et al.* (2006) , including the modifications of the International Union for Conservation of Nature (IUCN 2012), and Amphibia web (http://amphibiaweb.org/index.html).

We detected 97 species of alien amphibians transported to or within Australia in the period 1971-2011 (see data accessibility statement). Although we have consulted a large number of data sources to construct our database, it is possible that it does not include all transported amphibians. To estimate the reliability of our database we conducted a mark-recapture analysis using the presence/absence of each species in each different source. We have used the POPAN open-population model (Schwarz and Arnason 1996) implemented in MARK (White and Burnham 1999) for this analysis. We dealt with the different scope of the data sources by conducting analyses separately for alien and Australian species. In these analyses, each species was represented by an individual history of presence/absence in each of the data sources that provided the identity of more than one transported amphibian (range: 3-47 species). Sixteen POPAN models were run, in which we varied the parameters (survival probabilities, probabilities of entering the population and population size) to be source-specific as well as constant across all the sources. Model performance was assessed by means of an information-theoretic model selection approach (Burnham & Anderson, 2002; see statistical analysis for further details).

From the literature, we extracted nine different terms for defining the transport pathway of amphibians (see data accessibility statement). These were arranged into two categories based on whether the animals were transported intentionally or unintentionally: trade (including the terms 'pet trade', 'private keeping', 'intentional', 'zoo', 'research' and 'live import: non-commercial purposes, excluding household pets'); and stowaway ('cargo stowaway', 'accidentally entering' and 'nursery trade'). The first group includes 71 species and the second 38 species. Several species were transported through both pathways.

Threat status, extent of the native geographical range ($\log_{10}$km^2), latitudinal and longitudinal mid-point of the native distribution and body size have consistently been related to the transport and introduction stages of vertebrates (Cassey et al. 2004b; Blackburn et al. 2009; Tingley et al. 2010; Van Wilgen et al. 2010). These variables were obtained for each species from three sources: IUCN Red List (IUCN 2012), Amphibia web (http://amphibiaweb.org/index.html), the Encyclopedia of Life (http://eol.org/) and from Tyler and Knight (2011). Average body size was recorded as snout-vent length.

We expected unintentional transport of amphibians to be strongly influenced by the mobility of people, goods and services within and to Australia (Levine and D'Antonio 2003; McAusland and Costello 2004; Taylor and Irwin 2004; Christy et al. 2007; Westphal et al. 2008). We have obtained data on the annual value of imports to Australia (in US$) for 187 countries of the world from Lenzen *et al*. (2012; http://www.worldmrio.com/) for the period 1988-2012, and used these data as a proxy of the volume of the imports to Australia. We expected higher probabilities of transport associated to higher volumes of imports. We have also obtained data on the annual number of international flights per airport and the number of seats per airplane per airport travelling to Australia for the period 1996-2010 (from OAG Aviation Worldwide Ltd: http://analytics.oag.com/home/). We mapped the average value of imports, the annual average number of seats per airplane and the annual average number of airplanes flying to Australia in Arc GIS 10.0 (ESRI, Redland, CA, USA) and we constructed a worldwide grid (10º x 10º). The value of imports from 187 countries into Australia, the annual number of seats per airplane and the annual number of flights per airport showed no temporal trends: Imports (linear mixed model using country as random factor: slope = 3.70 ± 0.25 [estimate ± standard deviation], t-test for slope = 15.07, 4488 records, $p > 0.5$); Seats per airplane (linear mixed model using departure airport as random factor: slope = 0.68 ± 2.74, *t*-test for slope = 24.82, 40240 records, $p > 0.5$); Flights per airport (linear mixed model using departure airport as random factor: slope = 0.28 ± 0.01, *t*-test for slope= 33.77, 40249 records, $p > 0.5$). We therefore used their average values as proxies for the period for which we have data on amphibians (1971-2011).

Finally, we have assigned to each species transported a value of average imports, average number of planes and average number of seats per plane by calculating the interpolated grid value at the centre of the species distribution. These averaged values were used as variables in our models.

Statistical Analysis

We analysed the two different transport pathways independently, because the causes underlying these modes of transportation and their scopes differ greatly (Hulme et al. 2008; Wilson et al. 2009). First, we tested whether the transported amphibians are a random taxonomic sample, at the family level, of all extant species (Cassey et al. 2004b; Blackburn and Cassey 2007; Romagosa et al. 2009). Following Blackburn & Cassey (2007), we drew 10000 Monte Carlo random simulations, each one selecting from the pool of all 6940 extant amphibians a number of species equal to the observed number transported. We then calculated the expected number of species transported from each family under the hypothesis of a random-uniform distribution. We compared the observed and expected values considering all families together by means of paired permutation tests (Good 2005). We tested the differences between observed and expected values for each family individually by means of a Monte Carlo test. The resulting patterns of taxonomic non-randomness are particularly influenced by families with small numbers of extant species for which it is highly unlikely (by chance) that they would contain alien species. Geographical patterns of non-randomness in the origin of the transported amphibians were tested by comparing the latitudinal and longitudinal mid-points of the distribution of all extant amphibian species with those of transported species using also permutation tests.

We analysed correlates of transport for each of the two pathways. For the trade pathway, we considered the extent of the geographical native range, the conservation status (IUCN Red List categories; IUCN, 2012), and the longitudinal and latitudinal mid-point of the native distribution. For the stowaway pathway, we investigated the effects of extent of geographical native range, conservation status, longitudinal and latitudinal mid-point of the native distribution, average annual number of international flights, average number of seats per airplane, and the average estimated value of imports in the centre of the native range.

We compared the attributes of transported and non-transported amphibians through Generalized Linear Mixed Effects Models (Bolker et al. 2009) with a logit link function and binomially distributed errors. Amphibian family was included as a random effect to control for taxonomic non-independence (see Results). A set of models were tested for each pathway, and their performance was assessed by comparing the relative model support for each one (i.e., the weights of Akaike's information criterion corrected for small sample size, wAICc; Burnham & Anderson, 2002). We estimated evidence ratios by dividing the Akaike's weight of each model by the weight of the best model in the set. Finally, we calculated the conditional R^2 (percentage of the variance accounted for by the model) as described by Nakagawa & Schielzeth (2012) for GLMMs.

The selection of a set of non-transported species for comparison requires careful planning to avoid biasing the analysis (Cassey et al. 2004a). For drawing random samples of non-transported amphibians, we considered only species belonging to the same families as the transported amphibians. In order to obtain a reliable inference, the GLMMs were bootstrapped 1000 times (Good 2005). The coefficients of the best fitted models, Akaike's weights and R^2 values were calculated by bootstrapping (using the adjusted bootstrap percentiles, BCA, for 95% confidence intervals), whereas evidence ratios were estimated from the bootstrapped wAICc. We calculated the number of times that each model was top ranked, based on wAICc, over the 1000 bootstrap runs.

The analysis of the introduction stage was simpler. Taxonomic biases were tested using the same procedures described previously, but comparing the sample of introduced species with the random expectations drawn from the pool of all transported amphibians.

Family (no. species in the family)	Transported for trade Number (proportion)		Transported as stowaway Number (proportion)		Introduced Number (proportion)	
	Observed	Expected	Observed	Expected	Observed	Expected
Ambystomatidae (37 sps)	1.00 (0.01)	0.71 (0.01)			1.00 (0.05) (+)	0.19 (0.01)
Bufonidae (505 sps)			5.00 (0.13) (+)	3.19 (0.08)	1.00 (0.05)	0.95 (0.05)
Cryptobranchidae (3 sps)	1.00 (0.01) (+)	0.28 (0.004)				
Dendrobatidae (164 sps)	3.00 (0.04) (+)	2.13 (0.03)				
Dicroglosidae (164 sps)			1.00 (0.03)	1.00 (0.03)		
Hylidae (844 sps)	28.00 (0.39) (+)	9.94 (0.14)	18.00 (0.47) (+)	5.32 (0.14)	9.00 (0.47)	7.03 (0.37)
Leiopelmatidae (6 sps)	2.00 (0.03) (+)	0.07(0.001)				
Microhylidae (426 sps)	1.00 (0.01) (-)	5.04 (0.07)	1.00 (0.03) (-)	2.66 (0.07)	2.00 (0.11)	0.57 (0.03)
Myobatrachidae (128 sps)	28.00 (0.39)(-)	1.42 (0.02)	5.00 (0.13) (+)	0.76 (0.02)	5.00 (0.26)	6.08 (0.32)
Pelobatidae (4 sps)			1.00 (0.03) (+)	0.02 (0.001)		
Pipidae (31 sps)	1.00 (0.01)	0.36 (0.005)	1.00 (0.03) (+)	0.19 (0.005)		
Ranidae (315 sps)	1.00 (0.01)(-)	3.76 (0.05)	1.00 (0.03) (-)	1.90 (0.05)		
Rhacophoridae (285 sps)	1.00 (0.01)(-)	3.41 (0.05)	4.00 (0.11) (+)	1.90 (0.05)		
Salamandridae (74 sps)	4.00 (0.06)(+)	0.85 (0.01)	1.00 (0.03)	0.38 (0.01)	1.00 (0.05)	0.76 (0.04)

Table 2.1. Observed (and randomly expected) proportions of members of each amphibian family transported and introduced in Australia. Families with native representatives in Australia are emphasized in **bold letters**. See methods for further details. (+)/(-) significantly more/less observed species than expected (Monte Carlo test: $p<0.05$ in all comparisons).

Geographical biases were tested by comparing the latitudinal and longitudinal-mid points of the introduced vs. non-introduced species using a non-paired permutation test. The effect of body size, geographical extent, latitudinal and longitudinal mid-points, conservation status and the pathway of transport on introduction was investigated by means of a logistic regression, provided that we had not detected relevant taxonomic biases (see Results). We conducted these analyses without differentiating between the two pathways. In fact, we were specifically interested in the influence of the transport pathway in shaping the likelihood of introduction as previous research has highlighted the key role of the way by which animals are transported as a predictor of introduction probabilities (Kraus 2007, 2009; Krysko et al. 2011; Rago et al. 2012). We have included transport pathway (trade, stowaway, and both) as a factor in our logistic regression analysis. Model selection procedures were the same as outlined previously. Pseudo-R^2 was calculated based on the log-likelihoods of the models (Nagelkerke 1991). Where two models obtained similar support, we calculated the relative importance of each variable based on the sum of wAICc values of the models where they were included (Burnham and Anderson 2002). All statistical analyses were conducted in R (R Development Core Team 2015), using packages coin (Hothorn et al. 2007), lme4 (Bates 2005), rms and AICmodavg.

Results

Transported Amphibians

We estimated that 74.72 ± 12.44 (estimate ± SE; 95% Confidence Intervals: 50.35-99.10) Australian amphibian species have been transported outside their native range. The survival parameter, interpreted as the probability of finding every species in each source, was 0.65 ± 0.04. For alien species, the estimate was 36.20 ± 5.80 (95% CI: 24.83-47.57) species transported and the survival was 0.76 ± 0.17. These estimates indicate that we are missing only 12.6% of species transported and the number of species included in our database falls within the 95% confidence intervals of these estimates (64 domestic exotics and 33 aliens). We are therefore confident that our database of transported amphibians is a reasonable initial snapshot of reality.

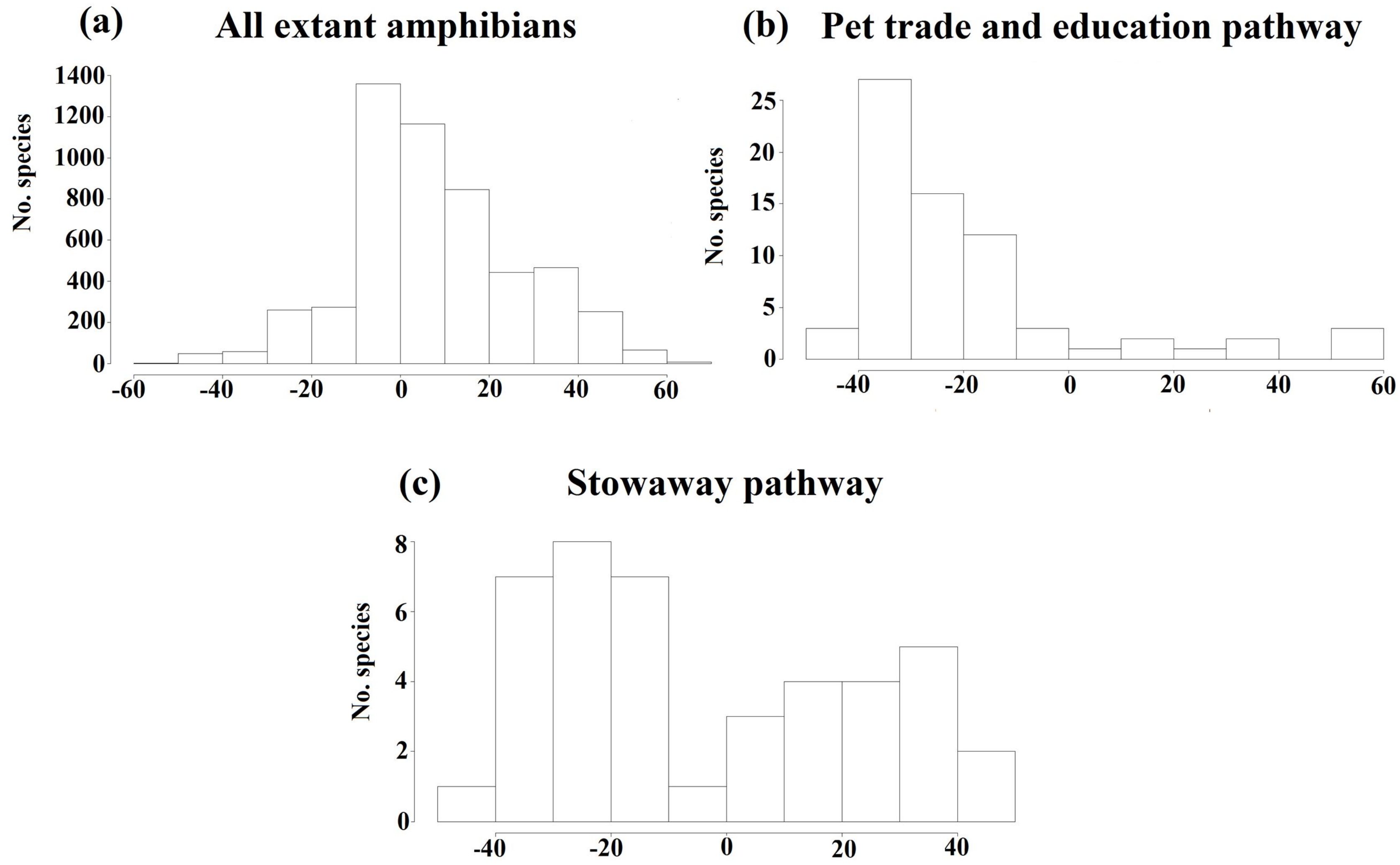
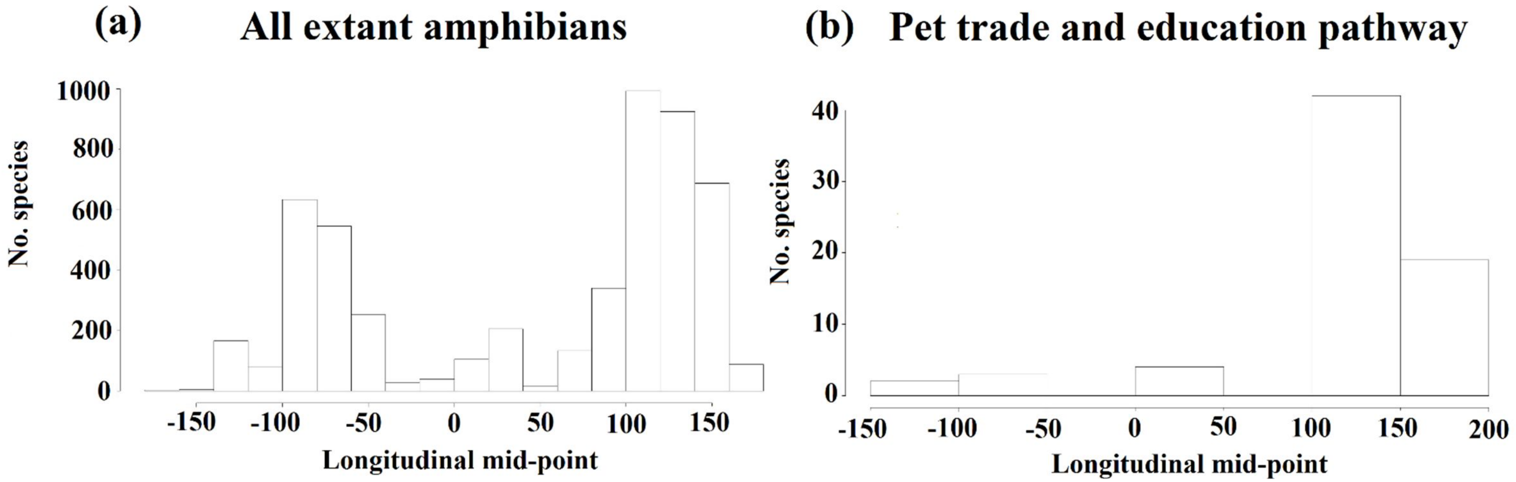


Fig. 2.1. Frequency distribution of latitudinal mid-points of the native range for (a) all extant amphibian species, (b) species transported for trade and (c) species transported as stowaways. Note the different scales of each histogram. Negative values refer to latitudes south of the equator.



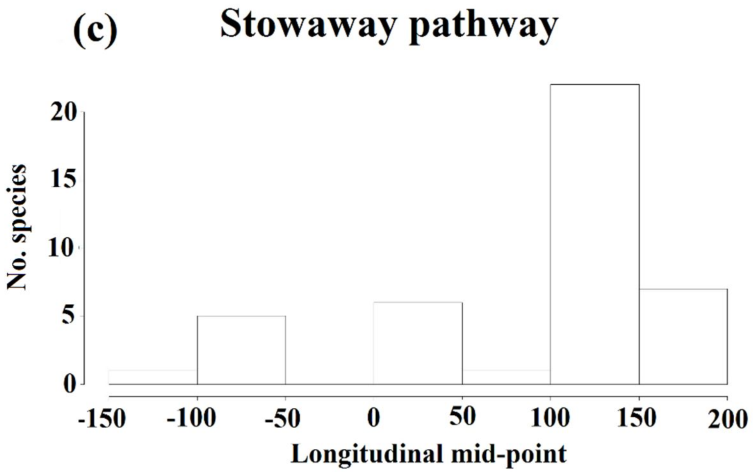


Fig. 2.2. Frequency distribution of longitudinal mid-points of the native range for (a) all extant amphibian species, (b) species transported for trade and (c) species transported as stowaway. Note the different scales of each histogram. Negative values refer to longitudes west of the 0° meridian.

Seventy one amphibian species belonging to only 11 families (out of 74 extant families: 16%) were detected as transported for trade. Of these, 56 species (79%) were native to Australia, while 15 (21%) were alien (see data accessibility statement and Appendix 1). Species were not distributed evenly among these families (Table 2.1), resulting in a biased composition relative to random expectations (Permutation test: T = 36, $p < 0.05$). The number of species from five families (Cryptobranchidae, Dendrobatidae, Hylidae, Leiopelmatidae and Salamandridae) exceeded the random expectations (Monte Carlo tests: $p < 0.05$ in all cases). For four families (Microhylidae, Myobatrachidae, Ranidae and Rhacophoridae), there were fewer species than expected in a random sample (Monte Carlo tests: $p < 0.05$ in any case). Two families transported were found in almost equal numbers from random sampling. The latitudinal and longitudinal mid-points differed between traded and all extant amphibians (Permutation test for latitude: T = 149865.6, $p < 0.001$; Permutation test for longitude: T = 419456.3, $p < 0.001$; Figs. 2.1 and 2.2; see also Appendix 1).

We tested eight models for transport probabilities in the trade pathway and the best-fitting model included only two variables, native range size and longitudinal mid-point of the native range (Table 2.2; Fig, 2.3a). This model had high support (wAICc = 0.99) and explained 83% of the variance (bootstrapped estimate ± standard error of R^2: 0.83 ± 0.09; Table 2). Moreover, this model was always the top ranked in the 1000 bootstrap replications. Estimates of the coefficients of the best fitted model are provided in Appendix 1. Models that included conservation status and latitude, as well as all other combinations of variables, had substantially lower support and R^2 (Table 2.2).

Thirty-eight amphibians from 10 families were found to be transported as stowaways. Again, there were strong taxonomic biases relative to all extant amphibian species (Permutation test: T = 40, $p < 0.05$; Table 2.1). Eighteen (47%) were Australian species and 20 (53%) were alien amphibians (see data accessibility statement and Appendix 1). Members of six out of 10 families (Bufonidae, Hylidae, Myobatrachidae, Pelobatidae, Pipidae and Rhacophoridae) were present in the pool of transported amphibians in higher numbers than expected from random transport (Monte Carlo tests: $p < 0.05$ in all cases). Two families (Dicroglossidae and Salamandridae) were represented by an equal number of species as would be expected from a random sample of amphibians of the world. Finally, two families (Microhylidae and Ranidae) occurred in a lower proportion than expected from random sampling (Monte Carlo tests: $p < 0.05$).

	wAICc **Estimate ± SE** **Bias** **95% CI**	**Evidence ratio**	**Top Rank**	**R^2** **Estimate ± SE** **Bias** **95% CI**
Area + longitude	0.99 ± 0.06 -0.01 0.89, 1.00	1.00	1000	0.83 ± 0.05 0.07 0.49, 0.93
Longitude	0.01 ± 0.06 -0.01 0.00, 0.08	0.01	0	0.60 ± 0.11 -0.07 0.42, 0.82
Latitude + longitude	0.00 ± 0.00 0.01 0.00, 0.00	0.00	0	0.60 ± 0.11 -0.06 0.41, 0.81
Area + conservation status	0.00 ± 0.00 0.00 0.00, 0.03	0.00	0	0.73 ± 0.09 0.07 0.36, 0.86
Area + latitude	0.00 ± 0.00 0.00 0.00, 0.00	0.00	0	0.44 ± 0.16 0.22 0.26, 0.59
Area	0.00 ± 0.00 0.00 0.00, 0.00	0.00	0	0.45 ± 0.11 0.03 0.27, 0.65
Latitude	0.00 ± 0.00 0.00 0.00, 0.00	0.00	0	0.08 ± 0.09 0.16 0.00, 0.14
Conservation status	0.00 ± 0.00 0.00 0.00, 0.00	0.00	0	0.35 ± 0.28 0.10 0.02, 0.86

Table 2.2. Adjustment and performance of the generalized linear mixed models for correlates of the probability of transport of amphibians for trade. Models are ordered by decreasing Akaike's weight (wAICc) values. Estimates of wAICc and R^2 were obtained by means of 1000 bootstrapped runs of the model (see methods). Area: log10 of the extent (km^2) of the native range; longitude: longitudinal mid-point of the native range; latitude: latitudinal mid-point of the native range; conservation status: IUCN categories of threat; SE: standard error; biases represent the difference between bootstrap and sample estimates. Evidence ratio: wAICc of the model / wAICc of the best model; top rank: no. of times that each model was the top ranked over the 1000 bootstrap runs.

	wAICc **Estimate ± SE** **Bias** **95% CI**	**Evidence ratio**	**Top rank**	**R^2** **Estimate ± SE** **Bias** **95% CI**
Area	0.55 ± 0.19 0.15 0.45, 0.77	1.00	551	0.69 ± 0.05 0.11 0.4, 0.84
Area + no. flights	0.19 ± 0.19 -0.01 0.11, 0.41	0.35	189	0.71 ± 0.11 -0.08 0.50, 0.87
Area + conservation status	0.16 ± 0.07 -0.06 0.10, 0.36	0.29	161	0.94 ± 0.02 0.01 0.65, 0.97
Area + value of imports	0.10 ± 0.04 -0.07 0.11, 0.25	0.18	99	0.71 ± 0.10 -0.02 0.37, 0.84
Longitude	0.00 ± 0.00 -0.00 0.00, 0.01	0.00	0	0.98 ± 0.01 -0.01 0.91, 0.99
Conservation status	0.00 ± 0.00 -0.00 0.00, 0.00	0.00	0	0.92 ± 0.02 0.02 0.63, 0.95
No. flights + value of imports	0.00± 0.00 -0.00 0.00, 0.00	0.00	0	0.71 ± 0.28 -0.11 0.12, 0.87
Value of imports	0.00 ± 0.00 -0.00 0.00, 0.00	0.00	0	0.24 ± 0.17 0.05 0.01, 0.55
No. seats per flight + value of imports	0.00 ± 0.00 -0.00 0.00, 0.00	0.00	0	0.25 ± 0.23 0.14 0.03, 0.54
No. flights	0.00 ± 0.00 -0.00	0.00	0	0.46 ± 0.31 -0.11 0.02, 0.74
Latitude	0.00 ± 0.00 -0.00 0.00, 0.00	0.00	0	0.01 ± 0.07 0.04 0.00, 0.10
No. seats per flight	0.00 ± 0.00 -0.00 0.00, 0.00	0.00	0	0.12 ± 0.33 -0.22 0.00, 0.33
No. flights + no. seats per flight	0.00 ± 0.00 -0.00 0.00, 0.00	0.00	0	0.89 ± 0.32 -0.23 0.16, 0.92

Table 2.3. Adjustment and performance of the generalized linear mixed models for correlates of the probability of transport of amphibians as stowaway. Models are ordered by decreasing Akaike's weight (wAICc) values. Estimates of wAICc and R^2 were obtained by means of 1000 bootstrapped runs of the model (see methods). No. flights: interpolated annual average number of airplanes flying to Australia taken at the centre of the native distribution; No. seats per flight: interpolated annual average number of seats per airplane taken at the centre of the native distribution; imports: interpolated annual average value of imports (USD) taken at the centre of the native distribution; other abbreviations as in Table 2. See methods for details.

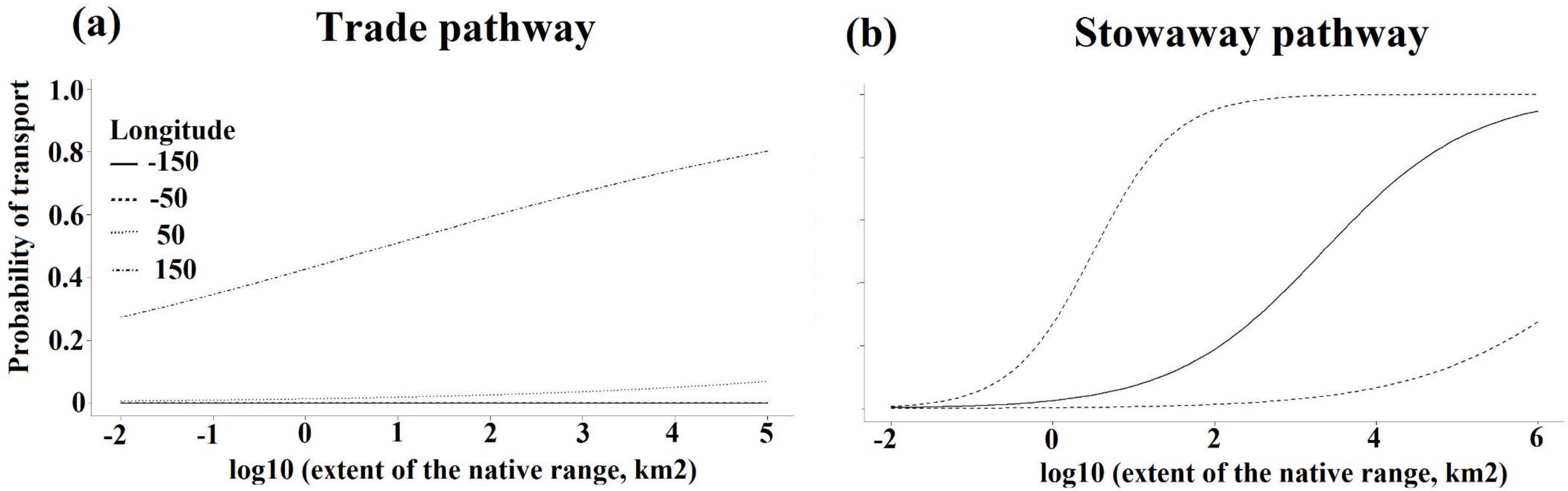


Fig. 2.3. Probability of transport of amphibians to or within Australia. (a) probability of transport for trade as a function of the extent of the native range (km2) and the longitudinal midpoint; (b) probability of transport for stowaway as a function of the extent of the native range (km2) and 95% confidence intervals derived from bootstrapping. Negative values of longitude refer to regions west of the 0° meridian. Data points are not plotted because zero values differ in each realisation of the models.

There were strong differences in the geographical origin of stowaway species compared to all extant amphibians (Permutation test for latitudinal mid-point: $T = 149865.6$, $p = 0.001$; Permutation test for longitudinal mid-point: $T = 419456.0$, $p < 0.001$; Figs. 2.1 and 2.2; see also Appendix S1).

Thirteen models were fitted to the data on amphibians transported as stowaways (Table 2.3). The best performing model explained a high percentage of the variance (bootstrapped estimate ± standard error of R^2: 0.69 ± 0.05; Table 2.3) and had considerable support (wAICc=0.54; top ranked 551 times out of 1000 bootstrap runs). Despite the relatively good performance of the model, the 95% confidence interval estimates of coefficients were visibly large (Fig. 2.3b; see Appendix 1). The likelihood of being transported as a stowaway increased with the geographical extent of the native range (Fig. 2.3b). Models including variables related to human mobility and transport of goods had lower relative model weights (wAICc values < 0.20; Table 2.3).

Introduced Amphibians

Only 19 out of 97 (20%) amphibians transported to, or within, Australia have been recorded as introduced, including representatives of only six different families (Table 2.1). The majority of introduced amphibians originated from localities within Australia (15 species: 79 %) and only four introduced species were non-native to Australia (21%). Considered together, there were no significant taxonomic differences compared to the random expectations (Permutation test: $T = 18$, $p = 0.31$; Table 2.1), although the family Ambystomatidae was found in higher numbers than expected (Monte Carlo test: $p < 0.05$). There were no statistically significant differences in the latitudinal mid-point (Permutation test: $T = -274.15$, $p = 0.81$) or the longitudinal mid-point (Permutation test: $T = 2309.32$, $p = 0.30$) of introduced compared to all transported species.

	wAICc	**Evidence ratio**	**Pseudo-R^2**
Pathway	0.55	1.00	0.46
Pathway + body size	0.45	0.82	0.48
Longitude	0.00	0.00	0.02
Area + longitude	0.00	0.00	0.05
Body size	0.00	0.00	0.02
Area	0.00	0.00	0.02
Conservation status	0.00	0.00	0.15
Latitude	0.00	0.00	0.00
Area + body size	0.00	0.00	0.03

Table 2.4. Adjustment and performance of the logistic models for correlates of the probability of introduction of amphibians. Models are ordered by decreasing wAICc values.

Nine models were conducted for introduced species (Table 2.4). Model selection procedures indicated that the logistic regression including only pathway as a factor was the best performing model (wAICc = 0.55; Pseudo-R^2 = 0.46; Table 2.4), although a model including pathway and body size as independent variables also obtained high support (wAICc = 0.45; Pseudo-R^2 = 0.48). The variable pathway had the highest relative importance (0.99), while body size had a relative importance of 0.45. All other variables had zero relative importance. The probability of introduction was higher for those species transported via both pathways (coefficient of the model [estimate ± standard error]: 0.47 ± 0.57), whereas the likelihood of introduction was negatively correlated when considering each pathway on its own (coefficient of trade pathway: -4.47 ± 1.16; stowaway pathway: -1.00 ± 0.70). Body size had a positive effect on the probability of introduction (coefficient of the model: 0.24 ± 0.22). All other models performed poorly (Table 2.4).

Discussion

We identified 97 amphibian species transported out of their natural range to Australia, 19 of these have been introduced (20%). To date, only four of these 19 introduced species have succeeded in establishing self-sustaining populations (21%), and these are three native Australian and one alien species (Kraus 2009; Tingley et al. 2014): *Limnodynastes tasmaniensis* Günther, 1858 (Spotted grass frog), *L. dorsalis* (Gray, 1841) (Western banjo frog), *Litoria ewingii* (Duméril and Bibron, 1841) (Ewing's tree frog) and *Lissotriton vulgaris* (Linnaeus, 1758) (Smooth newt).

There was significant taxonomic non-randomness in the families transported into Australia (Table 2.1), either for trade or as stowaways, which contrasts with the results of Romagosa et al. (2009), who found no evidence of non-randomness in the amphibian families traded in the United States. We also found significant geographical biases in the origin of transported species. Notably, the area delimited by the peaks of latitudinal and longitudinal mid-points of amphibians, included in the trade route, coincides approximately with the southern half of Australia, although there are other areas of origin of traded amphibians scattered in Asia, Europe, South Africa and South America (see Appendix 1). Australian legislation imposes strict constraints on the importation of alien species and only those species listed in the *List of specimens taken to be suitable for live import* (http://www.environment.gov.au/biodiversity/wildlife-trade/lists/import/pubs/live-import-list.pdf) can be legally transported. In the last update of this list (13 March 2013) only 11 amphibians are included. Thus, the trade on imported amphibians is strictly regulated, unlike other developed countries (e.g., United States) where the legal trade on amphibians is mostly deregulated (Schlaepfer et al. 2005; Defenders of Wildlife 2007; Smith et al. 2009). Meanwhile, the environmental legislation in Australia allowing for trading and keeping native species varies between states (see http://frogs.org.au/arc/legal.html for details). For example, in Victoria and New South Wales, wild frogs cannot be captured and a license is required to keep captive-bred native amphibians. These permissions allow keeping virtually any native amphibian species previously bred in captivity. Conversely, in South Australia, 19 of the 27 frogs present in the state (Tyler and Walker 2011) can be captured in the wild, maintained in captivity and even sold. Subsequently, native species are likely to be more frequently transported.

The case for the stowaway pathway is rather different, as the origins of the amphibians unintentionally transported can be tracked mostly back to two different source areas (see Appendix 1). One of the peaks of species richness encompasses the eastern half of Australia, which is a hotspot of frog species richness (Tyler and Knight 2011), and could increase the chances of unintentionally ‘hitchhiking’ and transporting an amphibian species. For example, Tyler and Knight (2011) and Tyler and Walker (2011) observed that tree frogs (family Hylidae) from Queensland are sometimes transported as stowaway in banana exports to other states. The other area of high species richness encompasses a large portion of eastern Asia (see Appendix 1), an area with important trade and demographic links with Australia (Lenzen et al. 2012; Lenzen et al. 2013).

Stowaway amphibians have larger native distributions than other species in the same families. Similarly, traded amphibians are also widespread, but the longitudinal mid-point of their distributions is included in the best fitted model and the relationship between probability of transport and longitude (Fig. 2.3b) tightly matches the geographical differences previously discussed. Establishment rates of amphibians in North America, Florida and worldwide are also influenced by native range size (Tingley et al. 2010; Poessel et al. 2012; Allen et al. 2013). Widespread species tend to occur in higher abundances than species with smaller ranges (Gaston 1996; Blackburn et al. 2006) and as a consequence they are more likely to be exposed to human activities. Readiness for capture also influences the transport of alien birds (Blackburn and Duncan 2001a; Cassey et al. 2004b; Blackburn et al. 2009). Contrary to our expectations (García-Díaz et al. 2016b), the results of the analysis for the stowaway pathway did not reveal any association between the probability of transport and the international linkages of Australia, perhaps because we have not accounted for movements within Australia, which will likely be responsible for the domestic transport of native species (Alacs and Georges 2008; Tyler and Knight 2011). Therefore, it seems that both the availability of amphibians to be captured and the limits imposed by Australian laws to import and keep amphibians drives the transport stage.

Regarding introduced species, we found no consistent taxonomic or geographical clustering. These findings contrast with the studies of Tingley et al. (2010) and Tingley et al. (2011) whose results on global patterns of amphibian introductions indicate that a high proportion of amphibian families have been introduced more or less frequently than expected by chance and these families originate mostly from the mid latitudes of the northern hemisphere, between 30º-50º.

Our results suggest that the likelihood of introduction is greater for those amphibians transported both as stowaways and for trade and reflect that most amphibian introductions in Australia are unintentional. Established alien amphibians and reptiles in Australia have been transported mostly as stowaway (Kraus 2009). It is plausible that transportation by both pathways involves the movement of higher number of animals than through only one pathway, and coupled with higher numbers comes higher probabilities of escape or release (Lockwood et al. 2005; Blackburn et al. 2013). Unfortunately, we do not have data to test the effects of propagule pressure on introduction of amphibians. Body size has been reported as a good predictor of introduction probability in birds, reptiles, mammals and fish (Cassey 2001; Cassey et al. 2004b; Forsyth et al. 2004; Jeschke and Strayer 2006; Blackburn et al. 2009; Van Wilgen et al. 2010). However, the exact shape of the relationship between body size and introduction appears to be complex and depends upon the taxonomic level assessed (Cassey 2001). Both positive and negative relationships have been described for alien birds and mammals (Cassey 2001; Cassey et al. 2004b; Forsyth et al. 2004; Jeschke and Strayer 2006). Whatever the relationship is, body size seems to have weak effects upon amphibian introductions (Tingley et al. 2010; Tingley et al. 2011; Rago et al. 2012). In our research, models including body size obtained moderate support (Table 2.4) suggesting some influence in introduction probabilities.

Preventing new incursions is the best practice to avoid the negative impacts of invaders (Clout and Williams 2009; Keller and Springborn 2013). Indeed, preventive strategies can return net economic profits when adequately implemented (Keller et al. 2007; Springborn et al. 2011). Managing, understanding and controlling the transport of species is essential for reducing the probability of an invasion (Romagosa et al. 2009; Smith et al. 2009; Perry and Farmer 2011). Obviously, a species that is not transported cannot become an invader, but as soon as it is taken outside its native range there is always some chances of escape or release into a new environment. We conclude that the differences in current environmental legislation in Australia have considerably affected which amphibian species are transported. Moreover, introduction depends on the vector of transport. Increased vigilance and biosurveillance are undoubtedly important in reducing the probability of introduction of amphibians. However, blanket bans to wildlife trade, as applied in Australia, do not entirely stop biological invasions and additional measurements are necessary (Carrete and Tella 2008; Perry and Farmer 2011; Keller and Springborn 2013; García-Díaz et al. 2016a). In Australia, legal trade is the source of the majority of transported and introduced amphibians, usually domestic exotics, highlighting the limitations of the current policy in avoiding invasions. Implementing a complementary policy of education and incentives for amphibian sellers, breeders and keepers could also help in diminishing the probabilities of future introductions (Perry and Farmer 2011). Finally, we reiterate that the transport and introduction stages are crucial in determining the outcome of a species travelling through the invasion pathway and considerably more research is needed on the factors that influence these steps.

Statement of Authorship

Title of Paper	Understanding the biological invasion risk posed by the global wildlife trade: propagule pressure drives the introduction and establishment of Nearctic turtles
Publication Status	☑ Published ☐ Accepted for Publication ☐ Submitted for Publication ☐ Unpublished and Unsubmitted work written in manuscript style
Publication Details	García-Díaz, P., Ross, J.V., Ayres, C. & Cassey, P. (2015). Understanding the biological invasion risk posed by the global wildlife trade: propagule pressure drives the introduction and establishment of Nearctic turtles. *Global Change Biology*, 21(3): 1078-1091. doi: 10.1111/gcb.12790.

Principal Author

Name of Principal Author (Candidate)	Pablo Garcia Diaz		
Contribution to the Paper	Planned and developed the research, compiled the data, developed the models and analysed the data, written the manuscript.		
Overall percentage (%)	80%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	14/02/2017

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Cesar Ayres		
Contribution to the Paper	Contributed to develop the original idea, data collection and edited the manuscript.		
Signature		Date	09/02/2017

Name of Co-Author	Associate Professor Joshua V. Ross		
Contribution to the Paper	Contributed ideas to the development of the research, contributed to the development of the modelling and analytical framework, revised and edited the manuscript		
Signature		Date	14/02/2017

Please cut and paste additional co-author panels here as required.

Name of Co-Author	Associate Professor Phillip Cassey		
Contribution to the Paper	Contributed ideas to the development of the research, contributed to the development of the modelling and analytical framework, revised and edited the manuscript		
Signature		Date	15/02/2017

Chapter 3. Understanding the Biological Invasion Risk Posed by the Global Wildlife Trade: Propagule Pressure Drives the Introduction and Establishment of Nearctic Turtles

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Publication: García-Díaz, P., Ross, J.V., Ayres, C. & Cassey, P. (2015). Understanding the biological invasion risk posed by the global wildlife trade: propagule pressure drives the introduction and establishment of Nearctic turtles. *Global Change Biology*, 21(3): 1078-1091. doi: 10.1111/gcb.12790.

Code accessibility: the annotated code for running the analyses in this Chapter is publically available at: https://github.com/pablogarciadiaz/PhD-thesis-code

Data accessibility: the databases of introduced Nearctic turtles and established slider turtles are publically available from the Dryad Repository: http://datadryad.org/resource/doi:10.5061/dryad.dc66k

Appendix: material accompanying this chapter can be found at Appendix 2 of this thesis.

Abstract

Biological invasions are a key component of human-induced global change. The continuing increase in global wildlife trade has raised concerns about the parallel increase in the number of new invasive species. However, the factors that link the wildlife trade to the biological invasion process are still poorly understood. Moreover, there are analytical challenges in researching the role of global wildlife trade in biological invasions, particularly issues related to the under-reporting of introduced and established populations in areas with reduced sampling effort. In this work, we use high-quality data on the international trade in Nearctic turtles (1999-2009) coupled with a statistical modelling framework, which explicitly accounts for detection, to investigate the factors that influence the introduction (release, or escape into the wild) of globally traded Nearctic turtles and the establishment success (self-sustaining alien populations) of slider turtles (*Trachemys scripta*), the most frequently traded turtle species. We found that the introduction of a species was influenced by the total number of turtles exported to a jurisdiction and the age at maturity of the species, while the establishment success of slider turtles was best associated with the propagule number (number of release events), and the number of native turtles in the jurisdiction of introduction. These results indicate both a direct and indirect association between the wildlife trade and the introduction of turtles and establishment success of slider turtles, respectively. Our results highlight the existence of gaps in the number of globally recorded introduction events and established populations of slider turtles, although the expected bias is low. We emphasize the importance of researching independently the factors that affect the different stages of the invasion pathway. Critically, we observe that the number of traded individuals might not always be an adequate proxy for propagule pressure and establishment success.

Keywords: global wildlife trade, hierarchical Bayesian models, invasion pathway, propagule pressure, reptiles, *Trachemys scripta*

Introduction

Alien species are an influential driver of biodiversity loss and a critical component of global biological change (Clavero and García-Berthou 2005; Lockwood et al. 2013; Richardson and Ricciardi 2013; Murphy and Romanuk 2014). Prior to the end of the 20th century many vertebrate species were intentionally introduced outside their native range, for the purpose of acclimatisation and the establishment of self-sustaining alien populations. Today, it is more likely that new introductions of alien vertebrates are accidental, through the escape or release of captive and pet species, and the unintentional incursion of stowaways (Hulme et al. 2008; Kraus 2009; Cassey and Hogg 2015). The characteristics of these two introduction pathways (intentional acclimatisation versus accidental release) are clearly different, and the outcome of introductions (i.e., whether a species establishes a self-sustaining population) may be strongly affected by these differences (Hulme et al. 2008; Wilson et al. 2009; Rago et al. 2012). In particular, species introduced intentionally (often in large numbers) are likely to have higher rates of establishment success (García-Berthou et al. 2005; Hulme et al. 2008; Blackburn et al. 2009; Rago et al. 2012). Within the unintentional pathway, the trade in vertebrate pets has continued to increase and has become an important contributor to new introductions of alien species worldwide (Hulme et al. 2008; Hulme 2009; Romagosa et al. 2009; Smith et al. 2009; Su et al. 2016). In Europe, pet escapes are currently one of the most important sources of new introductions of mammals, birds, reptiles and amphibians (Hulme et al. 2008).

The trade in alien pet reptiles has increased in developed countries since the 1980s (Romagosa et al. 2009; Tapley et al. 2011; Bush et al. 2014). A parallel increase in the number of new introductions of alien reptiles has also been observed (Kraus 2009; Van Wilgen et al. 2010; Henderson et al. 2011; Mateo et al. 2011). Freshwater turtles (Fig. 3.1) are a group that have experienced one of the largest increases in the number of new introductions, and establishment of alien populations, worldwide through the global trade in pet animals (Lever 2003; Kraus 2009; Masin et al. 2013). The most prominent example is the slider turtle (*Trachemys scripta*; Fig. 3.1a), the most frequently traded turtle in the world. The United States exported over 23.6 million slider turtles, between 1998 and 2002 alone, and the species has been introduced in at least 73 countries across all of the permanent ice-free continents (Lever 2003; Schlaepfer et al. 2005; Kraus 2009; Ficetola et al. 2012). Alien populations of slider turtles can have serious negative impacts in their alien range, because they outcompete native species (Cadi and Joly 2003, 2004; Polo-Cavia et al. 2010, 2011) and transmit diseases and parasites, such as *Mycoplasma* bacteria and a variety of nematode species (Hidalgo-Vila et al. 2009; Silbernagel et al. 2013). Pet turtles have also been recorded to transmit the bacteria *Salmonella*, which causes salmonellosis, to humans (Harris et al. 2009; Angulo et al. 2010; Hulme 2014). The slider turtle is the best known case of a widely established alien turtle species, but there are many more species available in the global turtle market that could pose a similar risk (Masin et al. 2013).

Here, we quantitatively consider the first two stages of the invasion pathway (introduction and establishment) for Nearctic turtles traded globally, particularly those species native to the United States (Fig. 3.1). First, we assessed the role of different factors on the introduction (release, or escape of individuals) of internationally traded Nearctic turtles. Second, we examined factors that are predicted to drive the establishment success of slider turtles (*Trachemys scripta*) at these sites. In particular, we have focused on the slider turtle because, given its widespread alien range, it is the only turtle species for which there is sufficient and adequate information on establishment success to conduct a robust comparative analysis. In doing so, we compiled a high-quality global database on the number of freshwater turtles exported by the United States of America (1999-2009), records of introductions of those species to the countries of import, and whether, following an introduction event, slider turtles are known to have become established. We complemented these records with data on factors consistently found to be related to the probability of introduction and establishment success of alien vertebrates (e.g., propagule pressure, life history and presence of congeneric species in the recipient region; see Table 3.1)(Jeschke and Strayer 2006; García-Berthou 2007; Blackburn et al. 2009; Tingley et al. 2010; Poessel et al. 2012; Van Wilgen and Richardson 2012; Allen et al. 2017).

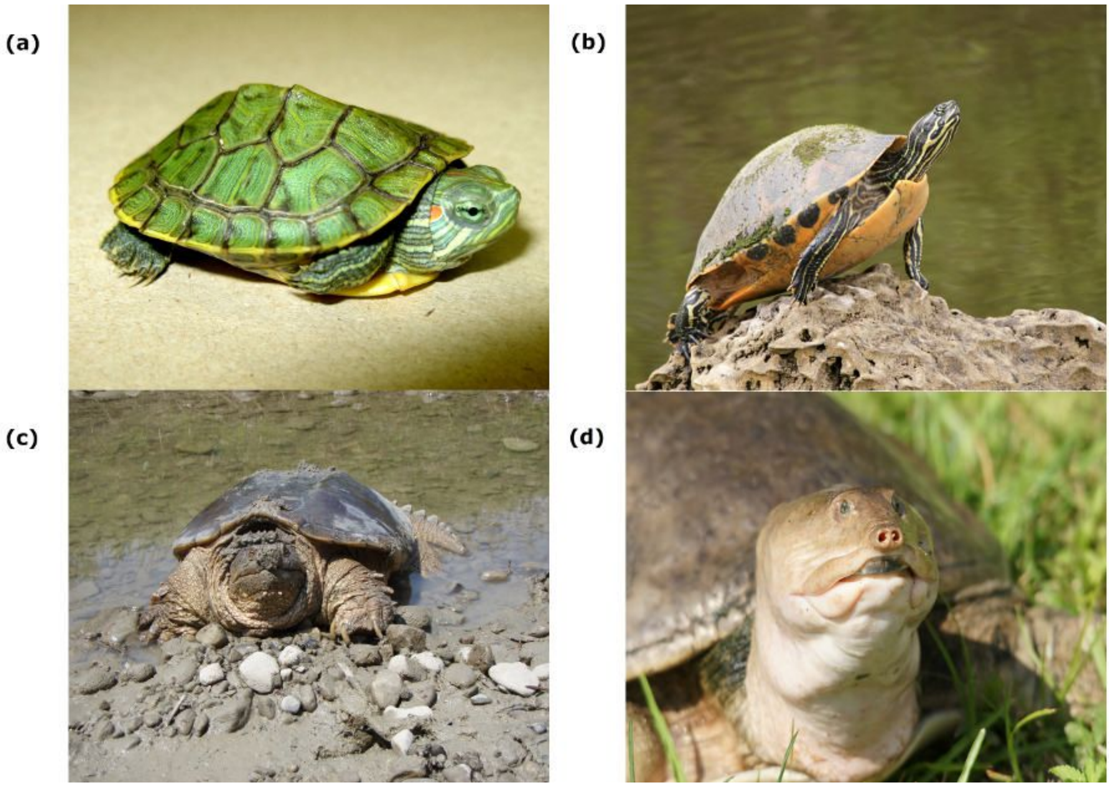

Fig. 3.1. Four representative examples of Nearctic turtles found in the global pet trade. (a) Juvenile Red-eared slider turtle (*Trachemys scripta elegans*) found at large (introduced) in Adelaide, Australia, in 2012 (photo source: Peter Bird, Biosecurity SA); (b) A river cooter (*Pseudemys concinna*) in its native habitat in Florida (photo source: Hans Hillewaert, licensed under Creative Commons); (c) Common snapping turtle (*Chelydra serpentina*) in Ontario, Canada (photo source: Wikipedia user Ontley, licensed under Creative Commons); (d) Florida softshell turtle (*Apalone ferox*) in its native habitat in Florida (photo source: Hans Hillewaert, licensed under Creative Commons).

The comparative study of alien species poses several analytical challenges (Cassey et al. 2004a; Sol et al. 2008), and estimating the link between the trade on alien species and their probabilities of introduction and establishment adds further complexity (Bradie et al. 2013; Leung and Steele 2013). One particular challenge is to ascertain whether the lack of data on the introduction of a given species into a jurisdiction is due to a real absence of introductions or to deficiencies in the jurisdictional sampling effort (Baillie et al. 2008; McGeoch et al. 2010; Jetz et al. 2012). Failing to account for this effect could have serious consequences upon the statistical inference regarding the processes involved during introduction and establishment phases of the invasion process (MacKenzie et al. 2002; MacKenzie et al. 2006; Lockwood et al. 2013; Guillera-Arroita et al. 2014b). We addressed this by developing a statistical model based on the stages of the invasion pathway that explicitly accommodates the uncertainty in detection while also allowing us to test the importance of other factors on the probabilities of introduction and establishment success.

Material and Methods

Data

To estimate the international trade in Nearctic turtles across global jurisdictions, we obtained, from the Office of Law Enforcement, United States Fish & Wildlife Service (USFWS), the specific identity and the total number of turtles exported from the US to other jurisdictions in the world, 1999-2009. This means that the origin of turtle species considered in this work was always the US. It is a legal imperative to obtain a license or permit to export turtles from the United States (see http://www.fws.gov/permits/). The database provided by the USFWS is composed of records for each occasion that turtles have been exported, the destination jurisdiction (usually country, but occasionally independent jurisdictions such as Hong Kong and Macau), the species exported, and the number of individual turtles exported (see Appendix 2). We were interested in obtaining the total number of individuals exported to each jurisdiction, 1999-2009, as it represents the abundance of the species in the destination market, and is therefore a reliable estimator of the availability of turtles. This is a reasonable assumption, since we are only aware of Nearctic turtles being farmed on a large scale outside the United States in China (Haitao et al. 2008; Zhou and Jiang 2008), and not further supplied to international trade. The global trade in US turtles provides a unique opportunity to critically examine the association between the wildlife trade and invasion outcomes, due to the thoroughness and accuracy of the records on the number of individuals traded.

We filtered and corrected the original database following the methods detailed in Fig. S3. Despite the reliability of the database, it is not exempt from mistakes (Schlaepfer et al. 2005; Defenders of Wildlife 2007; Pernetta 2009), and the taxonomy is out-dated. For 22% of all the individual exports (out of 25,355 exports) there was no species-specific identification. We recorded 36 freshwater turtle species in the export database, representing three-quarters of the 47 extant species of freshwater turtles in the US (see Fig. 3.1 for some examples of turtles)(Ernst and Lovich 2009). Our final database of exports from the USA comprised 747 events of 36 species for a total of 83 jurisdictions across the world (see data accessibility statement; see also Fig. 3.2a). Not all the species were transported to all the jurisdictions (Fig. 2a). The taxonomy of turtles follows that of van Dijk et al. (2012).

For each of the 747 records, we obtained information on whether the species exported have been introduced to a jurisdiction, during the period 1999-2013 (see data accessibility statement). We were interested in testing the role of the number of individuals imported on the probability of introduction, as well as assessing the effects of additional variables related to the introduction. Previous research on birds (Cassey et al. 2004a; Cassey et al. 2004b), fish, birds and mammals (Jeschke and Strayer 2006), and reptiles and amphibians (Van Wilgen et al. 2010; García-Díaz and Cassey 2014; Allen et al. 2017) has shown that the probability of introduction is related mainly to species-level variables. We gathered information on six life-history traits (see Table 1) (Wilson 2003; Ernst and Lovich 2009), as well as the area (km^2) of the jurisdiction that is freshwater (the higher the freshwater cover, the higher the potential habitat availability; information from The World Factbook: https://www.cia.gov/library/publications/the-world-factbook/).

For the establishment success of slider turtles (Fig. 3.3a), we considered the species as established in a jurisdiction if it has been present for greater than five years and has ever been known to successfully reproduce (Blackburn et al. 2011). We chose the five-year cut-off because it is the age at which all the females are sexually mature in alien populations (Perez‐Santigosa et al. 2008). We assessed the influence of the number of turtles imported, propagule number (the number of introduction events; Lockwood et al. 2009)(see data accessibility statement), and a series of jurisdiction-level and jurisdiction by species-level factors (Table 3.1). We only considered jurisdictions for which we had data on the number of slider turtles imported, 1999-2009. Thus, we only considered 56 out of the 73 (76.7%) jurisdictions where the species have been introduced worldwide (Kraus 2009; Ficetola et al. 2012). The presence and number of congeneric species, and the number of species of the same taxonomic group present in the recipient community has been shown to positively affect the establishment success and spread rates of reptiles (Ferreira et al. 2012; Poessel et al. 2012; Allen et al. 2013; Liu et al. 2014), and we obtained the total number of freshwater turtle species (species richness) in each jurisdiction from van Dijk et al. (2012). Climate is a key determinant of establishment success for alien reptiles (Bomford et al. 2009b; Van Wilgen et al. 2009; Jacobson et al. 2012; Van Wilgen and Richardson 2012). To determine the effects of climate on establishment success of slider turtles, we focused on the constraints imposed by ambient temperature, a key determinant of the biology and ecology of slider turtles (Bodie et al. 2000; Ernst and Lovich 2009). For each jurisdiction, we calculated the proportion of 2.5º x 2.5º (decimal degrees) cells whose ambient temperature are within the physiological limits of the species (defined as the critical thermal maximum and minimum).

The rationale for the use of this value and the procedures to obtain it are provided in Appendix 2. We used this value as a covariate in the models of establishment.

For the models of recorded introduction of turtles and recorded establishment success of slider turtles we included a covariate(s) representative of the sampling effort in each of the jurisdictions. Individuals are detected while searching specifically for turtles, but also while sampling other freshwater taxa, e.g., amphibians (P. García-Díaz & C. Ayres, *personal observations*). Moreover, it could be expected that larger species are more easily detected. To model the detection of introductions, we used three potential covariates as proxies for the sampling effort: (1) the cumulative number of records of amphibians and freshwater turtles (excluding alien US species), 1999-2013, stored in the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/) to approximate the biological sampling effort in the different jurisdictions (Guralnick et al. 2007); (2) the human population density in the jurisdictions; and (3) the carapace length of the turtle species. For modelling the detection of an established population of slider turtles, we proceeded in a similar manner but excluded carapace length as a covariate (as it would be the same for all events).

Modelling Approach

We developed a hierarchical stochastic model (Cressie et al. 2009; Kéry and Royle 2016). In this model, let $y_{i,j} \in \{0,1\}$ be the values indicating whether the species *j* has been recorded (in our database) as introduced in jurisdiction *i,* we modelled these values as the outcome of two processes: the first, ‘introduction’ in Table 3.2, is the expected status of the species in the jurisdiction (i.e., whether the species is expected to have been introduced in the jurisdiction), and the second, ‘detection’ in Table 3.2, indicates whether, once introduced, a species has been detected in the jurisdiction (i.e., a species could have been introduced in a jurisdiction but not yet detected). An important difference with other models for introduction, which do not include an independent component for detection (implicitly assuming that the recorded status of the species corresponds to the expected status), is that in our model the expected status of the species in a given jurisdiction is not directly recorded, but inferred from the structure of the model and the associated covariates. The probabilistic models and the components are described in Table 3.2.

Covariates	**Abbreviated name**	**Transformation and summary statistics (median ± standard deviation, and range)**	**Included in model selection for introduction**	**Included in model selection for establishment success of slider turtles**
Introduction / establishment				
Total no. of turtles exported to a jurisdiction	Import	Log_{10}, 2.29 ± 1.38 (0.00-7.38)	+	+
Propagule number (number of introduction events)	Propagule	Log_{10}, 0.48 ± 0.69 (0.00-2.50)		+
Average adult carapace length (centimetres)	CL	Log_{10}, 1.43 ± 0.20 (1.04-1.82)	+	
Average clutch size (no. of eggs)	Clutch	Square root, 3.61 ± 1.29 (1.00-6.00)	+	
Average no. of clutches / year (Factor)	Clutches	NA, 2.00 ± 1.29 (1.00- 6.00)	+	
Age at maturity (females)	Maturity	Log_{10}, 0.85 ± 0.17 (0.60-1.30)	+	
Maximum lifespan (years)	Lifespan	Log_{10}, 1.57 ± 0.22 (0.78-1.90)	+	
Food niche (factor: herbivorous, carnivorous omnivorous)	Food	NA	+	
Proportion of 2.5º x 2.5º cells in a jurisdiction whose ambient temperature is within the physiological limits (critical thermal maximum and minimum) of the species*	Temperature	NA, 0.86 ± 0.43 (0.00-1.00)		+
Total no. of native species of turtles in a jurisdiction	SPS	Log_{10} (+ 1), 0.48 ± 0.49 (0.00-1.61)		+
Surface of the jurisdiction covered by freshwater	Water	Log_{10} (+1), 2.75 ± 1.00 (0.00-5.11)	+	+
Detection				
Total no. of records of amphibians and freshwater turtles in a jurisdiction stored in the GBIF database	GBIF	Log_{10} (+1), 2.64 ± 1.16 (0.00-5.12)	+	+
Human population density in a jurisdiction	Density	Log_{10}, 0.15 ± 0.07 (0.03-0.60)	+	+
Average adult carapace length	CL	Log_{10}, 1.43 ± 0.20 (1.04-1.82)	+	

Table 3.1. Covariates (transformations and summary statistics) included in the model selection procedures for the recorded introduction of Nearctic turtles and establishment success of slider turtles.

This model is similar to that described by MacKenzie et al. (2002) and MacKenzie et al. (2006) for modelling occupancy data while accounting for imperfect detection, but it is adapted to the peculiarities of the invasion pathway and the data available. To link the set of components described in Table 3.2 to the stage of recorded introduction (introduction and detection of an introduction) with the covariates they are conditioned on, we assumed their functional forms, $f_1(N_{i,j}, S_j, V_i)$ and $f_2(C_i)$, are described by a logit link. This means that the relationship between the introduction, detection and the covariates is linear on the logit scale:

$$\text{logit}(I_{i,j}) = f_1(N_{i,j}, S_j, V_i) = \alpha_0 + \beta_1 N_{i,j} + \beta_2 S_j + \beta_3 V_i \qquad (3.1)$$

$$\text{logit}\,(D_{i,j}) = f_2(C_i) = \alpha_1 + \beta_4 C_i \qquad (3.2)$$

where α_n (intercepts) and β_n (slopes) are parameters of the regression. The model for the recorded establishment success of slider turtles in jurisdiction i (denoted $z_i \in \{0,1\}$ and representing the recorded establishment success of the species) is similar to the one outlined previously for the recorded introduction, but is instead composed of establishment and detection. Given the sequential nature of the invasion pathway (Williamson 1996; Blackburn et al. 2011), a species must be introduced before becoming established. Hence, we modelled the recorded establishment success of slider turtles conditional on its introduction in the jurisdiction (Table 3.2). We estimated $f_3(M_{i,j}, T_j, R_i)$ and $f_4(F_i)$ via a logit link:

$$\text{logit}(E_{i,j}) = f_3(M_{i,j}, T_j, R_i) = \alpha_2 + \beta_5 M_{i,j} + \beta_6 R_i \qquad (3.3)$$

$$\text{logit}\,(U_{i,j}) = f_4(F_i) = \alpha_3 + \beta_7 F_i \qquad (3.4)$$

where α_n (intercepts) and β_n (slopes) are parameters of the model.

Statistical Analyses and Inference

The models described in the *Modelling approach* are commonly parametized using data from multiple records of detection/non-detection of the same species at each jurisdiction to inform the detection component (MacKenzie et al. 2002; MacKenzie et al. 2006). This type of data is particularly difficult to gather for global studies. However, Lele et al. (2012) recently demonstrated, testing a related model and using penalized likelihoods, that it is possible to obtain reliable information using unique records as long as at least one of the continuous covariates used to model each component differs. By complying with this requirement, it is possible to fit the models with unique records, as in our case, and obtain robust, reliable, statistical inference.

For the analyses of the recorded introduction we divided the dataset (n = 747 events) into two sets, a training dataset (60% of records; n = 448), used to fit the models, and a test dataset (40%; n = 299) to evaluate the predictive performance of the models. Given the distribution of the records across genera, we defined the functional form of the introduction as a Generalized Linear Mixed Model (GLMM)(Bolker et al. 2009), including an intercept ($\alpha_{g(i)}$) to control for the non-independence of related species. This is the functional form of the introduction in Eq. 1 and was re-written to accommodate these intercepts as follows:

$$\text{logit}(I_{i,j}) = \text{f}_1(S_j, L_i) = \alpha_{\text{g(i)}} + \alpha_1 + \beta_1 S_j + \beta_2 L_i + \beta_3 U_i \qquad (3.5)$$

where $\alpha_{g(i)}$, is a genus-specific intercept value. The functional forms for the detection were included as a Generalized Linear Model (GLM) with a constant intercept. We fitted the models using Bayesian Markov Chain Monte Carlo (MCMC) methods (Congdon 2007), as implemented in JAGS through the interface RJAGS (Plummer 2003) for the R software environment (R Development Core Team 2015). JAGS implements the Gibbs sampling algorithm to estimate the joint posterior distribution of the parameters of the model (Plummer 2003). Although our Bayesian approach differs from the penalized likelihood methods used by Lele et al. (2012), Bayesian procedures are known to adequately handle analytical problems associated with similar types of models (Caley and Barry 2014).

The large number of covariates to be tested for the recorded introduction model (both for the introduction and the detection components; Table 3.1), results in a large number of potential combinations and hence candidate models. We used Bayesian variable selection to estimate the most likely model given the data (O'Hara and Sillanpää 2009; Tenan et al. 2014). For this purpose, we used only the data in the training dataset. We proceeded by using the method of Kuo and Mallick (1998) for Bayesian variable selection, which involves including an indicator parameter (θ_n) along with the slopes (β_n) and multiplying each covariate to be tested. To meet the constraint of including at least one different independent continuous covariate for each component of the model (introduction and detection), we discarded those MCMC iterations where the model proposed did not satisfy this constraint.

We first ran the model using 3 chains with 300,000 iterations each. After checking visually for convergence and mixing of the chains, and the autocorrelation of the parameters using the R package coda (Plummer et al. 2006), we simulated the model using 3 chains, with

300,000 iterations each, where the first 200,000 iterations were discarded, and with a thinning of 10, resulting in 30,000 draws of the posterior distributions. Following the approach of Hadfield and Nakagawa (2010), and to further control for the non-independence of related species, the prior for the genus-specific intercepts was drawn from a multivariate normal distribution ~ $N(-1, \Sigma)$. Σ is a genus-level phylogenetic correlation matrix derived from the phylogenetic tree of turtles published by Guillon et al. (2012) (see Appendix 2 for further details and the phylogenetic tree) using the vcv function in the R package ape (Paradis et al. 2004). We drew the priors for the other coefficients (slopes and intercepts) from a Normal distribution, ~ $N(-1, \sigma)$, with the variance component $\sigma^2 = 10$. As a sensitivity analysis, we changed the prior distribution for the parameters to ~ $N(0, \sigma)$, $\sigma^2 = 10$, and re-ran the models. The posterior parameter distributions did not change, indicating that our choice of priors, ~ $N(-1, \sigma)$, is adequate and therefore we conducted all the statistical inference by employing that prior on the parameters. The indicators were modelled as θ_n ~ Bernoulli (0.5). We used 0.5 as a prior to assign each potential model the same *a priori* probability during the model selection procedures (Tenan et al. 2014). We calculated the posterior probability of each candidate model as the proportion of MCMC iterations where the individual model was selected over all the iterations run (Congdon 2007; Tenan et al. 2014). Finally, we fitted the model with the highest posterior probability to the training dataset in order to estimate the intercepts and slopes. For all intercepts and slopes, we report the median ± standard deviation (SD) and the 97.5% Highest Posterior Density intervals (HPDI). See code accessibility for the code for fitting the model using MCMC methods.

Stage of the invasion pathway	**Model**		
	Introduction / Establishment	**Detection**	**Complete model**
Recorded introduction ($y_{i,j}$) Definition and criteria used in this work: recorded (in the literature) individuals released, or escaped, into the wild	$(I_{i,j} \mid N_{i,j}, S_j, V_i)$ Probabilistic model: $(I_{i,j} \mid N_{i,j}, S_j, V_i) \sim$ Bernoulli $[f_1(N_{i,j}, S_j, V_i)]$ Components: $I_{i,j}$: introduction $\epsilon \{0,1\}$ of the species j in the jurisdiction i $N_{i,j}$: no. of individuals of species j traded in the jurisdiction i S_j: characteristics of the species j V_i: characteristics of recipient jurisdiction i	$(D_{i,j} \mid I_{i,j}, C_i)$ Probabilistic model: $(D_{i,j} \mid I_{i,j}, C_i) \sim$ Bernoulli $[f_2(C_i) \text{ x } I_{i,j}]$ Additional components: $D_{i,j}$: values $\epsilon \{0,1\}$ indicating whether the species j has been detected in jurisdiction i C_i: sampling effort in jurisdiction i	$(y_{i,j} \mid N_{i,j}, S_j, V_i, C_i)$ Probabilistic model: $(y_{i,j} \mid N_{i,j}, S_j, V_i, C_i) \sim$ Bernoulli $[P(I_{i,j} = 1 \mid N_{i,j}, S_j, V_i) \text{ x } P(D_{i,j} = 1 \mid I_{i,j} = 1, C_i)]$ Additional components: $y_{i,j}$: values $\epsilon \{0,1\}$ indicating whether the species j has been recorded as introduced / established in jurisdiction i
Recorded establishment ($z_{i,j}$) Definition and criteria used in this work: the released individuals have been recorded (in the literature) as having formed a self-sustaining population – they survived for at least 5 years and have bred in the wild	$(E_{i,j} \mid I_{i,j}, M_{i,j}, T_j, R_i)$ Probabilistic model: $(E_{i,j} \mid I_{i,j}, M_{i,j}, T_j, R_i) \sim$ Bernoulli $[f_3(M_{i,j}, T_j, R_i) \text{ x } I_{i,j}]$ Additional components: $E_{i,j}$: establishment success $\epsilon\{0,1\}$ of the species j in the jurisdiction i $M_{i,j}$: propagule pressure of species j in jurisdiction i (= no. of individuals of species j released, or escaped, in jurisdiction i) T_j: characteristics of the species j by characteristics of recipient region i (i.e., climate) R_i: characteristics of the recipient jurisdiction i	$(U_{i,j} \mid E_{i,j}, F_i)$ Probabilistic model: $(U_{i,j} \mid E_{i,j}, F_i) \sim$ Bernoulli $[f_4(F_i) \text{ x } E_{i,j}]$ Additional components: $U_{i,j}$: values $\epsilon \{0,1\}$ indicating whether the species j has been detected as established in jurisdiction i F_i: sampling effort in jurisdiction i	$(z_{i,j} \mid I_{i,j}, M_{i,j}, T_j, R_i, F_i)$ Probabilistic model: $(z_{i,j} \mid I_{i,j}, M_{i,j}, T_j, R_i, F_i) \sim$ Bernoulli $[P(E_{i,j} = 1 \mid I_{i,j}, M_{i,j}, T_j, R_i) \text{ x } P(U_{ij} = 1 \mid E_{i,j} = 1, F_i)]$ Additional components: $z_{i,j}$: values $\epsilon \{0,1\}$ indicating whether the species j has been recorded as established in jurisdiction i

Table 3.2. Description and definition of the hierarchical stochastic model (and its components) developed to investigate the influence of the covariates in Table 1 upon the recorded introduction of Nearctic turtles and the recorded establishment success of slider turtles. Functional forms were always modelled using a logit function.

We evaluated the model performance by calculating the Area Under the Curve of the Receiver Operative Characteristic curve (AUC ROC) of the models fitted using the training data, while the predictive ability of the models was estimated by calculating the AUC for the test dataset (Swets 1988; Pearce and Ferrier 2000). AUC values range from 0.5 (performance/predictive ability expected by chance) to 1 (perfect performance/predictive ability). AUC values were estimated using the package ROCR (Sing et al. 2005). We calculated the AUC values for each chain's iterations (and hence report on the median ± standard deviation and the 97.5% HPDI) as well as the AUC values obtained when using the median values of the coefficients (i.e., we estimated the median values for each coefficient first, and then used those coefficients to fit the model and calculate the predicted values, and the AUC; one AUC value per model).

In the case of the recorded establishment success of slider turtles, we used similar procedures as previously outlined for the recorded introduction, but we fitted the models by comparing successful establishment events of sliders with the total pool of slider introductions (Cassey et al. 2004a). Although our modelling approach allowed us to explicitly consider unreported introductions, we assumed that there was not enough information to assess whether there has been sufficient time after the introduction for the species to have become established (Jeschke and Strayer 2005). Hence, we only considered those jurisdictions where we were confident the species have been recorded as introduced for greater than five years. In the models for recorded establishment success, both the intercept and the slopes were constant. We used a training dataset (80% of recorded introduction events; 45 records) and a testing dataset (20%; 11 records). With the exception of the prior for the intercept in (3.3), which was specified as $N(-1, \sigma^2 = 10)$ because it is constant across all the data, the other priors, the variable/model selection procedure, and the structure of the models were the same as outlined for the recorded introduction analysis.

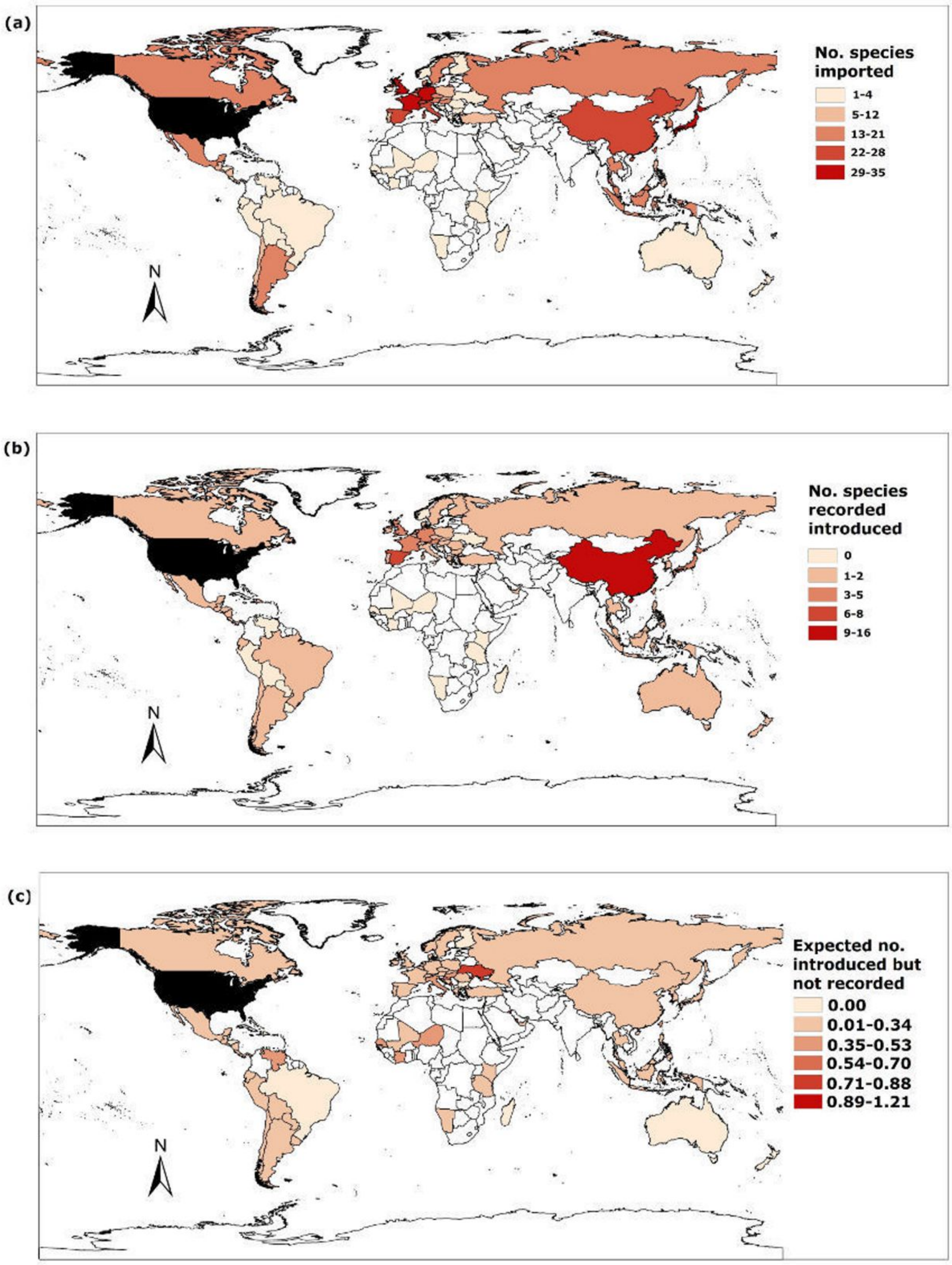

Fig. 3.2. Distribution of the number of turtle species (a) imported to 83 global jurisdictions, and (b) recorded in the literature as introduced (out of all the imported species). The expected number of turtle species introduced to a jurisdiction, but not recorded in the literature (c), is derived from the 'introduction' component of the top-ranked model. Values rank from 0 (no difference between the expected and recorded number of introduces species) to 1.21 (1.21 species expected introduced but none recorded). White areas indicate jurisdictions with no data, and the USA, the origin for the Nearctic species analysed here, is depicted in black.

Results

Recorded Introduction

Alien Nearctic turtle species have been widely introduced globally (Figure 3.2b). Model performance and predictive ability measurements indicated the reliability of the top-five-ranked models in matching the recorded pattern of introductions (Table 3.3; and see also Appendix 2 for the distribution of the posterior probabilities of all candidate models). Hereafter, we focus on the inference drawn from the top-ranked model.

Introduction of turtles was associated with the number of turtles exported and the age at maturity, while the detection of an introduction was influenced by the number of GBIF records. The number of turtles imported to that jurisdiction positively influenced the introduction of a turtle species (slope coefficient [median ± standard deviation]: 0.47 ± 0.14; 97.5% HPDI: (0.19, 0.76)), while the age at maturity had a strong negative effect (slope coefficient: -2.42 ± 0.96; 97.5% HPDI: (-4.24, -0.48)). The detection of an introduction increased with the number of GBIF records of freshwater turtles and amphibians in the jurisdiction (slope coefficient: 1.30 ± 1.40; 97.5% HPDI: (0.32, 5.51)). Although the model for the recorded introduction included a covariate for detection, the mean difference between the expected (introduction component of our model) and the recorded number of species introduced (in the database) per jurisdiction was low (Fig. 3.2c), with 1.21 being the maximum value obtained corresponding to Macau.

The introduction of turtles was also influenced by genus-specific differences (Fig. 3.4; see Appendix 2). The genus with the highest estimate for introduction was *Trachemys* (coefficient: 0.96 ± 0.92; 97.5% HPDI: (-0.70, 2.94)) and the genus *Sternotherus* (Musk turtles) had the lowest (coefficient: -2.75 ± 1.00; 97.5% HPDI: (-5.01, -1.11)). However, there was high variability and overlap in all of the estimates for the genus-specific intercepts (Fig. 3.4). Estimates for all model coefficients are provided in Appendix 2.

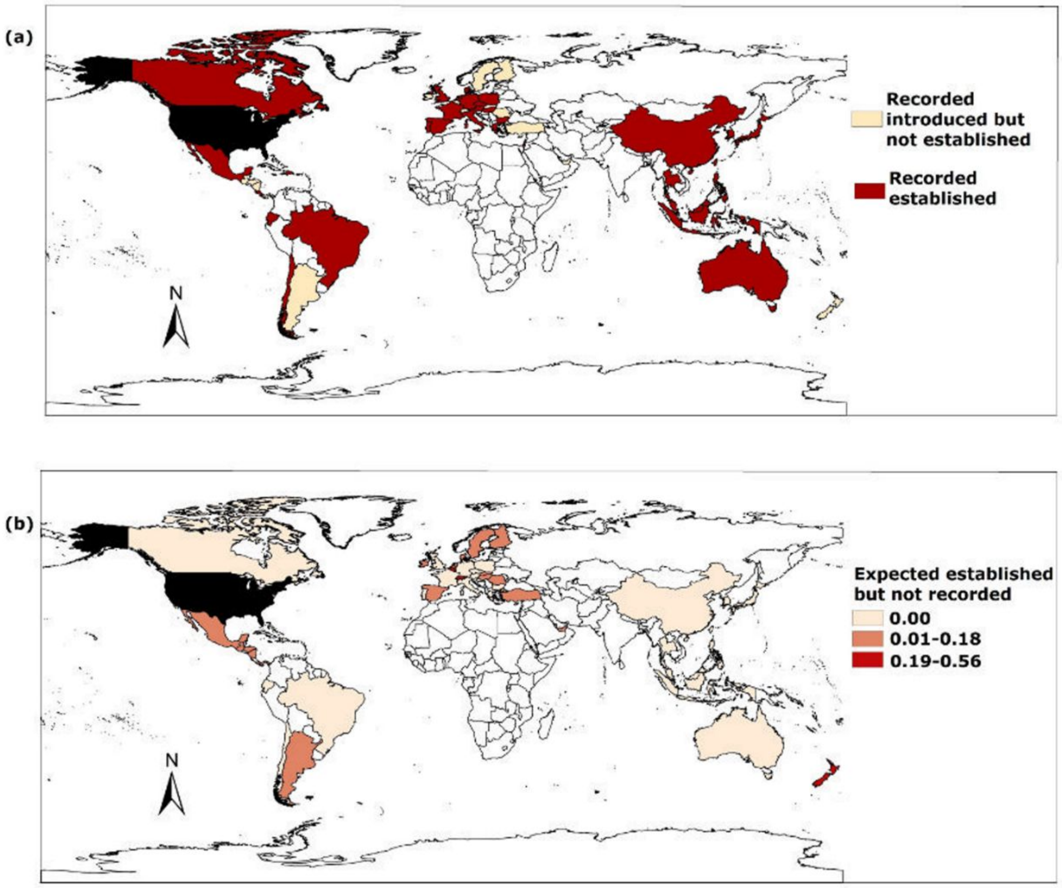

Fig. 3.3. Recorded distribution and status of alien populations of slider turtle for (a) those jurisdictions where it has been recorded as imported in our database, and (b) the expected establishment success of slider turtles in a jurisdiction, but not recorded in the literature. Expected establishment is derived from the 'establishment' component of the top-ranked model (see Table 3.3). Values can rank from 0 (no difference between the expected and recorded establishment success) and 1 (expected established but not recorded), although in this case the maximum value is 0.56.

Model structure	**Posterior probability**	**AUC train (iterations) Median ± standard deviation 97.5% HPDI**	**AUC test (iterations) Median ± standard deviation 97.5% HPDI**	**AUC train (median coefficients)**	**AUC test (median coefficients)**
Recorded introduction					
Introduction: Import + maturity Detection: GBIF	0.077	0.99 ± 0.01 (0.98, 1.00)	0.70 ± 0.04 (0.61, 0.77)	0.99	0.92
Introduction: Import + maturity Detection: GBIF + CL	0.055	0.99 ± 0.01 (0.98, 1.00)	0.69 ± 0.04 (0.61, 0.77)	0.99	0.92
Introduction: Import + maturity Detection: Density + GBIF	0.033	0.99 ± 0.01 (0.98, 1.00)	0.68 ± 0.04 (0.60, 0.77)	0.99	0.92
Introduction: Import + maturity Detection: Density + GBIF + CL	0.033	0.99 ± 0.01 (0.97, 1.00)	0.68 ± 0.04 (0.60, 0.76)	0.99	0.92
Introduction: Import Detection: GBIF	0.028	0.99 ± 0.01 (0.98, 1.00)	0.69 ± 0.04 (0.61, 0.78)	0.99	0.92
Recorded establishment success of slider turtles					
Establishment: Propagule + SPS Detection: GBIF	0.108	0.97 ± 0.07 (0.75, 1.00)	0.70 ± 0.13 (0.42, 0.90)	0.99	0.83
Establishment: Propagule + SPS Detection: Density	0.098	0.96 ± 0.08 (0.75, 1.00)	0.63 ± 0.16 (0.30, 0.92)	0.99	0.83
Establishment: Propagule + temperature + SPS Detection: GBIF	0.057	0.96 ± 0.08 (0.72, 1.00)	0.67 ± 0.13 (0.40, 0.90)	0.99	0.80
Establishment: SPS Detection: Density	0.052	0.96 ± 0.08 (0.73, 1.00)	0.43 ± 0.15 (0.17, 0.75)	0.99	0.50
Establishment: Propagule + temperature + SPS Detection: Density	0.048	0.91 ± 0.09 (0.71, 1.00)	0.57 ± 0.17 (0.27, 0.87)	0.99	0.80

Table 3.3. Posterior probability and Area Under the Receiver Operative Curve (AUC) for the top five ranked models for the recorded introduction and recorded establishment success of slider turtles. Covariate names follow abbreviations in Table 3.1. ‘Iterations’ indicate that those AUC values were calculated for each iteration, while ‘median coefficients’ denote the AUC values calculated from a model whose coefficients are the median values derived from all iterations.

Recorded Establishment Success of Slider Turtles

We have reported self-sustaining populations of slider turtles in 35 out of the 56 (62.5%) jurisdictions where the species has been introduced and present at large for at least five years (Fig. 3.3a). Our five top-ranked models for the recorded establishment success of slider turtles had good performance and predictive abilities (Table 3.3; and see also Appendix 2 for the distribution of the posterior probabilities of all candidate models). We focus on the results obtained from the top-ranked model, although the three top-ranked models had similar posterior probabilities (Table 3.3).

The establishment success of slider turtles was best explained by the propagule number and by the number of native freshwater turtles in the jurisdiction. The detection of established alien populations was associated with the number of GBIF records (Table 3.3). There was a strong influence of the propagule number (slope coefficient: 2.12 ± 1.69; 97.5% HPDI: (0.25, 6.55); Table 3.4), which was also similar to the estimate for the number of native freshwater turtle species (slope coefficient: 2.12 ± 2.23; 97.5% HPDI: (0.36, 4.83); Table 3.4). The cumulative number of GBIF records had a strong influence on the detection of established populations of slider turtles (slope coefficient: 1.10 ± 1.71; 97.5% HPDI: (-0.36, 6.09); Table 3.4). The mean difference between the expected (establishment component of our model) and the recorded establishment success (in the database) per jurisdiction was low (Fig. 3.3b), 0.56 being the maximum value obtained (Belgium), and indicating that established populations of slider turtles have been adequately reported in our database. All estimates for model coefficients are provided in Table 3.4.

	Median ± SD	**97.5% HPDI**
Establishment		
Intercept	-1.15 ± 0.91	(-2.75, 0.62)
Slope of propagule	2.12 ± 1.69	(0.25, 6.55)
Slope of SPS	2.12 ± 2.23	(0.36, 4.83)
Detection		
Intercept	1.01 ± 1.86	(-1.50, 5.84)
Slope of GBIF	1.10 ± 1.71	(-0.36, 6.09)

Table 3.4. Median posterior estimates (and 97.5% HPDI) of coefficients obtained from the top-ranked model for the recorded establishment of slider turtles (see Table 3.3). Covariate names follow abbreviations in Table 3.1. Estimates were obtained from 3 chains each with 300,000 iterations, discarding the first 200,000 iterations and a thinning of 10.

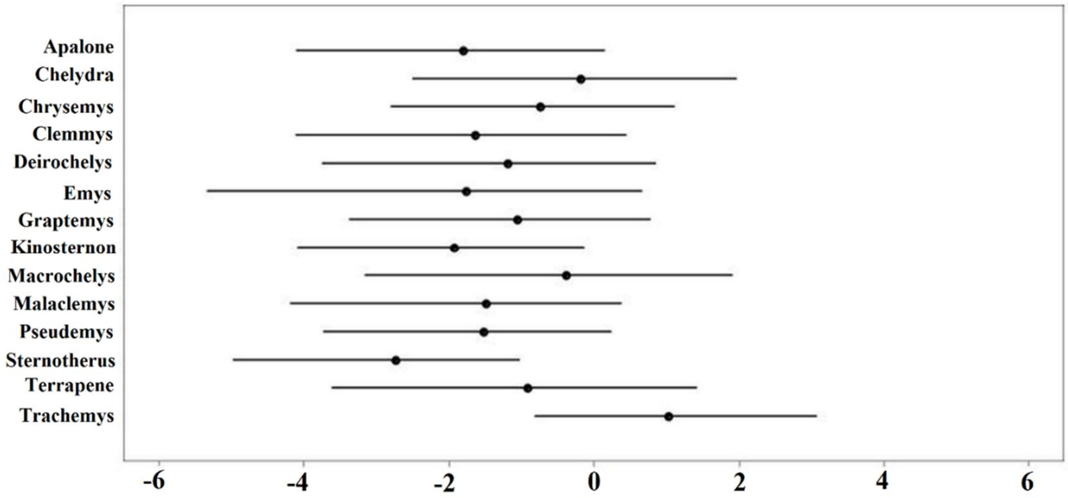

Fig. 3.4. Median posterior estimates (and 97.5% HPDI) of genus-specific intercepts obtained from the top-ranked model for the recorded introduction of Nearctic turtles (see Table 3.3).

Discussion

We found a clear association between the number of Nearctic turtles exported in the global wildlife trade and the introduction at a global scale, but we found no relationship between numbers traded and the establishment success of slider turtles, the most widespread species of alien turtle in the world. The introduction was driven by the number of imported turtles and the age at maturity. Alternately, the establishment success of slider turtles was driven by the number of release events and the availability of an adequate habitat for the species in the jurisdiction (as indicated by the association with the number of native turtle species). These results provide evidence that the global trade in turtles directly influences their introduction, while the relationship between establishment and trade is indirect, relying on the pressures of introduction (release or escape) to drive establishment success. Our study is one of the first to address explicitly the influence of detection on the outcomes of global comparative analyses of vertebrate invasions.

There is scarce research on the factors that influence the introduction (release or escape of individuals) of alien vertebrates and it is commonplace for transport and introduction to be addressed simultaneously (Cassey et al. 2004a; Cassey et al. 2004b; Jeschke and Strayer 2006; Leung et al. 2012; García-Díaz and Cassey 2014). Cassey et al. (2004b), Jeschke and Strayer (2006), and García-Díaz and Cassey (2014) working on alien parrots globally, fish, mammals and birds in Europe and North America, and on amphibians in Australia, respectively, found introduction probability to be related to the ease of transport of those groups and with proxies for the number of individuals transported. Our results support the hypothesis that the higher the number of turtles imported, the higher the introduction probability to a jurisdiction. Similar to the findings of Jeschke and Strayer (2006) for alien fish introduced to North America and Europe, we found that the age at maturity of turtles influenced their introduction. Previous studies have reported high likelihoods of establishment for reptiles and amphibians that attain maturity at young ages (Fujisaki et al. 2010; Van Wilgen and Richardson 2012). However, the underlying process determining why the age at maturity correlates to the introduction must be different than the process driving the relationship for establishment success. We can think of three plausible explanations for this relationship: (1) through the captive husbandry of species, some Nearctic turtles are known to become aggressive during the mating period (Highfield 1996; Luison and Redaelli 2008). This aggressiveness could drive the release (i.e., discard) and escape of particular species, which reach sexual maturity at an earlier age; (2) species that mature earlier can be bred in captivity earlier than late-maturing species. This could lead to an increased number of new captive individuals, and subsequently increase the chances of release; and (3) earlier sexual maturity implies reaching large body sizes earlier, fostering the release of big individuals that are more difficult to be cared for (Highfield 1996; Luison and Redaelli 2008).

The global establishment success of slider turtles was best associated with an increase in the number (species richness) of a jurisdiction's native turtles and a greater propagule number (measured as the number of release events). The presence of congeneric species has been demonstrated to positively influence the establishment success of mammals (Jeschke and Genovesi 2011), and amphibians and reptiles. This positive relationship most likely reflects the general suitability of the environment for freshwater turtles, including the alien slider turtle (Fridley et al. 2007; Tingley et al. 2011; Ferreira et al. 2012; Poessel et al. 2012; Liu et al. 2014). Even though this association is likely to reflect a response of alien turtles to similar environmental gradients, it suggests a link of potential conservation concern. Alien slider turtles are known to transmit a variety of diseases to native turtles in the recipient community (Hatcher et al. 2012; Hulme 2014), and an association with high number of native turtles would mean increasing the chances that these diseases will affect native species.

The role of propagule number in explaining establishment success is well established in the literature on alien vertebrates (Lockwood et al. 2005; Colautti et al. 2006; Simberloff 2009), and our results support this general evidence. However, our findings indicate that it is the number of release events (propagule number) rather than the number of imported turtles that drives their establishment success. This contrasts to results for other pet species relating the abundance of aquarium fish (either in shops or imported) to high rates of establishment success (Duggan et al. 2006; Gertzen et al. 2008; Bradie et al. 2013), but concurs with Carrete and Tella (2008) and Fujisaki et al. (2010) who found no relationship between the number of birds traded in Spain, and reptiles imported to Florida, and their establishment success, respectively.

Our results have broad implications for the fields of invasion ecology and alien species management. We have demonstrated that models explicitly accommodating detectability provided reasonable accuracy in matching recorded introductions and established populations. This confirms that some introduction events and established, self-sustaining, populations are likely under-reported (McGeoch et al. 2010; Lockwood et al. 2013), although the expected bias seems to be relatively small (see Fig. 3.2c and Fig. 3.3b). Our modelling framework provides a reliable, yet flexible, way to account for detection in comparative studies of introduction and establishment success to gain robust conclusions on the process of invasion. We advise to base the inference about the models (either on the effects sizes and/or the predictions) upon the median values derived from the complete set of iterations, given that this provides a better predictive framework as shown by the AUC values in Table 3.3.

Our results pose certain challenges for the management of invasions. Firstly, species-based risk assessments rely on the assumption that it is possible to predict the introduction and establishment success based on the characteristics of species and recipient environments and then ban those high risk species (Keller and Springborn 2013; Ricciardi et al. 2013). We indeed found that one species-specific trait (age at maturity) and a jurisdiction-specific covariate (the number of native species of turtles) influenced the introduction and establishment success, respectively. However, our findings also support the evidence that the number of turtles imported and propagule number have key roles influencing introduction and establishment success. Therefore, to manage turtle introductions it will remain important to focus not only on the attributes of the species and the jurisdiction, but critically also in reducing the number of specimens imported and kept. Finally, we reiterate that the factors influencing the introduction and establishment success of biological invasions are frequently different. It is particularly important to stress the value of researching the factors that affect the individual stages of the invasion pathway independently.

Statement of Authorship

Title of Paper	The illegal wildlife trade is a likely source of alien species	
Publication Status	☑ Published ☐ Submitted for Publication	☐ Accepted for Publication ☐ Unpublished and Unsubmitted work written in manuscript style
Publication Details	García-Díaz, P., Ross, J.V., Woolnough, A.P. & Cassey, P. (2016). The illegal wildlife trade is a likely source of alien species. *Conservation Letters*, early view. doi: 10.1111/conl.12301.	

Principal Author

Name of Principal Author (Candidate)	Pablo Garcia Diaz		
Contribution to the Paper	Planned and developed the research, compiled the data, developed the models and analysed the data, written the manuscript.		
Overall percentage (%)	80%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	14/02/2017

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Associate Professor Joshua V. Ross		
Contribution to the Paper	Contributed ideas to the development of the research, contributed to the development of the modelling and analytical framework, revised and edited the manuscript		
Signature		Date	14/02/2017

Name of Co-Author	Dr Andrew P. Wooolnough		
Contribution to the Paper	Contributed ideas to the development of the research, supported data compilation, and revised and edited the manuscript		
Signature		Date	14/02/2017

Name of Co-Author	Associate Professor Phillip Cassey		
Contribution to the Paper	Contributed ideas to the development of the research, revised and edited the manuscript		
Signature		Date	15/02/2017

Chapter 4. The illegal Wildlife Trade is a Likely Source of Alien Species

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Publication: García-Díaz, P., Ross, J.V., Woolnough, A.P. & Cassey, P. (2016). The illegal wildlife trade is a likely source of alien species. *Conservation Letters*, early view. doi: 10.1111/conl.12301.

Code accessibility: the annotated code for running the analyses in this Chapter is publically available at: https://github.com/pablogarciadiaz/PhD-thesis-code

Data accessibility: the databases are publically available from the webpage of the supplementary material of the publication in *Conservation Letters* (Open Access): http://onlinelibrary.wiley.com/doi/10.1111/conl.12301/full

Appendix: material accompanying this chapter can be found at Appendix 3 of this thesis.

Abstract

The illegal wildlife trade is driving biodiversity declines worldwide, yet its role in transporting alien species with a high likelihood of establishment is seldom considered. We demonstrate the threat posed by the illegal reptile trade in Australia. We modelled the establishment success of alien reptiles in Australia, revealing the importance of both minimum number of release events and the body length of the species. Using our model, we screened 28 alien reptiles illegally traded in Victoria, Australia. Establishment risk varied widely across species, and a whole-pathway analysis revealed that five out of the 28 species (17.9%) are likely to become established if released. The global dimension of the illegal wildlife trade calls for a tight transnational collaboration, via multilateral cooperation agreements arranging the share of resources. Complementary to this, we encourage conducting campaigns to raise public awareness about the risk and legal consequences of participating in the wildlife black market.

Keywords: alien reptile, Australia, biological invasion, biosecurity risk, establishment success, multilateral cooperation, propagule pressure, risk management, transport pathway

Introduction

The illegal wildlife trade is a threat to the persistence of animal populations worldwide, mainly due to overexploitation to meet the black market demand (Rosen and Smith 2010; Patel et al. 2015). An additional conservation concern is the potential for the illegal trade to be a source of alien invasive species and diseases in regions receiving illicitly traded animals (Smith et al. 2009). Alternately, regulating the wildlife trade as a pathway for invasive species might unintentionally foster the illegal trade in wildlife. Biosecurity policies aim to prevent the establishment of self-sustaining populations of new alien species, and commonly rely on conducting risk assessments to evaluate the likelihood of establishment of alien species; with species scored as high risk being banned from importation into the jurisdiction (Leung et al. 2012; Keller and Springborn 2013). Unfortunately, a risk-based system that prohibits species from importation might create the perverse outcome of making those species more desirable for wildlife enthusiasts, thus promoting the illegal wildlife trade (Rivalan et al. 2007). The interplay between alien species and the illegal wildlife trade has been largely neglected by researchers and decision-makers when addressing either the conservation issues of the illegal wildlife trade or the management of alien species.

Here we demonstrate the important role of the illegal wildlife trade as a source for alien species (biological invasion risk, hereafter), using the case example of the black market of alien reptiles in Australia. There is an existing legal trade in pet reptiles native to Australia (Swan 2008), but alien reptiles cannot be legally imported for private trade (Department of Environment, Government of Australia: https://www.environment.gov.au/biodiversity/wildlife-trade/exotics). Nevertheless, since 1999 alien reptiles are the group of vertebrates most commonly intercepted at the border, and by on-shore Australian biosecurity agencies (Henderson et al. 2011). An exceptional record of illegal alien reptiles has been maintained by one mainland Australian State, Victoria. This record was generated during a confiscation campaign, deployed as an amnesty for people to surrender alien species to authorities, and a concerted policing effort to seize alien species; over the period 1999-2012 (Fig. 4.1). The intensiveness of the campaign, and its long-term deployment (13 years) offers a rare snapshot of the wildlife black market and provides us with the unique opportunity to assess the biological invasion risk posed by the illegal trade in alien reptiles.

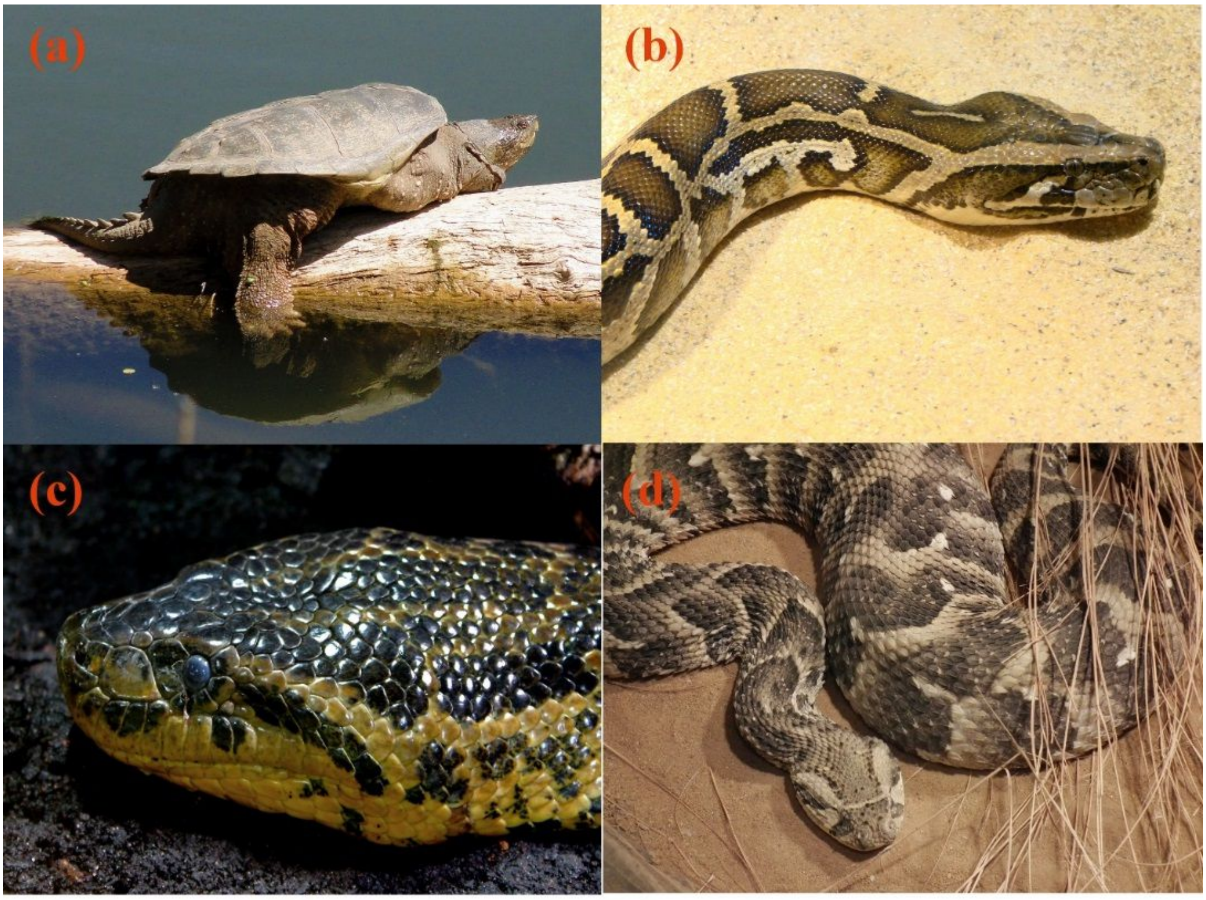


Fig. 4.1. The four top-ranked alien reptiles illegally traded in Australia based on the risk of establishment if released at moderate propagule number (n=3 releases; see Figure 4.3 and Appendix 3). (a) Common snapping turtle (*Chelydra serpentina*), mean posterior probability of establishment success in mainland Australia: 0.70 (photo source: Wikipedia user Leejcooper, licensed under Creative Commons); (b) Burmese python (*Python bivittatus*), mean posterior probability of establishment success: 0.59 (photo source: Wikipedia user Vassil, work released to the public domain); (c) Yellow anaconda (*Eunectes notaeus*), mean posterior probability of establishment success: 0.57 (photo source: Wikipedia user H. Zell, licensed under Creative Commons); (d) Puff adder (*Bitis arietans*), mean posterior probability of establishment success: 0.56 (photo source: Wikipedia user 4028mdk09, licensed under Creative Commons).

We conducted a two-stage process to evaluate the biological invasion risk of illegal alien reptiles. First, we developed and tested a predictive model for the establishment success of introduced reptile species in Australia. Second, we used our predictive model to screen 28 species that have been detected by the Victorian Government as being traded illegally within the jurisdiction. We evaluated the biological invasion risk posed by the black market pathway as a whole (i.e., how many species being illegally traded would likely become established if released?), and for each of the species traded (i.e., what is the likelihood of establishment success of a traded species if released?).

Material and Methods

Data

We gathered information on: (i) the identity of introduced reptile species into mainland Australia (the main continental landmass and Tasmania) and Australian island territories (Christmas Island, Cocos [Keeling] Islands, Lord Howe Island, and Norfolk Island); and (ii) whether these species are established or not, from sources including compilations on introduced reptiles globally and regionally (Kraus 2009; Henderson et al. 2011) and detection data provided by the Australian Government Department of Agriculture and Water Resources. We complemented these data sources with information obtained from a comprehensive literature review and from web pages reporting missing pets (see data accessibility statement). An introduced species was defined as one that has been released, or has escaped into the wild, in an area outside its native range (Blackburn et al. 2011). Our definition of introduced species encompasses both species whose native range does not include any part of jurisdictional Australia (alien species) and species whose native range includes part of jurisdictional Australia, but that have been introduced to other parts of the country not included within the limits of their native range (i.e., domestic exotic species) (Guo and Ricklefs 2010). We considered a species as established if it has been present for over ten years in the wild and has been reported as breeding (Blackburn et al. 2011). The final dataset contained 71 species-by-region (mainland / islands) records of 63 reptile species introduced anywhere in Australia, and their invasive status in the region (see data accessibility statement); between 1840 and 2005. Sixty species have been introduced to mainland Australia, five to Christmas Island, four to Cocos (Keeling) Islands, one to Lord Howe Island, and one to Norfolk Island (11 reptile species introduced to islands). Species introduced to mainland Australia belong to two extant reptile Orders: Testudines (turtles and tortoises; 13 species) and Squamata (lizards and snakes; 47 species), whereas all species introduced to islands are squamates. There was no information available on the establishment success of three of the 63 (5%) introduced species on the mainland, all of them domestic exotic species (namely, *Elseya dentata* [Gray, 1863], *Elusor macrurus* Cann & Legger 1994, and *Gehyra dubia* [Mackleay, 1877]). We treated the establishment success of these species as missing data.

For the 71 species-by-region records, we recorded six covariates for modelling the establishment success of introduced reptiles in Australia. Our choice of covariates was informed by existing knowledge of the factors related to the establishment success of introduced reptiles (Bomford et al. 2009b; Fujisaki et al. 2010; Van Wilgen and Richardson 2012; Mahoney et al. 2014; García-Díaz et al. 2015; Tingley et al. 2016a; Allen et al. 2017). The definition of the covariates, units, and transformations are provided in Table 1, and the data sources can be found in Appendix 3. We defined propagule number following Lockwood et al. (2005) as the minimum number of independent release events that have occurred regardless of the number of individuals released, for which there is no information available. The absolute thermal safety margin (aTSM) was defined following Clusella-Trullas et al. (2011) as the absolute difference between the species' preferred body temperature and the median average temperature of the warmest quarter in an area within 50 km of towns and cities in the region of introduction (see Appendix 3 for a description of methods and caveats of using aTSM values).

The Victorian Government has conducted an intensive campaign for recording, seizing and intercepting illegal alien wildlife during the period 1999-2012 (see data accessibility statement). Thirty-three alien reptile species were identified during the campaign, but we discarded those that have already been introduced into the country, and were used for fitting our own establishment model. In total, 28 alien reptiles new to Australia were evaluated (84.9% of the 33). For these species, we also compiled information on the same covariates potentially influencing establishment success as for the introduced species (see Appendix 3).

Covariate	**Definition and transformation**	**Summary statistics** **Mean ± standard deviation, and range**
Propagule number	Minimum number of independent release events ($\log_{10}$)	Turtles (n=13): 0.21 ± 0.30 (0.00-0.95) Squamates (n=58): 0.18 ± 0.23 (0.00-0.70) Total (n=72): 0.18 ± 0.24 (0.00-0.95)
Body length	Average adult body length, cm ($\log_{10}$) Turtles: carapace length Squamates: snout-vent length	Turtles (n=13): 1.43 ± 0.22 (1.00-1.82) Squamates (n=50): 1.39 ± 0.62 (0.60- 2.48) Total (n=63): 1.40 ± 0.56 (0.60-2.48)
Fecundity per breeding season	Number of eggs per clutch (oviparous species) Number of juveniles born per season (viviparous) (Squared root)	Turtles (n=13): 3.32 ± 0.81 (2.45-5.48) Squamates (n=50): 2.51 ± 1.19 (1.00-4.90) Total (n=63): 2.67 ± 1.6 (1.00-5.48)
Number of congeneric species	Total number of species of the same genus present in Australia ($\log_{10}$+1)	Turtles (n=13): 0.38 ± 0.40 (0.00-0.85) Squamates (n=58): 0.62 ± 0.63 (0.00-2.06) Total (n=72): 0.57 ± 0.60 (0.00-2.06)
Preferred body temperature	Average body temperature during activity bouts (° C)	Turtles (n=7): 26.19 ± 5.11 (21.80-37.00) Squamates (n=41): 31.73 ± 3.05 (22.50-38.10) Total (n=48): 31.01 ± 3.82 (21.80-31.80)
Area	Area of the region, km^2 / 10,000 ($\log_{10}$)	Mainland Australia: 2.89 Christmas Island: -1.87 Cocos (Keeling) Islands: -2.85 Lord Howe Island: -2.84 Norfolk Island: -2.46

Table 4.1. Definitions and summary statistics for the six covariates used for modelling establishment success of introduced reptiles in Australia and external Territories. Differences in sample sizes are because propagule number and the number of congeneric species vary across regions and alien species, whereas length and fecundity are species-specific covariates. Preferred body temperature was not a covariate in the model, but rather it was used to calculate the absolute Thermal Safety Margin. However, as there were missing data for body temperatures (15 species with missing data), we illustrate here the distribution for the species for which we had data, and which we used for the Bayesian imputation procedures.

Modelling Establishment Success

We modelled the probability of establishment success of introduced reptiles in Australia and the external Territories (pe_i for species i) as a function of the covariates through a regularised Bayesian logistic regression. We controlled for the potential effects of autocorrelation among taxonomic orders (Testudines vs. Squamata), the origin of the introduced reptiles (alien vs. domestic exotics), and the location of introduction (mainland vs. island) on the establishment by including an Order-specific, an origin-specific, and a location-specific intercept. The final model was defined as follows:

$$\text{logit}(pe_i) = \alpha_{or(i)} + \alpha_{g(i)} + \alpha_{og(i)} + \sum_{j=1}^{6} \beta_j X_{i,j} \qquad (4.1)$$

$$E_i \sim \text{Bernoulli}(pe_i) \qquad (4.2)$$

where $E_i \in \{0, 1\}$ is the establishment success of species i in Australia, $\alpha_{or(i)}$ represents the order-specific intercept, $\alpha_{g(i)}$ is the location of introduction-specific intercept (mainland and island), $\alpha_{og(i)}$ is the origin-specific intercept (alien and domestic exotics), β_j are the covariate coefficients (slopes), and $X_{i,j}$, j=1,…6, are the six putative covariates (Table 1). In order to obtain a Bayesian regularised model, we constructed a full model (i.e., including all the covariates in the logistic regression), and used a Laplace prior for the slopes $\sim Laplace(0, b)$ $b \sim Uniform(0.1, 2)$ (Gelman et al. 2013).

For the taxonomic Order, origin, and location-specific intercepts, we used a multivariate Normal prior, $\sim MVN(0, \Sigma)$, where Σ is the Order, origin or location-level variance-covariance matrix. We used an uninformative Wishart prior for Σ, where the variances (diagonal values) were $\sigma^2 = 100$, and the covariances (off-diagonal values) were set to zero (i.e., no autocorrelation between the levels of the intercepts). The degrees of freedom for the Wishart prior were set to two.

We ran the model using three chains, with 810,000 iterations each and with a thinning of five, discarding the first 400,000 iterations after checking for mixing and convergence of the chains. This procedure produced 246,000 draws from the posterior marginal distribution of the parameters. We conducted the Bayesian analyses using the R statistical software (R Development Core Team 2015) interface to the JAGS software (Plummer 2003) (see code accessibility statement). We report the mean and 95% Credible Interval (CI) values from the marginal posterior distribution for each parameter.

We assessed the performance of our model in matching the recorded patterns of establishment success by calculating the Area Under the Curve of the Receiver Operative Characteristic curve (AUC) and the Bayesian realised residuals. In both cases, we excluded the four species with missing data for establishment success. Bayesian realised residuals were calculated as (E_i - pe_i), and vary from -1 (predicted to establish but not recorded as established) to 1 (recorded as established but not predicted to establish), with zero indicating a perfect fit of the model (Gelman et al. 2013). We calculated the Bayesian realised residuals and AUC values for each iteration of the chains, and we report the means and 95% CIs.

Biological Invasion Risk of the Illegal Trade

We assessed the biological invasion risk posed by the illegal reptile trade using the full regularised model to estimate the establishment success (E_i, for species i) and the probability of establishment success (pe_i) for the illegally traded alien reptiles. We obtained posterior estimates of E_i, and pe_i for illegally traded reptiles for mainland Australia by inputting values for the covariates for each species in our model.

We evaluated the pathway-level risk by estimating the total number of the twenty-eight alien reptiles being illegally traded that would likely become established if released (Te), by summing across all the species' establishment success values:

$$Te = \sum_{i=1}^{28} E_i \qquad (4.3)$$

We had no information on the propagule number for the illegally traded species, given that they have never been introduced, so we performed analyses across a range of propagule number values (minimum number of release events regardless of the number of individuals), ranging from 1 to 20 releases, to represent a broad range of situations. In order to aid in the interpretation of our analyses, and to put our estimates for the probability of establishment success in context, we focussed on estimates of propagule numbers of one, three, and seven (low, moderate, and high propagule numbers, respectively). These corresponded to the lower 95 % CI, mean, and upper 95% CI values for propagule numbers for introduced reptile species already established in mainland Australia (19 species; obtained from our database on the introduced reptiles introduced into the country).

Results

Establishment Success

From 60 reptile species introduced into mainland Australia and territorial islands, and for which we had reliable information on their establishment success (out of a total of 63 species introduced), 23 have succeeded in establishing self-sustaining populations (38.3%), comprising 17 squamates (73.9% out of 23 established species) and six turtles (26.1%). Our regularised logistic model demonstrated good predictive performance (AUC, mean = 0.84; 95% Credible Intervals: [0.74, 0.90]; Bayesian realised residual, mean = 0.003; 95%CI: [-0.07, 0.11]), and revealed, after controlling for the effects of the taxonomic Order, origin, and location, that the establishment success of introduced reptiles in Australia was driven by propagule number, body length, and the area of the region where the species has been introduced.

Propagule number positively and strongly influenced establishment success (slope coefficient mean: 3.33; 95% CI: [0.48, 6.96]), whereas both body length and the area of the region of introduction had negative effects on the establishment success of introduced reptiles (Fig. 4.2 and Appendix 3). The species' fecundity had a marginally positive effect on establishment success (Fig. 4.2).

Biological Invasion Risk of the Illegal Trade

Species-specific estimates of the probability of establishment success varied across the pool of the 28 illegal species screened (Fig. 4.3 and Appendix 3). The only turtle species found in the illegal market, *Chelydra serpentina* (Linnaeus, 1758), always had the highest probabilities of establishment success of the 28 species. Alternately, two species of snakes always had the lowest probabilities of establishment success (*Micruroides euryxanthus* [Kennicott, 1860] and *Crotalus durissus* [Linnaeus 1758]).

The illegal reptile trade represents a biological invasion risk regardless of the simulated propagule number (Fig. 4.4 and Appendix 3). Our findings indicate that if illegal alien reptiles were released a moderate number of times (number of releases = 3), and in the absence of further on-shore management, approximately 12 of the 28 illegal species would be likely to become established (mean: 12.42; 95%CI: [4, 22]).

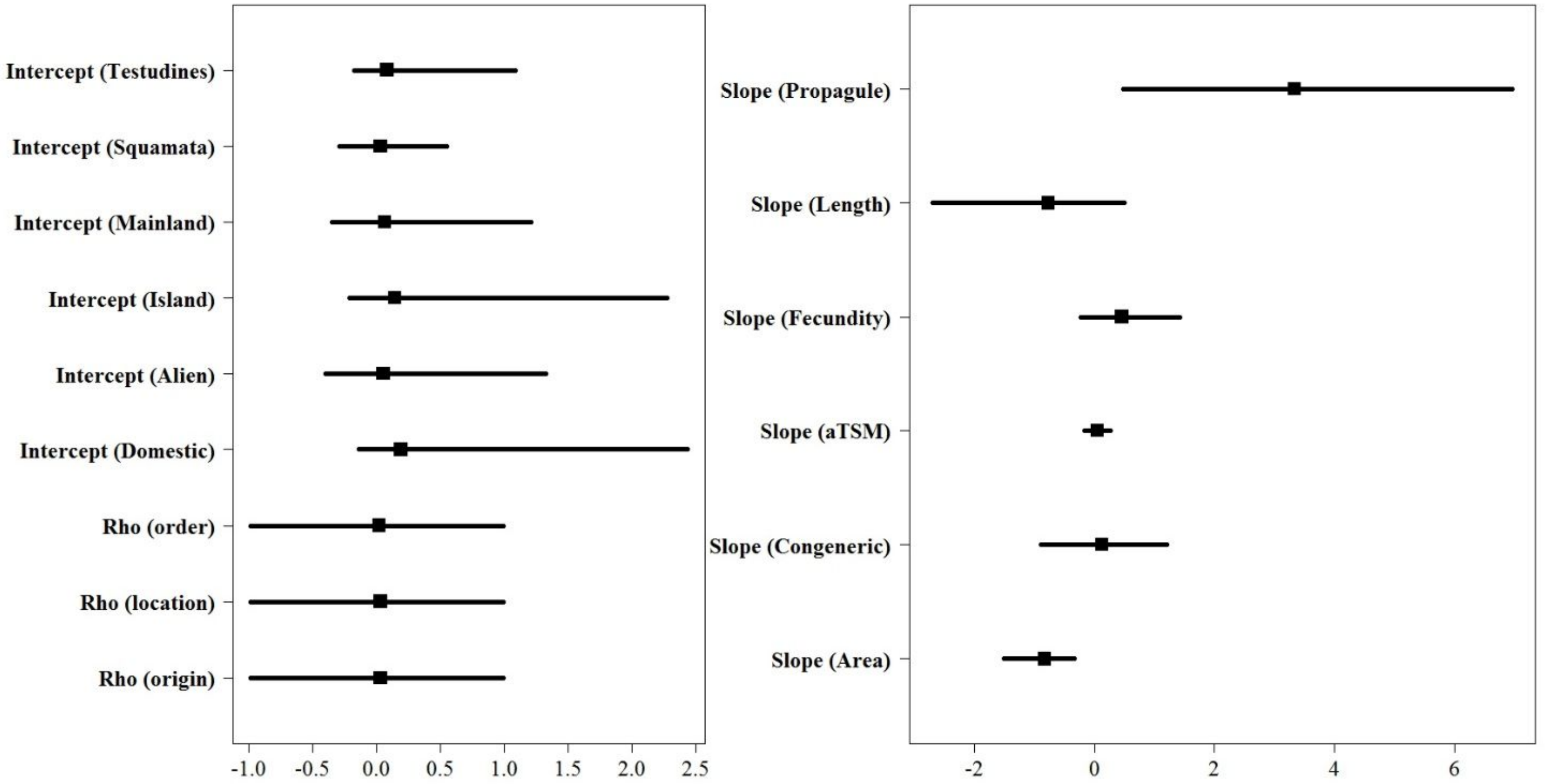
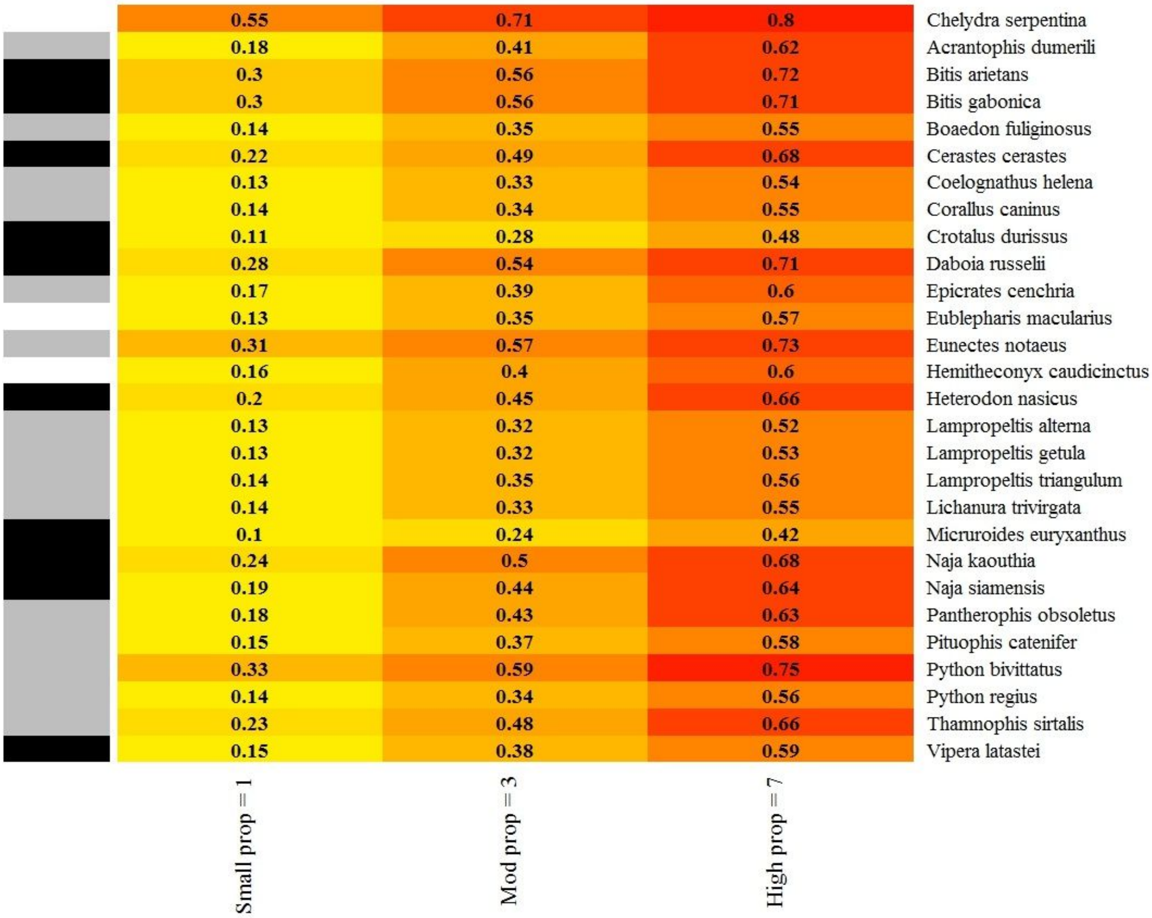


Fig. 4.2. Posterior estimates (mean and 95% Credible Intervals) of the effect sizes of the order- origin- and location-specific intercepts and of the covariates on the establishment success of introduced reptiles in Australia. Note that the values of the covariates were transformed (see Table 4.1). Rho are the intercept correlation coefficients between the groups.



	Small prop = 1	Mod prop = 3	High prop = 7	
	0.55	0.71	0.8	Chelydra serpentina
▒	0.18	0.41	0.62	Acrantophis dumerili
■	0.3	0.56	0.72	Bitis arietans
■	0.3	0.56	0.71	Bitis gabonica
▒	0.14	0.35	0.55	Boaedon fuliginosus
■	0.22	0.49	0.68	Cerastes cerastes
▒	0.13	0.33	0.54	Coelognathus helena
▒	0.14	0.34	0.55	Corallus caninus
■	0.11	0.28	0.48	Crotalus durissus
■	0.28	0.54	0.71	Daboia russelii
▒	0.17	0.39	0.6	Epicrates cenchria
	0.13	0.35	0.57	Eublepharis macularius
▒	0.31	0.57	0.73	Eunectes notaeus
	0.16	0.4	0.6	Hemitheconyx caudicinctus
■	0.2	0.45	0.66	Heterodon nasicus
▒	0.13	0.32	0.52	Lampropeltis alterna
▒	0.13	0.32	0.53	Lampropeltis getula
▒	0.14	0.35	0.56	Lampropeltis triangulum
▒	0.14	0.33	0.55	Lichanura trivirgata
■	0.1	0.24	0.42	Micruroides euryxanthus
■	0.24	0.5	0.68	Naja kaouthia
■	0.19	0.44	0.64	Naja siamensis
▒	0.18	0.43	0.63	Pantherophis obsoletus
▒	0.15	0.37	0.58	Pituophis catenifer
▒	0.33	0.59	0.75	Python bivittatus
▒	0.14	0.34	0.56	Python regius
▒	0.23	0.48	0.66	Thamnophis sirtalis
■	0.15	0.38	0.59	Vipera latastei

Fig. 4.3. Mean posterior probability of establishment success in mainland Australia for 28 illegally traded alien reptile species. Values are plotted for three scenarios where the propagule number was varied (low, moderate and high propagule number). Colours rank species by their mean probability of establishment, in a range from yellow (low risk) to red (high risk). The first species, the Common snapping turtle (*Chelydra serpentina*) is the only turtle species, and all other species belong to the order Squamata. Rows coloured to the left are snakes, and a black cell indicates venomous species. Note, to improve interpretability, propagule number values are not transformed here. Posterior estimates (mean and 95% CIs) can be found in Appendix 3.

Discussion

The illegal trade in alien reptiles can pose genuine biological invasion risks. It is likely that the next alien reptile invader may already be present within an Australian jurisdiction. We found that introduced reptile species that had been released more frequently (higher propagule number) than other introduced reptiles were more likely to form a self-sustaining population in Australia. The importance of propagule number as a determinant of establishment success is a pervasive finding in invasion ecology and introduced reptiles are no exception (Bomford et al. 2009b; Mahoney et al. 2014; García-Díaz et al. 2015). Larger reptiles were less likely to become established, an effect previously reported to influence the establishment success of introduced reptiles (Mahoney et al. 2014; Tingley et al. 2016a). We suggest that the effect of body length, combined with the marginal positive effect of fecundity, upon establishment success of introduced reptiles in Australia indicates a positive relationship with fast-paced life histories (Vitt and Caldwell 2009; Herrando-Pérez et al. 2012; Allen et al. 2017).

Illegal alien reptiles, released at moderate or even low propagule numbers, could potentially become established in Australia (Figs. 4.3 and 4.4). Once established, it is exceedingly difficult to control or eradicate alien reptiles, and any potential impact would likely be very difficult to manage (Engeman et al. 1998; Kraus 2009). It is particularly concerning that ten out of the 28 species illegally traded are venomous snakes, which could be a serious hazard for the human and native wildlife populations if they were to become established in Australia (Fig. 4.3 and Appendix 3). Thus, the illegal trade in alien reptiles represents a risk in terms of both the likelihood of establishment and the high hazard for people and wildlife (Mazza et al. 2013).

We have focussed on the biological determinants of the risk posed by the illegal wildlife trade, but human factors would clearly add to the overall risk (Perry and Farmer 2011). Particularly, we recommend more research into the dynamics of the black market and the motivations for keeping and releasing animals, which will determine the propagule number. Such research would serve to highlight potential policing targets (Perry and Farmer 2011; UNODC 2016). For the purposes of our work, we have assumed that reptile species detected in Victoria represent an adequate sample of illegal species available across Australia. Smugglers act across States indicating that our assumption is reasonable (see for example this article: http://goo.gl/XiZjkl). Complementary information about the species traded in each State will produce a more nuanced image of the biological invasion risk posed by illegal reptiles in Australia. Nonetheless, we expect that such information would be difficult to obtain, and it is not clear whether it will lead to substantial changes in policies (Canessa et al. 2015).

Our work has important policy implications for the management of alien species and the illegal wildlife trade, closely aligned with the proposals recently made by the United Nations Office on Drugs and Crime in the *World Wildlife Crime Report* (UNODC 2016). The demand created by the illegal trade in wildlife must be tackled in concert with regulations and policy for the legal wildlife trade to ensure that both are adequately acknowledged and managed as important components of the overall biological invasion risk from the trade in wildlife. The illegal wildlife trade is an international issue and, therefore, the receiving jurisdictions should cooperate with potential exporting jurisdictions for addressing the biological invasion risks posed by the pathway (Wyatt 2013; Challender et al. 2015). Receiving jurisdictions could aim to identify potential source regions, and explicitly incorporate into their legislation the need for transnational cooperation including the allocation of appropriate resources for the task (Rosen and Smith 2010; Banks et al. 2015; Patel et al. 2015). It is possible that the trade in one species is legal in the exporting country, but illegal in the receiving jurisdiction (UNODC 2016). In this situation, we suggest the development of multilateral agreements and frameworks to address globally the risks posed by the trade of wildlife. These agreements will provide policy and legislative certainty about the demanded roles and responsibilities of the signatory countries. In any case, all policies will also require appropriate public awareness campaigns, strongly emphasising not only the risks posed by illegally traded animals but also the legal repercussions associated with their illegal possession (TRAFFIC 2008; Moorhouse et al. 2016).

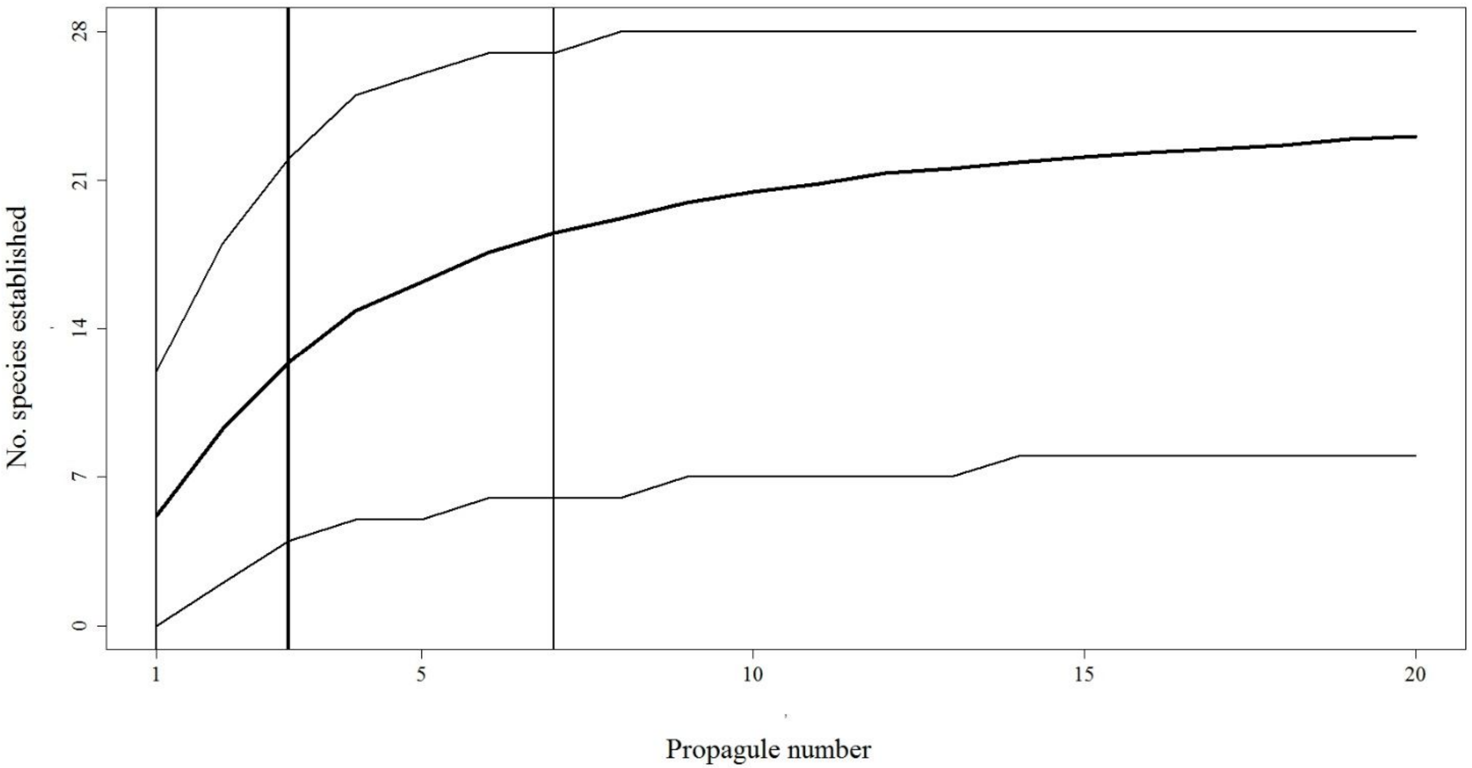


Fig. 4.4. Posterior estimate of the total number of illegally traded alien reptiles in mainland Australia (mean and 95% Credible Intervals) that would likely become established if introduced at various propagule numbers (maximum = 28 species established). Vertical lines indicate low, moderate, and high propagule numbers (one, three, and seven, respectively). Note, to improve interpretability, propagule number values are not transformed here. Posterior estimates (mean and 95% CIs) can be found in Appendix 3.

Statement of Authorship

Title of Paper	Transport pathways shape the biogeography of alien freshwater fishes	
Publication Status	☐ Published ☑ Submitted for Publication	☐ Accepted for Publication ☐ Unpublished and Unsubmitted work written in manuscript style
Publication Details	García-Díaz, P., Kerezsy, A., Unmack, P.J., Lintermans, M, Beatty, S.J., Butler, G.L., Freeman, R., Hammer, M.P., Hardie, S., Kennard, M.J, Morgan, D.L., Pusey, B.J., Raadik, T.A., Thiem, J.D., Whiterod, N., Cassey, P. & Duncan, R.P. (submitted). Transport pathways shape the biogeography of alien freshwater fishes. Submitted to *Global Change Biology*.	

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Contribution to the Paper	Planned the article, data collection and curation, developed the statistical models, performed the analyses, interpreted the data and results, and wrote the manuscript.		
Overall percentage (%)	70%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Contribution to the Paper	Assisted with development of project, conducted the primary data collection, edited the manuscript.		
Signature		Date	16th Feb 2017

Name of Co-Author	Phillip Cassey		
Contribution to the Paper	Contributed ideas to the development of the research, revised and edited the manuscript		
Signature		Date	16th Feb 2017

Chapter 5. Transport pathways shape the biogeography of alien freshwater fishes

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Publication: García-Díaz, P., Kerezsy, A., Unmack, P.J., Lintermans, M., Beatty, S.J., Butler, G., Freeman, R., Hammer, M.P., Hardie, S., Kennard, M.J., Morgan, D.L., Pusey, B.J., Raadik, T.A., Thiem, J., Whiterod, N., Cassey, P. & Duncan, R.P. (submitted). Transport pathways shape the biogeography of alien freshwater fishes. *Global Change Biology*, submitted.

Code accessibility: the annotated code for running the analyses in this Chapter is publically available at: https://github.com/pablogarciadiaz/PhD-thesis-code

Data accessibility: the presence data and the identity of the alien fishes will be publically available from FigShare after the embargo expires. For the purposes of marking, the data can be downloaded from the following link: https://figshare.com/s/72579e1bd4839e09ac2b

Appendix: material accompanying this chapter can be found at Appendix 4 of this thesis.

Abstract

Changes in human activities can cause alterations in the suite of alien species that are transported and spread, but the mechanisms shaping these changes are poorly understood. We assessed the extent to which changes in human usage of alien freshwater fishes has determined and altered their biogeography in Australia. We analysed alien fish species richness pre-1970 and post-1970, examining changes in the original transport pathways for each species established, and modelled richness based on drainage features. We recognised four distinct international transport pathways for alien fishes in Australia: acclimatisation, aquaculture, biocontrol, and ornamental. The importance of each pathway has changed substantially between the two periods, and these shifts have been accompanied by similar drainage-level changes in richness patterns and the influence of covariates on alien fish richness. Pre-1970, most of the species were purposefully transported by acclimatisation societies (64% of species) leading to higher richness in plain inland drainages impacted by human activities, located at a higher elevation compared to drainages with fewer alien fishes. Our findings for this period reflect the European colonisation and settlement of Australia. In contrast, the post-1970 period was characterised by the establishment of ornamental fishes (68% of species), resulting in higher richness mainly in north-eastern tropical and sub-tropical coastal drainages that tended to be topographically steeper than drainages with fewer species. Our results demonstrate that temporal changes in human uses of alien fishes have produced a cascade of processes modifying both the biogeographical patterns and the underlying processes. Moreover, our conclusions suggest a need for caution when using historical richness data to assess potential future patterns in alien species richness. The continuing introduction of alien species will further alter ecological communities, to the extent that traditional biogeographical units may no longer be identifiable in the foreseeable future.

Keywords: acclimatisation, Australia, community alteration, human-induced environmental change, ornamental trade, turnover

Introduction

Modern biogeographic patterns are increasingly shaped by human activities (Lockwood and McKinney 2001; Dirzo et al. 2014; Lewis and Maslin 2015). Introductions of alien species, for example, alter biogeographic patterns by overcoming natural dispersal barriers and impacting on the composition of the recipient ecological communities, leading to biotic homogenisation (Olden et al. 2004; Helmus et al. 2014; Capinha et al. 2015). As human societies change, there are often shifts in the pathways involved in the transport of alien species, such that past changes to species distributions resulting from alien introductions may not predict likely future changes (Wilson et al. 2009; Hulme 2015; Petchey et al. 2015). Acclimatisation societies, defined as those organisations that purposely introduced species to new areas as either a food resource or recreational species, were a major driver of alien vertebrate introductions in the nineteenth and early twentieth (Lever 1992; Duncan et al. 2006; Hulme 2015). More recently, transport pathways such as the wildlife trade and the unintentional transport of stowaways have become the primary sources of new alien species (Hulme 2015). This shift is likely to alter the type of species being introduced and the locations in which they establish.

Changes in the importance of different introduction pathways over such short time periods suggest that the biogeographical changes associated with alien species introductions are more dynamic than what may occur in natural systems (Holt et al. 2013; Capinha et al. 2015). Determining the occurrence, extent, and causes of changes to biogeographical dynamics due to changes to transport pathways is thus an essential goal for explaining how biogeographical dynamics are shaped by human activities (Gaston and Blackburn 2008; Lomolino et al. 2010). Factors influencing alien species richness can be understood in terms of event-level factors (unique to specific introduction events, such as the number of individuals released and the frequency of releases), environmental factors (features of the release site such as habitat characteristics and the presence of native species), and species-specific factors (features of the alien species such as life-history traits) (Duncan et al. 2003; Pyšek et al. 2010a; Pyšek et al. 2010b). Changes in human behaviour can affect the biogeography of alien species by influencing each of these three groups of factors; for example through changes in the taxonomic pool of alien species transported to a region, the numbers of individuals being transported, and the locations where they are released (Blackburn and Duncan 2001a; García-Berthou et al. 2005; de Miguel et al. 2016).

Alien freshwater fishes can have substantial negative impacts on the environments they invade (Cucherousset and Olden 2011; Closs et al. 2015; Howeth et al. 2016), and can alter the composition of native fish communities (Rahel 2010; Marr et al. 2013; Toussaint et al. 2016). In Australian freshwater systems, which boast a highly endemic aquatic fauna (Unmack 2013), alien fishes have been linked to declines in native fishes through predation, competition, disease spillover, and habitat alteration (Crowl et al. 1992; Lintermans 2004; Olden et al. 2008; Lymbery et al. 2014). Forecasting the threat and likely impacts of future introductions of alien fishes relies on understanding transport pathways and how these are changing over time. Here we assess the influence of recent changes in transport pathways in shaping the biogeography of alien freshwater fishes in Australian drainages. We compiled a comprehensive database of the alien freshwater fish species richness in 144 drainages in Australia. We used the data to examine the alien fish richness in each drainage in two periods: pre-1970, where most species were intentionally released for acclimatisation purposes; and post-1970 where most species originated through the ornamental aquarium trade. We examined how the change in transport pathways led to concomitant shifts in the influence of the characteristics of the recipient drainage basins on alien fish species richness, by constructing and comparing models that explained alien fish richness pre-1970 and post-1970 using location-specific covariates (Kéry and Royle 2016).

Materials and Methods

Data

We considered alien freshwater fish species to be taxa whose native range does not include any part of Australia and that have established reproductive, self-sustaining, populations in the freshwater reaches of at least one Australian drainage (Blackburn et al. 2011). We compiled a database of alien fish richness and identified how many became established in each freshwater drainage in Australia in two periods, pre- and post-1970. We used the drainages delineated in the Australian Hydrological Geospatial Fabric, Geofabric, as our geographical units for compiling the richness data (Stein et al. 2014). Data on alien fishes were sourced from an extensive literature review (see Appendix 4 for full details), records obtained during recent field surveys conducted by us, museum records, and state fish distribution databases. See the data accesibility statement for the presence data and the identity of the alien fishes. The predominant transport pathway by which each species initially established was obtained from Lintermans (2004) and Harris (2013), subsequent publications and expert assessment by the authors, and assigned to one of four categories: acclimatisation, ornamental, aquaculture, and biocontrol (Fig. 5.1c). The final database consisted of records of 32 alien freshwater fish species established in at least one of 144 drainages across Australia (Fig. 51 a, b). Fourteen alien species had established in 121 drainages pre-1970, whereas 31 species established in 82 drainages post-1970.

To model alien fish richness, we gathered information on eight geographical and environmental features of the drainages consistently reported in the literature to be associated with the richness and establishment of alien fishes (García-Berthou 2007; Gozlan et al. 2010; Clavero 2011; Howeth et al. 2016; Liew et al. 2016; Liu et al. 2017). The covariates are described in Table 5.1 and were collected from publications and online databases (Wildlife Conservation Society and Center for International Earth Science Information Network 2005; Jetz et al. 2012; Kriticos et al. 2012; Stein et al. 2014). See the data accessibility statement for information on obtaining the databases. Colonisation pressure, the total number of alien species introduced, including those that failed to establish, at each location is an important predictor of alien species richness, including fishes (Marchetti et al. 2004; Lockwood et al. 2005; Lockwood et al. 2009). Unfortunately, these data were not available for most drainages. We mitigated the potential impact of this lack of data by only analysing the 144 drainages where at least one alien fish species had established; these were all drainages subject to some degree of activity associated with alien fish introductions.

Statistical Analyses

We examined spatial changes in alien fish species richness between periods by calculating species turnover at the drainage level. The turnover was calculated by dividing post- 1970 species richness by the total species richness (species established post-1970 + species established pre-1970) in each drainage. The index varies between 0 (all species established pre-1970) to 1 (all species established post-1970).

To identify how changes in transport pathways may have altered the relationship between the characteristics of the drainages and their alien fish richness, we modelled alien fish richness in each of the 144 drainages during each time period as a function of the eight covariates. As the models were only of species richness in each period, the model post-1970 models did not include species established in the same drainage pre-1970. This is because we wanted to examine the patterns of richness in each period independently. We used a Bayesian Markov Chain Monte Carlo regularised Poisson-log regression to model the alien fish richness as a function of the eight covariates along with topographic drainage division-specific intercepts included in the models. This was done to account for the potential autocorrelation between drainages within a same hydrological division (topographic divisions are made up of drainages) (Bolker et al. 2009). We used the topographic divisions described in Geofabric (Stein et al. 2014), and the 144 drainages considered here belong to 11 independent topographic divisions (out of 13 total divisions in Australia; Fig. 5.2).

We constructed Bayesian regularised models by including all covariates and specifying a Laplace prior for each slope, ~ *Laplace*(0, *b*), *b* ~ *Uniform*(0.1, 5). This procedure shrinks slope estimates towards zero when the association between alien fish species richness and the covariate is weak (Hooten and Hobbs 2014). Covariates were standardised by subtracting the mean and dividing by the standard deviation. We used a multivariate normal prior for the topographic division-specific intercepts, ~ *MVN(*0, Σ_{dv}), where Σ_{dv} is the division-specific variance-covariance matrix. We used a Wishart prior for Σ_{dv} with variance σ^2 = 100, and covariances set to zero (meaning no correlation between topographic divisions). The degrees of freedom of the Wishart distribution were configured to be the total number of topographic divisions plus one (i.e., 12). The inclusion of a multivariate normal prior for topographic division-specific intercepts allowed us to account jointly for alien fish richness patterns not captured by the eight covariates and the potential non-independence of topographic divisions (e.g., due to their spatial closeness). We assessed the fit of our models to the alien fish species richness data by calculating the R^2, following Gelman and Pardoe (2006). We ran all the Bayesian regularised Poisson-log models using JAGS (Plummer 2003) as interfaced to the R statistical environment (R Development Core Team 2015). See the code accessibility statement for the annotated JAGS code. We fitted the models using three chains with 400,000 iterations each and no thinning. We discarded the first 10,000 iterations of each chain as burn-in after visually checking for adequate mixing and convergence of the chains. This procedure produced 1,170,000 values of the posterior marginal distribution for each coefficient in the models.

We examined whether there had been temporal changes in how the eight covariates were associated with alien fish species richness. To do this, we assessed the magnitude of change in the covariates between periods by subtracting the pre-1970 posterior marginal values of the slopes from the post-1970 values and then calculating the proportion of these differences that were greater or less than zero. Situations where the difference pre- and post-1970 was greater or less than zero, indicate substantive changes in a coefficient estimate, implying that its association with alien fish species richness had changed over time.

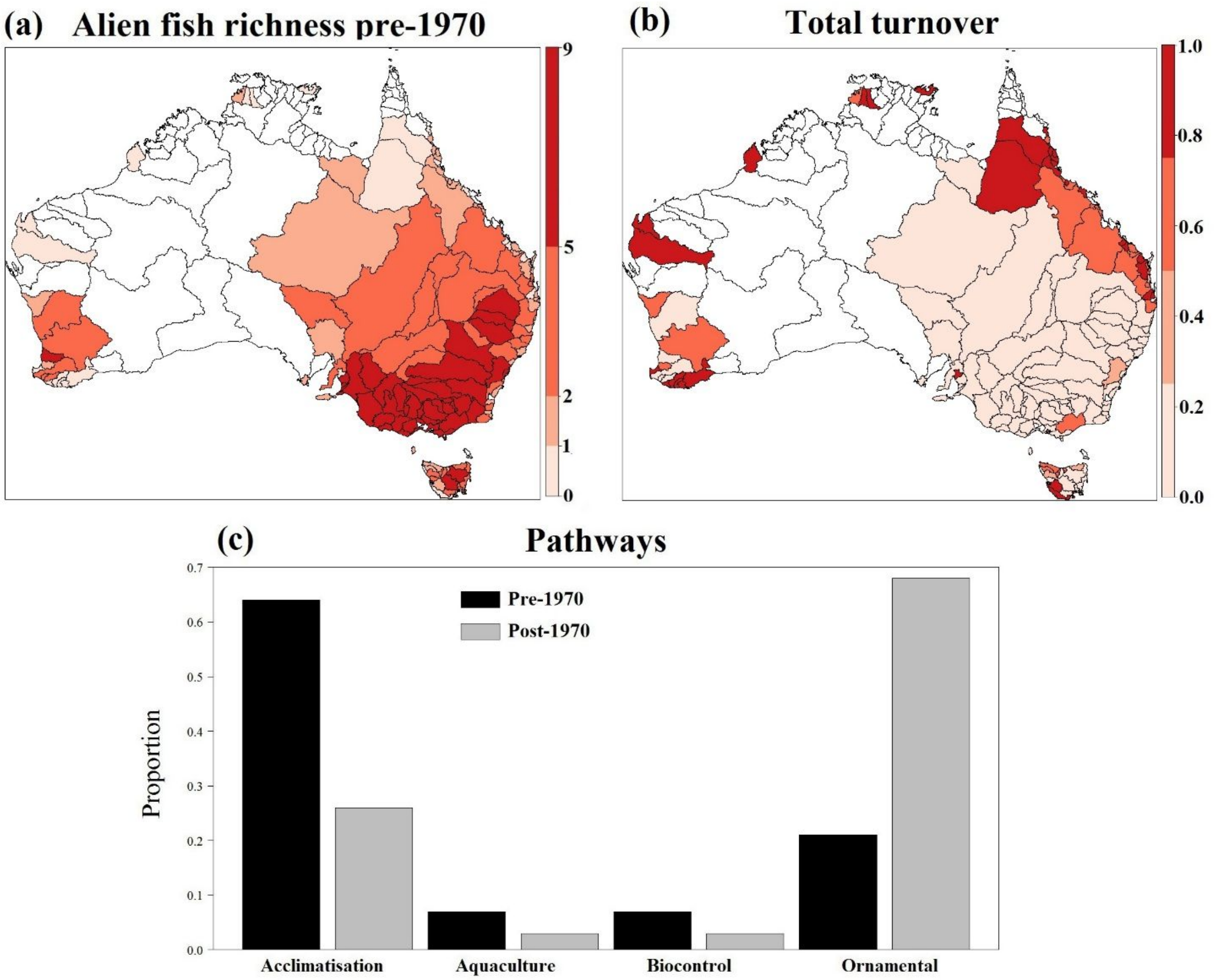


Figure 5.1. (a) Alien fish richness in 144 drainages in Australia, pre-1970; (b) turnover in alien fish communities in 144 drainages in Australia; and (c) the proportion of established alien fish species initially transported via four pathways for each period. White drainages were those were no alien fish occurred and were not included in the analyses.

Covariate	**Type of covariate**	**Definition**	**Summary statistics; Mean ± standard deviation (minimum, maximum)**
Area	Geographical: drainage-specific	Area of the drainage, km^2	28460.30 ± 77970.61 (153.70, 699162.00)
Human influence index (HII)	Environmental: drainage-specific	Median human influence index across the drainage	18.38 ± 11.28 (0.00, 75.00)
Flow length	Geographical: drainage-specific	Median number of upstream drainage 1-km^2 cells across the drainage	13.13 ± 5.11 (4.00, 36.00)
Flow accumulation	Geographical: drainage-specific	Median total number of upstream drainage 1-km^2 cells across the drainage	120.91 ± 41.75 (41.00, 334.00)
Upstream slope	Geographical: drainage-specific	Median average slope across the drainage	192.00 ± 166.96 (7.00, 681.50)
Upstream elevation	Geographical: drainage-specific	Median average elevation across the drainage	259.00 ± 204.22 (47.00, 1043.00)
Minimum temperature	Environmental: drainage-specific	Median minimum temperature in January across the drainage	15.85 ± 4.63 (7.05, 25.60)
Maximum temperature	Environmental: drainage-specific	Median maximum temperature in July across the drainage	15.40 ± 5.37 (7.30, 31.10)

Table 5.1. Description and summary statistics of the eight covariates used for modelling the alien fish species richness in 144 drainages in Australia. Summary statistics are of the covariate values before they were standardised for analysis. Note that the 144 drainages were the same for both pre-1970 and post-1970 periods.

Results

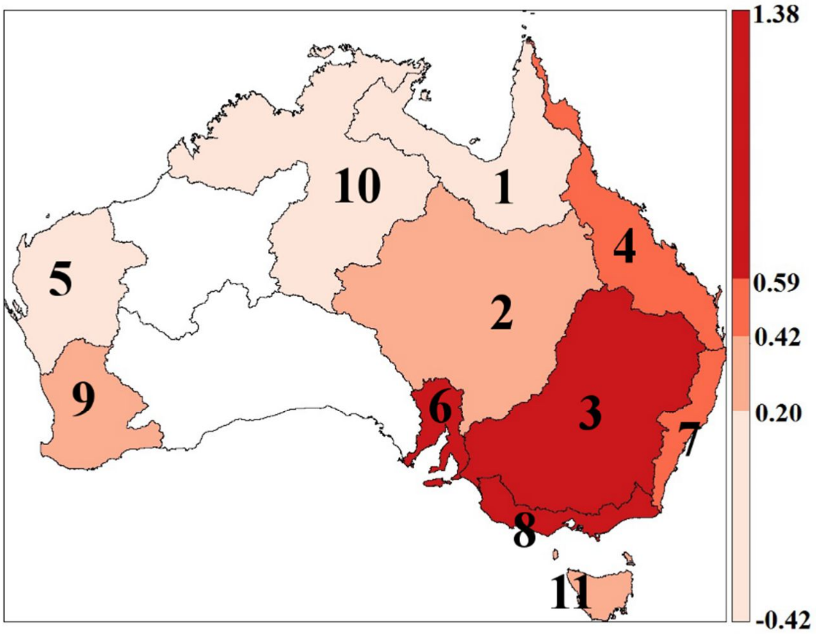
Species Richness Patterns, Turnover and Transport Pathways

The south-eastern part of Australia generally had the highest alien fish richness pre-1970, with the Murray-Darling Basin, southern Victoria and Tasmania being the major hotspots of alien fishes (Figs. 5.1a and 5.2a). Turnover of alien fishes pre- and post-1970 was highly variable across the 144 drainages, with areas of high turnover in tropical and sub-tropical drainages of the north, eastern, and western coasts (Fig. 5.1b). There was also high turnover in a few drainages of the northern and western coasts of Tasmania. The large inland drainages had lower turnover and all were less than 0.2 (Fig. 5.1b). Across all drainages, the mean turnover was 0.34 ± 0.39 (mean ± standard error), with over half of the drainages having low turnover <0.2 (54% of 144), and 27 drainages having high turnover >0.8 (19% of 144).

Coefficient	**Pre-1970**	**Post-1970**
Topographic division-specific intercepts		
Carpentaria Coast	-0.01 ± 0.51 (-1.12, 0.98)	-0.40 ± 0.54 (-1.52, 0.48)
Lake Eyre Basin	0.19 ± 0.59 (01.03, 1.30)	-0.21 ± 0.76 (-1.75, 1.40)
Murray-Darling Basin	1.37 ± 0.14 (1.09, 1.66)	-0.70 ± 0.30 (-1.34, 0.07)
North East Coast	0.56 ± 0.22 (0.00, 0.96)	0.50 ± 0.22 (0.07, 0.96)
Pilbara-Gascoyne	-0.42 ± 1.01 (-3.21, 0.84)	-0.27 ± 0.61 (-1.69, 0.64)
South Australian Gulf	0.63 ± 0.19 (0.25, 1.00)	-0.84 ± 0.52 (-2.15, -0.19)
South East Coast (New South Wales)	0.43 ± 0.18 (0.04, 0.77)	-1.03 ± 0.37 (-2.03, -0.52)
South East Coast (Victoria)	1.12 ± 0.18 (0.78, 1.47)	-0.04 ± 0.48 (-1.22, 0.58)
South West Coast	0.28 ± 0.23 (-0.21, 0.71)	0.20 ± 0.33 (-0.45, 0.77)
Tanami-Timor Coast	0.14 ± 0.55 (-0.96, 1.32)	-0.11 ± 0.49 (-1.20, 0.62)
Tasmania	0.25 ± 0.22 (-0.15, 0.72)	-0.01 ± 0.45 (-1.16, 0.52)
Covariates		
Area	0.10 ± 0.10 (-0.08, 0.30)	-0.11 ± 0.14 (-0.43, 0.13)
Human influence index (HII)	0.26 ± 0.07 (0.12, 0.38)	0.21 ± 0.12 (-0.02, 0.44)
Flow length	-0.02 ± .14 (-0.33, 0.24)	0.16 ± 0.18 (-0.18, 0.52)
Flow accumulation	0.04 ± 0.14 (-0.23, 0.34)	0.08 ± 0.17 (-0.26, 0.42)
Upstream slope	-0.23 ± 0.08 (-0.39, 0.07)	0.18 ± 0.11 (-0.02, 0.39)
Upstream elevation	0.20 ± 0.07 (0.06, 0.34)	0.08 ±0.10 (-0.11, 0.28)
Minimum temperature	-0.11 ± 0.19 (-0.51, 0.25)	-0.25 ± 0.56 (-1.78, 0.33)
Maximum temperature	-0.42 ± 0.24 (-0.89, 0.03)	0.54 ± 0.48 (-0.01, 1.71)

Table 5.2. Posterior coefficient estimates (median ± standard error, and 95% Credible Intervals) of the models of alien fish richness in 144 Australian freshwater drainages in two periods.

(a) Pre-1970



(b) Post-1970

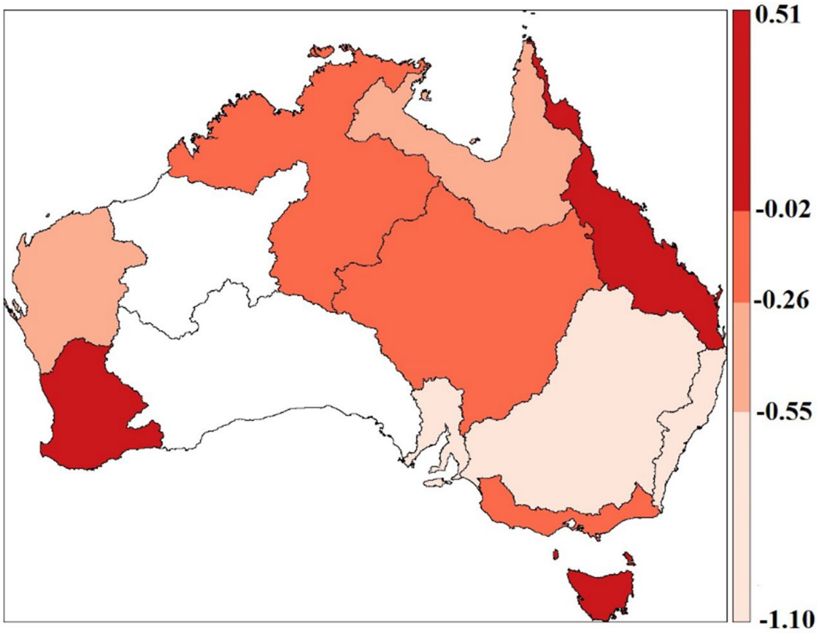


Fig. 5.2. Distribution of the topographic division-specific intercepts (means of the posterior distributions; see Table 5.2 for full estimates) in two periods, (a) pre-1970 and (b) post-1970. Warmer colours indicate topographic divisions where there were higher alien fish richness not explained by the eight covariates included in the models, and represent hotspots of alien fishes (see text). Names: 1: Carpentaria Coast; 2: Lake Eyre Basin; 3: Murray-Darling Basin; 4: North-East Coast; 5: Pilbara-Gascoyne; 6: South Australian Gulf; 7: South East Coast (New South Wales); 8: South East Coast (Victoria); 9: South West Coast; 10: Tanami-Timor Sea Coast; 11: Tasmania.

Acclimatisation and ornamental introductions were the two major transport pathways for the initial establishment of alien fishes in Australia, but their relative importance has changed over time (Fig. 5.1c). Pre-1970, most established alien fishes were transported by acclimatisation societies (64%; 9 of 14 species established in this period) whereas post-1970 most arrived as ornamental fishes (68% of the 31 species established). Meanwhile, introductions for aquaculture and biocontrol made up a much smaller proportion of established alien fishes, and the importance of both has declined over time (Fig. 5.1c).

Correlates of Species Richness

Our Bayesian regularised Poisson-log models adequately fitted the data for both pre-1970 and post-970 (R^2 = 0.98 in both cases). Our models revealed, after accounting for the effects of topographic division autocorrelation, that alien fish richness pre-1970 was positively associated with the topographical features and human influence in the drainages (Table 5.2). The Human Influence Index had a positive effect (HII slope, mean ± SE: 0.26 ± 0.07, 95%CI: [0.13, 0.38]), meaning that drainages more heavily impacted by human activity were more likely to be inhabited by a higher number of alien fishes. Drainages where the terrain was flatter and located at higher elevations compared to other drainages were more heavily invaded (positive association with the upstrean elevation and negative with upstream slope; Table 5.2). Additionally, there was a tendency for alien fish richness to be negatively associated with the maximum summer temperature in this period (Table 5.2), although the 95% CI slightly overlapped zero indicating we cannot be completely confident the coefficient was negative (-0.42 ± 0.24, 95% CI: [-0.89, 0.03]). Therefore, pre-1970 alien fish richness tended to be higher in colder drainages. In contrast, alien fish richness increased with increasing upstream slope post-1970 (positive estimate of the slope, 0.18 ± 0.11, 95% CI: [0.01, 0.39]), whereas all the other covariates did not show a certain effect in this period (Table 5.2). Nonetheless, alien fish richness post-1970 tended to be positively associated with the maximum summer temperature, although again the 95%CI slightly overlapped zero (0.41 ± 0.27, 95% CI: [-0.03, 1.00]). This latter effect suggests that alien fish richness was higher in drainages experiencing warmer temperatures during the Austral summer. Differences between coefficient estimates pre-1970 and post-1970 uncovered a shift over time towards alien fishes occurring in relatively steeper and warmer drainages (negative change in the upstream slope and maximum summer temperature coefficients; Fig. 5.3).

Topographic division-specific intercepts revealed important variability among divisions in their alien fish richness that was not captured by the covariates (Fig. 5.2 and

Table 5.2). Five divisions had relatively large posterior estimates pre-1970, indicating relatively higher richness (Table 5.2), while only one topographic division had a positive posterior estimate post-1970 (North East Coast, encompassing drainages with a high turnover). Another three topographic divisions had comparatively large negative estimates implying lower species richness post-1970 (Fig. 5.2b and Table 5.2). Notably, the intercepts for three topographic divisions changed signs from positive pre-1970 to negative post-1970 (Table 5.2), indicating that, relative to other topographic divisions, they hosted a higher number of alien fishes pre-1970 than post-1970. Posterior estimates of the correlation matrices for both periods are available in Appendix 4.

Discussion

Our findings show that changing transport pathways have had a major impact in altering the biogeography of alien freshwater fishes in Australia. The shift from fish introduced primarily by acclimatisation societies pre-1970 to ornamental introductions post-1970 (Fig. 5.1c), has been associated with a substantial shift in the distribution of drainages inhabited by a higher number of alien fishes (Figs. 5.1b and 5.2), and also with changes in covariates associated with alien fish richness (Fig. 5.3). In summary, the biogeography of alien fishes in Australia has experienced a major temporal shift caused by a switch from the organised and purposeful release of angling and biocontrol species pre-1970 to the more haphazard introduction of ornamental aquarium fish post-1970.

Alien fish richness pre-1970 (Figs. 1a and 2a) was a result of the intentional release of alien fishes for acclimatisation and biocontrol purposes (Fig. 1c) in south-eastern inland drainages heavily impacted by human activities (higher standardised HII), located at a relatively higher elevation than the average across all drainages (higher standardised upstream elevation), and generally characterised by streams flowing through plain type terrain (smaller standardised upstream elevation). This mirrors the pattern of European settlement and agricultural development during this period within these regions, which was accompanied by the active efforts of acclimatisation societies to establish both angling species and fish to control mosquito-borne diseases in south-eastern Australia (Lever 1992; Clarke 2002; Jupp 2002; Pyke 2008; Van Den Hurk et al. 2013). This is further apparent in the alien fishes that were widely released in this period for angling (e.g., European perch, brown trout and rainbow trout) and the eastern mosquitofish, released for mosquito biocontrol (see data accesibility statement).

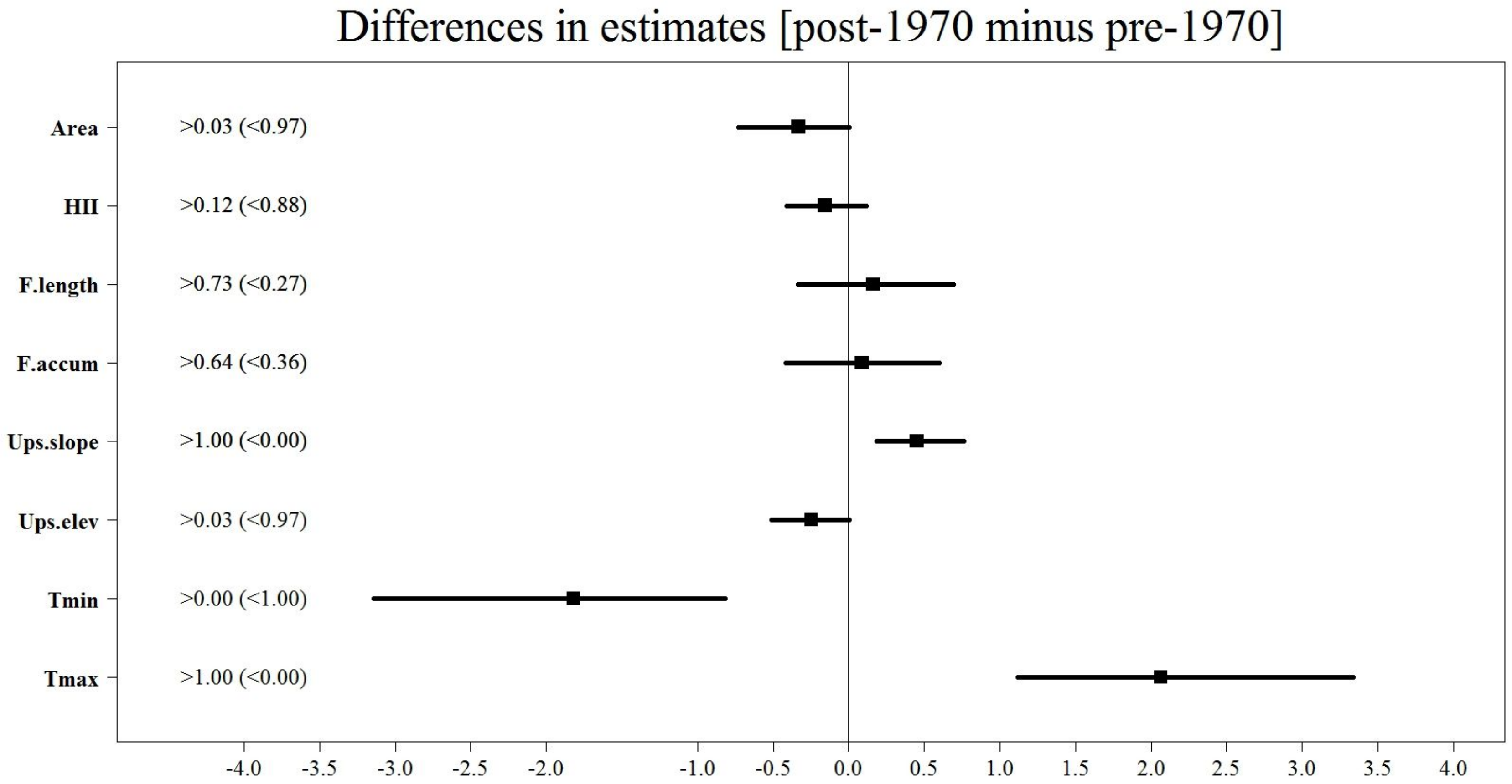


Fig. 5.3. Differences in the posterior estimates (mean and 95% Credible Intervals) of the slopes of the eight covariates between two periods (pre-1970 and post-1970). Values on the left of the graph indicate the proportion of posterior iterations where the estimate of post-1970 was higher (smaller) than the estimate of pre-1970. HII: Human influence index. All the covariates were standardised for the analyses. Refer to Table 5.1 for a description of all of the covariates.

In contrast, post-1970 richness patterns were dominated by a shift to ornamental alien fishes mainly establishing in tropical and sub-tropical coastal drainages in northern, eastern, and western Australia (Figs. 5.1b and 5.2b). The presence of a high number of alien fishes in north-eastern Australia post-1970 has been reported previously (Koehn and MacKenzie 2004; Lintermans 2004; Olden et al. 2008; Webb 2008). We also identified two other regions of high alien fish turnover during this period that could not be attributed to the presence of ornamental species (Fig. 5.1b; see data accessibility statement). The group of high turnover drainages on the south-west coast was likely due to the establishment of the eastern mosquitofish, whereas the establishment of three salmonids (rainbow trout, brown trout, and brook trout, *Salvelinus fontinalis*) for angling and aquaculture were responsible for the high turnover in western Tasmania (Jackson et al. 2004; Lintermans 2004). The current dominance of alien ornamental fishes is consistent with the growth in the aquarium trade in Australia, an industry that imported *c.* 1.5 million fish between 1964-65 and rose to *c.*12 million fish one decade later (Lintermans 2004; Whittington and Chong 2007). This growth in the aquarium industry is consistent across the world, with steady increases over the last three decades (Gozlan et al. 2010; Bradie et al. 2013). Thus, shifts similar to those shown here for Australia can be expected in other countries where there is a substantial market for alien ornamental fishes (Mancera-Rodríguez and Álvarez-Leon 2008; Maceda-Veiga et al. 2013; Howeth et al. 2016).

Our model post-1970 indicated that drainages characterised by a steeper terrain and experiencing warmer conditions, relative to all other drainages, were most likely to host more alien fish species (higher standardised upstream slope and maximum summer temperatures), in concordance with the dominance of alien fishes in tropical and sub-tropical drainages during this period. Moreover, there was a tendency for alien fish richness to increase with the Human Influence Index (Table 5.2), in agreement with the high turnover in drainages encompassing major human population hubs such as Darwin (Finniss River drainage, Northern Territory), Adelaide (Torrens River, South Australia), Brisbane (Brisbane River, Queensland), and Townsville (Ross River, Queensland). This points to the potential role of human populations in increasing the likelihood of establishment of ornamental fishes due to greater colonisation and propagule pressure (Marchetti et al. 2004; Lockwood et al. 2005). Escaped and discarded aquarium fishes comprise most of the introductions of ornamental fishes in Australia, which may explain the lack of association between fish establishment and some of the covariates we tested, because escapes and discards are often unsystematic or occur in discrete population centres that were not well captured in the drainage-level features that we included (Lever 1996; Lintermans 2004).

Our findings demonstrate that changes in societal uses for fishes have triggered shifts in the locations inhabited by them, leading to the alteration of the biogeography of this group of alien vertebrates in Australia. A key outcome of our models was that the covariates explaining alien fish richness differed between the two time periods, implying that historical models are unlikely to be suitable for forecasting future distribution patterns. Explaining the patterns of alien species richness on a spatio-temporal scale, as we have done here, is fundamental to inform the development of strategies aimed at preventing new introductions (Lodge et al. 2016). Currently, the drainages with the highest number of alien ornamental fishes tend to be in regions of eastern Queensland associated with towns and cities. However, it is clear that there are a large number of drainage basins in other tropical and sub-tropical regions potentially suitable for hosting more alien fishes, particularly considering the positive effects of the maximum summer temperatures. The dominance of ornamental fishes suggests that conducting campaigns to raise public awareness about the impacts of alien fishes may be required to reduce the frequency of releases of unwanted pets (Moorhouse et al. 2016). Moreover, preventive strategies would benefit from an improved understanding of the economic and social values of alien species, which likely drive the contemporary movement and introduction of alien species (Romagosa 2014; Vaz et al. 2017).

Our conclusions are likely to extend to other groups of alien species for which similar temporal shifts in the importance of transport pathways have been reported (Pyšek et al. 2011; Hulme 2015), warranting further research to investigate the generality of our findings across taxa and locations. Future advances and diversification in the technology and uses of animals by humans will likely create a new assortment of transport pathways and expand the potential sources of alien species (Hajkowicz 2015; Hulme 2015; Early et al. 2016). Such anthopogenic-induced changes can happen at a much faster pace than the natural processes of colonisation, speciation, and extinction that shape natural biogeographic patterns (Gaston and Blackburn 2008; Lomolino et al. 2010; Pimm et al. 2014), to the extent that traditional biogeographic regions may no longer be recognisable based on their current inhabitants (Abell et al. 2008; Holt et al. 2013; Capinha et al. 2015).

Statement of Authorship

Title of Paper	A framework for designing and implementing early detection surveys for alien reptiles.
Publication Status	☐ Published ☐ Accepted for Publication ☑ Submitted for Publication ☐ Unpublished and Unsubmitted w ork w ritten in manuscript style
Publication Details	*García-Díaz, P., Ross, J.V., Vall-llosera, M. & Cassey, P.* (submitted). A framework for designing and implementing early detection surveys for alien reptiles. *Submitted to Methods in Ecology and Evolution.*

Principal Author

Name of Principal Author (Candidate)	Pablo Garcia Diaz
Contribution to the Paper	Planned and developed the research, conducted the fieldwork, compiled the data, developed the models and analysed the data, written the manuscript.
Overall percentage (%)	80%
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.
Signature	Date 15/02/2017

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Associate Professor Joshua V. Ross
Contribution to the Paper	Contributed ideas to the development of the research, contributed to the development of the modelling and analytical procedures, supported the planning of the fieldwork, revised and edited the manuscript
Signature	Date 15/02/2017

Name of Co-Author	Dr Miquel Vall-llosera Camps		
Contribution to the Paper	Contributed ideas to the development of the research, supported the planning of the fieldwork, conducted the fieldwork, revised and edited the manuscript		
Signature		Date	14/02/2017

Name of Co-Author	Associate Professor Phillip Cassey		
Contribution to the Paper	Contributed ideas to the development of the research, supported the planning of the fieldwork, revised and edited the manuscript		
Signature		Date	16/02/2017

Chapter 6. A Framework for Designing and Implementing Early Detection Surveys for Alien Reptiles

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Publication: García-Díaz, P., Ross, J.V., Vall-llosera, M. & Cassey, P. (submitted). A framework for designing and implementing early detection surveys for alien reptiles. *Methods in Ecology and Evolution*, submitted.

Code accessibility: the annotated code for running the analyses in this Chapter is publically available at: https://github.com/pablogarciadiaz/PhD-thesis-code

Data accessibility: the detection data of all the alien reptile species and the posterior estimates of the probability of absence given no reptiles is detected will be publically available from FigShare after the embargo expires. For the purposes of marking, the data can be downloaded from the following link: https://figshare.com/s/0e079b373d05a328a65b.

Appendix: no supplementary material accompanies this chapter.

Abstract

Early detection of new introductions is critical for stopping alien species before they can produce impacts, yet scarce research has examined the practicalities of implementing early detection surveys. We aim to fill this gap by developing and evaluating a quantitative early detection framework. Our framework is based on three consecutive stages: (i) identification of key sites with high likelihood of introduction of new species; (ii) surveying those sites for species already present in the area to establish baseline probabilities of detection; and (iii) use of the estimates obtained in the previous stage to estimate the probability of absence of new alien species given none are detected via Bayes' rule. We apply our framework to the case of detecting alien reptile species on Christmas Island, a remote Australian Territory. We identified 34 surveillance sites, where we surveyed for five alien reptiles on repeated occasions (three during the day and three during the night; 10 minutes surveying on each occasion). We used mixture Poisson-Binomial models, fitted using Bayesian methods, for jointly estimating the abundance and the probabilities of individual detection of the five alien species. Estimated abundances and probabilities of individual detection varied widely across species and sites, with averages ranging from 0.01 to 0.33. Despite the variation, our findings indicate that the probabilities of individual detection were higher during night time surveys for three of the five species surveyed. The surveying effort required for attaining a high probability of absence, given no alien individuals were detected, was estimated to be relatively high and was influenced by the prior beliefs and knowledge about whether a new species has been introduced into the region. In order to implement reliable early detection surveys, it is paramount to account for the variability between species in their probabilities of individual detection and to justify and disclose existing prior beliefs and knowledge about the presence of new alien species. Early detection surveys are a challenging task, but we encourage their widespread application for better managing the risks posed by alien species. We provide a tested quantitative framework for their successful implementation.

Keywords: biosecurity; Christmas Island; environmental management; invasive species; mixture Poisson-binomial model; surveillance

Introduction

Early detection of new introductions is of paramount importance for avoiding the establishment and impacts of new self-sustaining populations of alien species (Vander Zanden et al. 2010; Jarrad et al. 2015). Designing effective survey activities for early detection of new introductions is a challenging task, because the observers are surveying for 'unknown unknowns' – that is, it is not known whether there has been a new introduction, and in that case, the identity of the alien species (Wintle et al. 2010; Jarrad et al. 2011; Jarrad et al. 2015). Early detection activities cannot be tailored to detect a particular species given that its potential identity is unknown. Moreover, new introductions are usually more difficult to detected because they are formed by a small number of individuals (McCarthy et al. 2013). In this context, early detection surveys face many uncertainties, particularly when deciding how much surveying effort is required to confidently declare that no new alien species have been introduced (Ramsey et al. 2011; Guillera-Arroita et al. 2014a). Adding further complexity, it is increasingly difficult to justify surveying for novel alien species at a time where resources for environmental conservation are particularly limited (McCarthy et al. 2010; Jarrad et al. 2015).

Reptiles are a group of emergent alien species that have produced serious environmental impacts in recipient regions worldwide (Dorcas et al. 2012; Kraus 2015). Once established, alien reptiles are difficult to eradicate and, therefore, early detection is fundamental to averting their potential impacts. Unfortunately, reptiles are difficult to survey in the wild due to their cryptic habits and characteristics (Kéry 2002; Christy et al. 2010; Sewell et al. 2012; Smith et al. 2012a; Durso and Seigel 2015; Lardner et al. 2015; Rodda et al. 2015), and surveys may typically require deploying labour-intensive methods such as trapping that may not be adequate in situations typical of early detection activities (Doan 2003; McDiarmid et al. 2011; Reed et al. 2011). Alien reptiles are often transported unintentionally, as stowaways in shipping or air traffic cargo, and the accelerating volume of global traffic has increased their chances of introduction into new regions (Kraus 2009; Helmus et al. 2014; Li et al. 2016).

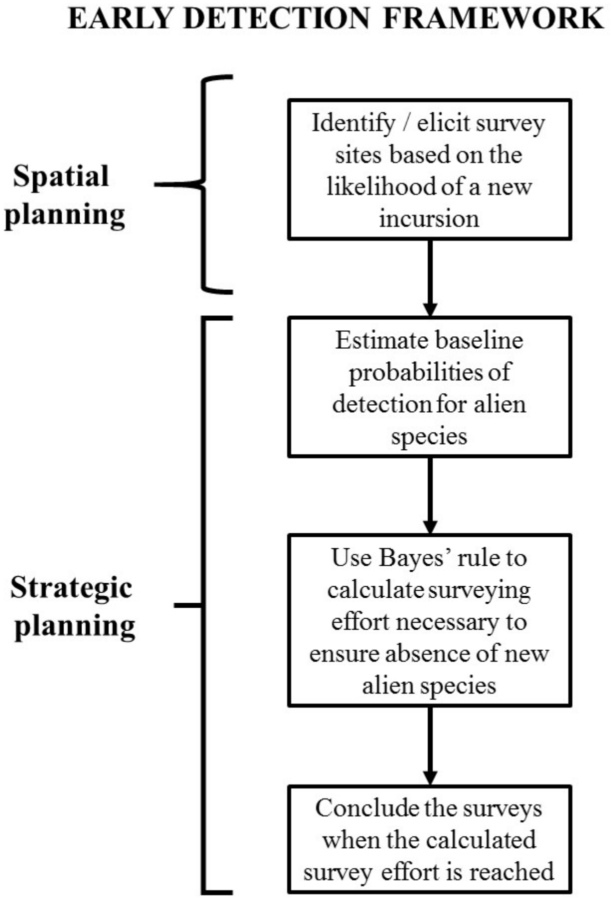


Fig. 6.1. Outline of our framework for developing, designing and undertaking early detection programs for alien species. We illustrate the application of each stage using the case example of alien reptiles in Christmas Island.

Early detection of new introductions of alien reptiles is an important but challenging activity. Here we develop and evaluate a framework (Fig. 6.1) for effectively implementing robust, rapid assessments for the early detection of alien reptiles incorporating spatial (i.e., where to survey?) and strategic (i.e., how to survey and when to stop surveying?) planning components (Groves and Game 2016). We designed our early detection framework based on three consecutive stages (Fig. 1): (i) prioritising and focussing the survey effort on those key sites with a higher likelihood of introduction of a new alien species (Brockerhoff et al. 2006; Yemshanov et al. 2015); (ii) Poisson-Binomial models for estimating baseline probability of individual detection (Royle 2004; Kéry and Royle 2016); and (iii) using Bayes' rule for estimating the survey effort necessary to ensure with a very high probability that no new individuals of a new species are present given that none have been detected (Anderson et al.

2013; Guillera-Arroita et al. 2015). Mixture Poisson-Binomial models account for the abundance-detection relationship by estimating the probability of detecting an individual of an alien species, a parameter that can then be used in the third stage of our framework to estimate the probability of absence given no individuals are detected.

In our framework, it is necessary to estimate baseline detection probabilities. We argue that such baseline detection probabilities can be estimated from the detection probabilities of species already present in the region where the early detection surveys would be conducted. The species surveyed do not necessarily have to be alien to the region, as detection probabilities of native species may also provide important baseline information. Nonetheless, we suggest that, if alien reptiles are present, the baseline detection probabilities may be better estimated from surveying those alien species already present in the area (as conducted here).

We apply and demonstrate our framework to the particular case study of detection of alien reptiles on Christmas Island (Fig. 6.2). The remoteness of the island requires all goods and commodities to be imported via shipping and air traffic routes, increasing the potential risks of transporting alien reptiles into the island, but also limiting the number of potential pathways of transport onto the island (Kraus 2009; Helmus et al. 2014). To date, Christmas Island has been invaded by five species of alien reptiles belonging to four families of extant reptiles (Smith et al. 2012b). These are the common house gecko (*Hemidactylus frenatus*), the stump-toed gecko (*Gehyra mutilata*), the grass skink (*Lygosoma bowringii*), the flowerpot snake (*Indotyphlops braminus*), and the wolf snake (*Lycodon capucinus*). The presence of these invaders at varying abundances and the remoteness of the island offers the unique opportunity to evaluate the feasibility of our framework in identifying surveillance sites and estimating baseline detection probabilities for a range of alien reptiles (Kraus 2009; García-Díaz et al. 2016a). Our example provides key lessons transferable to the planning and implementation of early detection surveys in other places around the world.

Material and Methods

Study Area and Surveillance Sites

Christmas Island is an Australian oceanic territory located in the Indian Ocean, 10º 30’ S 105º 40’ E (Fig. 6.2). The island has an area of 135 km^2, of which approximately 63% is a National Park. The island has a tropical climate, with rainforest covering most of it, although phosphorus mining has transformed some areas (Fig. 6.2). The island has a permanent population of approximately 2,200 people who mostly live in a settlement in the north-east of the island (http://goo.gl/esM3Dy). The island's landscape and habitat features are described in greater detail elsewhere (Claussen 2005; Smith et al. 2012b). The island's native biota has suffered a catastrophic extinction crisis since its human colonisation in the 1890s, with most of its terrestrial vertebrate species, except birds, extinct as a consequence of the impacts caused by humans and alien species (Tidemann et al. 1994; Wyatt et al. 2008; Martin et al. 2012; Smith et al. 2012b). In the case of the native reptiles, only one of the five pre-European settlement species, the giant gecko (*Cyrtodactylus sadleiri*), is still extant on the island while the rest are declared extinct, or only survive in captivity (Smith et al. 2012a; Smith et al. 2012b).

The first stage in our framework was to identify the sites with a high likelihood of incursion of a new alien reptile, where the surveying effort will be focussed (Fig. 6.1). We identified 34 surveillance sites (Fig. 6.2) through expert consultation with representatives of the Christmas Island National Park and Natural Resource Management Board (S. Flakus, B. Tiernan, D. Maple, M. Misso) and the Australian Government Department of Agriculture and Water Resources (J. Matthews). The surveillance sites were located in areas receiving and storing the goods and commodities imported to the island, as these sites were deemed to be the principal potential points of entry of alien reptiles (Brockerhoff et al. 2006; Yemshanov et al. 2015).

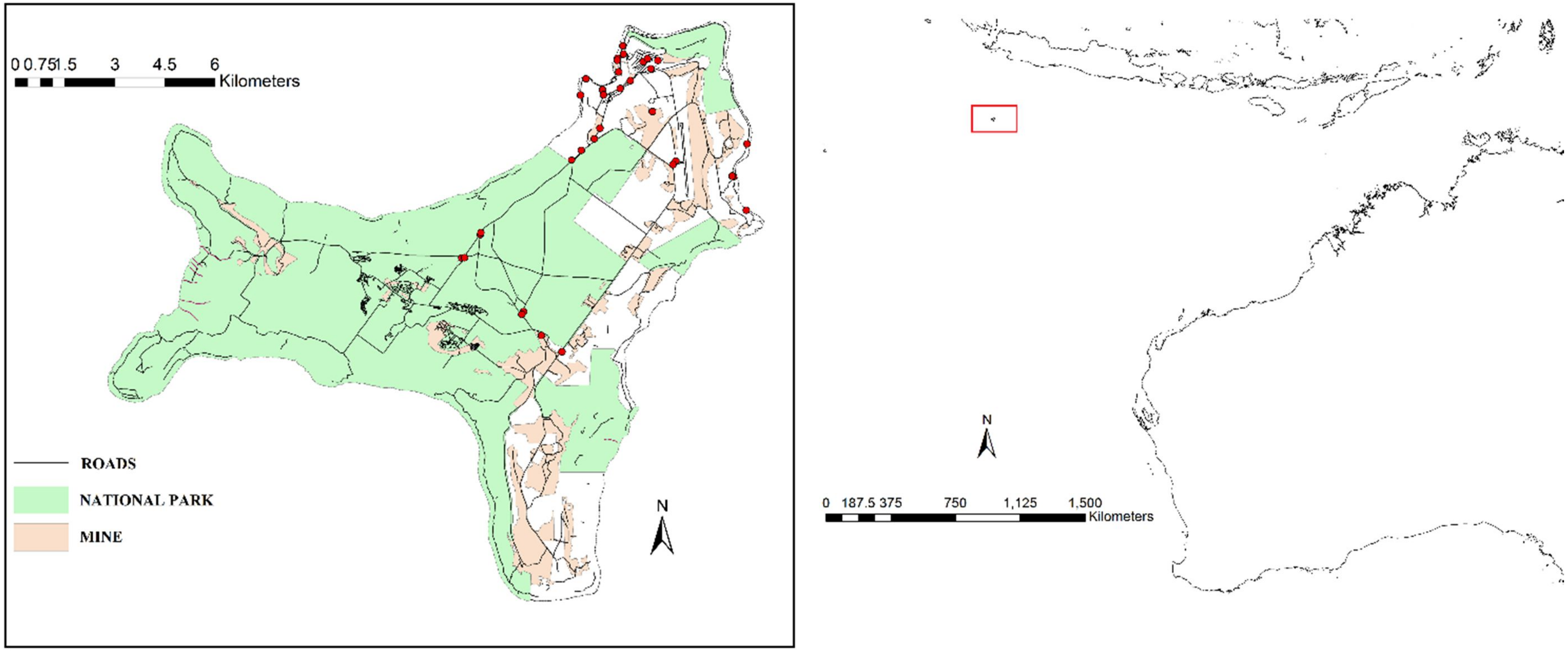


Fig. 6.2. Geographical location of Christmas Island illustrating its remoteness and position with respect to Australia and Indonesia (box in right panel map). Left panel: major land uses in Christmas Island and the geographical distribution of the 34 surveillance sites (red dots).

Estimating Abundance and Detection Probabilities

The second stage of our early detection framework was to estimate baseline detection probabilities for alien reptiles, which can be used for informing decisions on survey efforts required for confirming absence (Fig. 6.1). We surveyed for alien reptiles in the 34 sites during the dry season, 8th July to 7th August 2015. The island has a tropical climate, so reptiles are active all year round including during the dry season. Each site was surveyed on six occasions (three after sunset, during night time 18:20-20:40, and three after sunrise, during the day time 8:00-11:30) to estimate probability of individual detection of alien reptiles (Royle 2004; Kéry and Royle 2016). We conducted day and night surveying occasions to ensure a good coverage of surveying conditions in the surveillance sites. We conducted the fieldwork exclusively during the dry season to minimise interferences and problems due to weather conditions.

The sites were surveyed using a minor modification of the methodology employed by Christmas Island National Park Staff (Smith et al. 2012a; Smith et al. 2012b). In each of the surveillance sites, we intensively searched for alien reptiles during 10 minutes along a linear transect that varied in length from site to site (mean ± standard error: 182.71 ± 72.59; range: 60-1384 metres). Our models indicate that the wide range of distances surveyed did not influence the results of the surveys (Table 6.1). We intensively surveyed the surveillance sites by searching for alien reptiles under rocks, other fallen structures (e.g., logs), and individuals in the vegetation, both during the day and night surveys (using a head torch during night surveys). The combination of transect and visual encounter surveys is known to be effective in detecting reptiles in tropical environments (Doan 2003; McDiarmid et al. 2011; Smith et al. 2012a).

During each survey occasion we recorded the number of individuals of each alien reptile detected and the temperature (ºC) at four different heights in the habitat (Table 6.1) (Vitt and Caldwell 2009). For each surveillance site, we collected information on ten covariates believed to influence the abundance in the site by alien reptiles; including vegetation cover and geographical features (Table 1). We defined the cover of different micro-habitat characteristics in each site following the semi-quantitative Braun-Blanquet scale (Sutherland 2006). We gathered information on the altitude (metres above sea level; sourced from the National Park digital elevation map), and the Euclidean distance from the surveillance site to the port (metres). The port has been the point of entrance for all the alien reptiles to the island and closer sites might be more likely to have higher abundances despite the apparent widespread distribution of all alien reptiles in the island (Smith et al. 2012b). All the continuous covariates for modelling abundance and individual probabilities of detection were standardised (centred by their mean and scaled by their standard deviation). See data accessibility statement for information on where to obtain the data. We assumed that the number of animals counted ($Nd_{i,z}$) at surveillance site i during surveying occasion z follows a stochastic Binomial distribution with parameters N_i and $p_{i,z}$:

$$Nd_{i,z} \sim \text{Binomial}(N_i, p_{i,z}) \tag{6.1}$$

where N_i is the abundance of the species, and $p_{i,z}$ is the probability of individual detection (Royle 2004; Kéry and Royle 2016).We modelled the abundance of a species at a surveillance site, N_i, as a function of the covariates described in Table 6.1 via a Poisson-log regression, after confirming that there was no over-dispersion in the models and data (using a Negative-binomial regression performed on the same data). The abundance model was defined as follows:

$$N_i \sim \text{Poisson}(\lambda_i), \tag{6.2}$$

$$\log(\lambda_{\text{i}}) = \alpha_1 + \sum_{j=1}^{10} \beta_j X_{i,j}, \tag{6.3}$$

where α_1 and β_j (j = 1, …, 10) are the intercepts and the slopes, respectively, of the model of the mean abundance, λ_i, in surveillance site i and X_i is a vector of the 10 covariates used for modelling the mean abundance (see Table 6.1). We modelled the probability of individual detection using a logistic regression:

$$\text{logit}(p_{\text{i,z}}) = \alpha_d + \sum_{r=1}^{11} \beta_r T_{i,z,r} \tag{6.4}$$

where α_d are the time of the day specific intercepts (day and night), β_r (r = 1, …, 11) are the slopes of the model of the probability of individual detection, $p_{i,z}$, during surveying occasion z at surveillance site i, and $T_{i,z}$ is a vector of the 11 covariates used for modelling the probability of individual detection (see Table 6.1).

We employed Bayesian regularisation to construct robust model structures for abundance and probability of individual detection as a function of the covariates (Hooten and Hobbs 2014). The models were constructed and independently fitted for all the alien reptile species on Christmas Island. The models were fitted using the jagsUI interface for R environment (R Development Core Team 2015) to the JAGS software (Plummer 2003). We used relatively uninformative priors for the intercepts in the model, ~N(0, $\sigma^2 = 10$), and uninformative Laplace priors for all the slopes to construct regularised models, ~Laplace(0, *b*), *b*~Uniform*(0.1, 5*). All the models were run using three chains with 150,000 iterations each, and no thinning. After visually checking for convergence and mixing of the chains, we discarded the first 30,000 iterations as a burn-in time, resulting in 360,000 draws of the posterior distribution of all the parameters in the models. We used posterior mean absolute errors of species counts in each surveying occasion and surveillance site to measure the fit of our Poisson-binomial models to the detection data (see code accessibility statement).

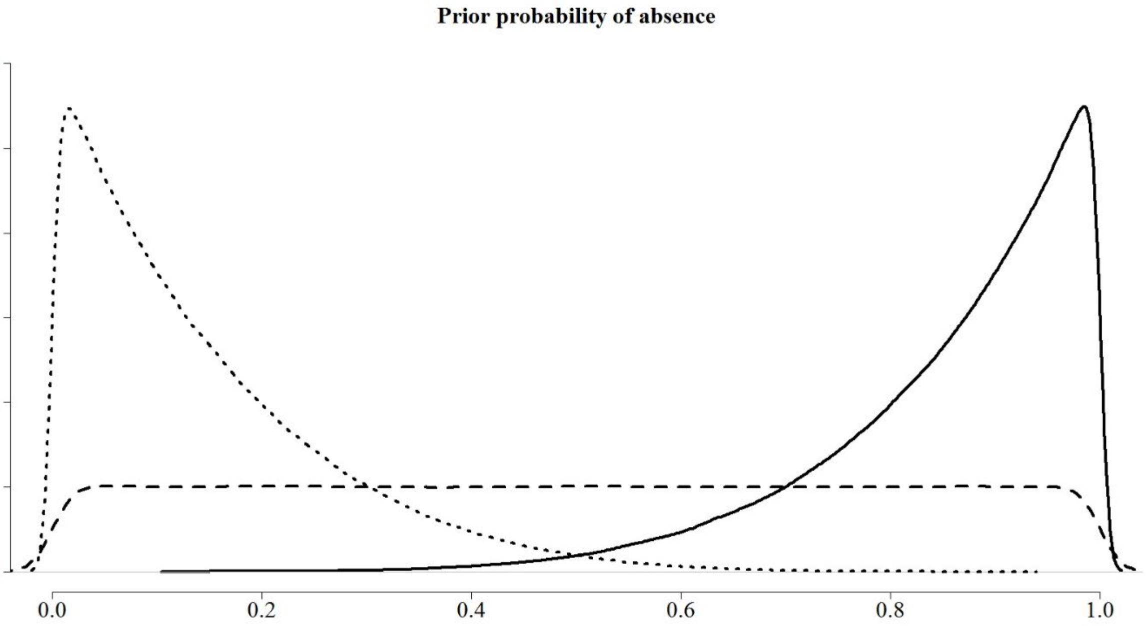


Fig. 6.3. The three prior probabilities of absence for new alien reptiles used to represent three alternative scenarios for management of an early detection program. Dotted line: Scenario 1 (strong belief that new alien reptiles are absent, *~Beta[6, 1]*); Dashed line: Scenario 2 (no strong belief in the presence or absence of new alien reptiles, *~Beta[1, 1]*); Solid line: Scenario 3 (strong belief that new alien reptiles are present, *~Beta[1, 6]*).

Confirming Absence of New Introduced Species

Ensuring absence of new alien reptiles, given that none have been detected during the surveys, is the central and last stage of our framework (Fig. 6.1). The key question is, how much survey effort should be conducted to ensure, with a very high probability, that there are no alien reptiles. We used Bayes' rule for determining the probability of absence of an individual alien reptile in a given surveillance site given that the surveys detected none (Anderson et al. 2013):

$$P(A \mid D^{-}) = \frac{P(A)}{1 - P_t(1 - P(A))} \qquad (6.5)$$

where $P(A \mid D^{-})$ is the probability that the alien reptile is absent from the surveillance site given that none are detected, $P(A)$ is the prior probability of absence from the surveillance site (the probability of absence before the current survey occasion), and P_t is the probability of individual detection of the alien species during a survey occasion in the surveillance site (i.e., the probability of individual detection $p_{i,z}$).

Prior probabilities of absence, $P(A)$, before any survey occasion has been conducted, reflect the beliefs, knowledge, and confidence of the environmental managers about whether there has been a new introduction or not (Ramsey et al. 2011). We evaluated three alternative scenarios, with three different prior distributions, that represent realistic cases of interest for the management of early detection activities (Fig. 6.3):

> Scenario 1: strong belief that new alien reptiles are absent, prior ~Beta*(6, 1)*
>
> Scenario 2: no strong belief in the presence or absence of new alien reptiles, prior ~Beta*(1, 1)*
>
> Scenario 3: strong belief that new alien reptiles are present, prior ~Beta*(1, 6)*

Scenarios 1 and 3 represent risk-prone and risk-averse environmental decision-making situations, respectively (Groves and Game 2016), whereas Scenario 2 is a neutral case where the environmental managers state their ignorance regarding the presence/absence of new alien species. We calculated $P(A \mid D^{-})$ for each species based on one million runs of equation (6.5). We estimated P_t by sampling values at random of the posterior distribution of all day or night $p_{i,z}$ values in each of the million simulations. Therefore, each run of equation (6.5) represents a surveillance site and surveying occasion chosen at random.

Results

Abundance and Detection Probabilities

Our Poisson-log regressions showed that abundances were influenced by different covariates depending on the species (Table 6.1), with the exception of the flowerpot snake for which all our posterior slope estimates widely overlapped zero. Both the common house gecko and the grass skink were less abundant in surveillance sites located at higher altitudes relative to all other surveillance sites (Table 6.1), but that was the only commonality in the associates of abundance of the five alien reptiles.

Our Bayesian regularised models were an adequate fit to the count data (Table 6.1), and revealed that the survey time (day vs. night) was the main driver of the probability of individual detection across the five alien reptiles (Table 6.1). Only in the case of the common house gecko was the probability of individual detection influenced by any of the 11 covariates included in the models (seven out of 11 covariates did not overlap zero; see Table 1 for details). The highest probability of individual detection was for the common house gecko during night time surveys (0.33 ± 0.01; 95% CIs: [0.19, 0.50]). The smallest probability of individual detection was estimated for stump-toed geckos during day time surveys (0.00 ± 0.01; 95% CIs: [0.00, 0.02]). For three of the five alien reptiles (Table 1), the detection probabilities were higher during night time surveys, whereas only for the grass skink was detection probability higher during day time surveys. There were no differences between day and night time surveys for the wolf snake (Table 6.1).

Confirming Absence of New Introduced Species

The surveying effort required to confirm absence at the surveillance site level varied widely across species and depending on the time of the day. Our estimates were also dependent on the prior probability of absence for each of the three scenarios tested (Figs. 6.4-6.6). The required number of consecutive surveys with no detections of a single individual was smallest for Scenario 1 (strong belief in absence, Fig. 6.4), whereas large numbers of consecutive surveys have to be conducted to confirm absence for Scenario 3 (strong belief in the presence of a new alien reptile; Fig. 6.6). See data accessibility agreement for posterior estimates of the probability of absence given no individual reptiles are detected for each species.

	Common house gecko (*Hemidactylus frenatus*)	Stump-toed gecko (*Gehyra mutilata*)	Grass skink (*Lygosoma bowringii*)	Flowerpot snake (*Indotyphlops braminus*)	Wolf snake (*Lycodon capucinus*)
Mean absolute error	1.46 ± 0.07 (1.34, 1.60)	0.20 ± 0.02 (0.16, 0.25)	0.15 ± 0.02 (0.12, 0.19)	0.12 ± 0.01 (0.10, 0.15)	0.10 ± 0.01 (0.07, 0.12)
Abundance: **Poisson-log regression**					
Intercept (α_1)	3.01 ± 0.30 (2.55, 3.78)	0.29 ± 0.46 (-0.52, 1.28)	-0.90 ± 0.88 (-2.57, 1.00)	-0.50 ± 0.48 (-1.37, 0.51)	-0.38 ± 1.20 (-2.73, 2.04)
Distance to port (standardised)	0.01 ± 0.07 (-0.12, 0.14)	0.72 ± 0.22 (0.29, 1.15)	0.31 ± 0.33 (-0.21, 1.06)	0.04 ± 0.22 (-0.39, 0.50)	-0.03 ± 0.30 (-0.67, 0.57)
Cover of trees	0.07 ± 0.23 (-0.39, 0.55)	-0.03 ± 0.31 (-0.73, 0.57)	-0.32 ± 0.44 (-1.33, 0.37)	0.23 ± 0.31 (-0.26, 0.95)	-0.28 ± 0.44 (-1.34, 0.44)
Cover of bush (<30cm tall)	-0.21 ± 0.20 (-0.67, 0.12)	-0.07 ± 0.27 (-0.63, 0.50)	-0.41 ± 0.47 (-1.49, 0.36)	-0.15 ± 0.27 (-0.79, 0.32)	-0.10 ± 0.37 (-0.97, 0.56)
Cover of bush (>30cm tall)	-0.51 ± 0.26 (-1.03, -0.01)	-0.01 ± 0.28 (-0.63, 0.55)	-0.21 ± 0.35 (-1.00, 0.39)	0.07 ± 0.27 (-0.44, 0.66)	0.03 ± 0.35 (-0.70, 0.77)
Cover of grass (<30cm tall)	-0.63 ± 0.29 (-1.38, -0.20)	0.32 ± 0.39 (-0.20, 1.34)	0.72 ± 0.47 (-0.07, 1.72)	-0.05 ± 0.24 (-0.58, 0.42)	1.08 ± 0.65 (-0.02, 2.53)
Cover of grass (>30cm tall)	-0.04 ± 0.25 (-0.56, 0.51)	-0.09 ± 0.22 (-0.58, 0.31)	-0.75 ± 0.51 (-1.92, 0.06)	0.16 ± 0.25 (-0.26, 0.73)	0.23 ± 0.40 (-0.40, 1.21)
Cover of rocks and stones	0.12 ± 0.13 (-0.14, 0.38)	-0.10 ± 0.27 (-0.66, 0.42)	0.21 ± 0.40 (-0.46, 1.16)	0.06 ± 0.23 (-0.38, 0.57)	0.14 ± 0.36 (-0.51, 0.98)
Cover of human structures	0.89 ± 0.20 (0.52, 1.31)	0.54 ± 0.50 (-0.40, 1.46)	-0.08 ± 0.32 (-0.75, 0.56)	-0.13 ± 0.27 (-0.76, 0.35)	0.26 ± 0.41 (-0.40, 1.24)
Transect length (standardised)	-0.11 ± 0.07 (-0.26, 0.03)	-0.12 ± 0.20 (-0.56, 0.23)	0.60 ± 0.42 (-0.07, 1.52)	-0.05 ± 0.23 (-0.56, 0.38)	0.21 ± 0.32 (-0.35, 0.94)
Elevation (standardised)	-0.32 ± 0.09 (-0.49, -0.15)	-0.05 ± 0.20 (-0.46, 0.33)	-0.81 ± 0.37 (-1.59, -0.13)	-0.11 ± 0.23 (-0.63, 0.31)	0.03 ± 0.32 (-0.62, 0.70)

(cont.)

***Probability of individual detection:* logit regression**					
Intercept (day)	-4.38 ± 0.35 (-5.17, -3.77)	-6.77 ± 1.44 (-10.07, -4.46)	-1.19 ± 1.28 (-3.81, 1.18)	-2.21 ± 0.66 (-3.60, -1.03)	-3.95 ± 1.23 (-6.50, -1.68)
Intercept (night)	-0.75 ± 0.37 (01.65, -0.14)	-1.18 ± 0.73 (-2.79, 0.09)	-4.94 ± 1.28 (-7.61, -2.59)	-1.82 ± 0.65 (-3.21, -0.67)	-4.10 ±1.22 (-6.64, -1.87)
Ground temperature (standardised)	0.05 ± 0.11 (-0.16, 0.26)	-0.33 ± 0.62 (-1.97, 0.54)	-0.14 ± 0.18 (-0.53, 0.16)	-0.05 ± 0.24 (-0.59, 0.41)	0.05 ± 0.24 (-0.43, 0.55)
Temperature 10cm above ground (standardised)	0.11 ± 0.16 (-0.19, 0.44)	-0.10 ± 0.44 (-1.23, 0.66)	-0.17 ± 0.26 (-0.78, 0.26)	0.01 ± 0.38 (-0.57, 0.61)	0.01 ± 0.28 (-0.56, 0.61)
Temperature 10cm underground (standardised)	0.03 ± 0.10 (-0.17, 0.21)	0.34 ± 0.33 (-0.20, 1.10)	-0.01 ± 0.25 (-0.56, 0.49)	0.16 ± 0.29 (-0.35, 0.83)	0.19 ± 0.27 (-0.26, 0.82)
Temperature 120cm above ground (standardised)	0.48 ± 0.18 (0.13, 0.83)	0.18 ± 0.48 (-0.58, 1.42)	0.29 ± 0.37 (-0.27, 1.17)	0.02 ± 0.29 (-0.58, 0.62)	-0.12 ± 0.31 (-0.85, 0.42)
Cover of trees	-0.83 ± 0.31 (-1.45, -0.19)	0.48 ± 0.72 (-0.44, 2.40)	0.20 ± 0.56 (-0.63, 1.69)	-0.11 ± 0.35 (-0.93, 0.55)	-0.10 ± 0.35 (-0.91, 0.56)
Cover of bush (<30cm tall)	0.93 ± 0.24 (0.46, 1.43)	-0.17 ± 0.54 (-1.43, 0.82)	0.19 ± 0.55 (-0.65, 1.62)	-0.14 ± 0.32 (-0.87, 0.46)	-0.08 ± 0.32 (-0.80, 0.52)
Cover of bush (>30cm tall)	0.64 ± 0.36 (0.02, 1.39)	0.29 ± 0.85 (-1.03, 2.48)	0.21 ± 0.39 (-0.44, 1.14)	-0.28 ± 0.39 (-1.21, 0.32)	0.01 ± 0.32 (-0.66, 0.67)
Cover of grass (<30cm tall)	1.00 ± 0.33 (0.45, 1.82)	-0.54 ± 1.00 (-3.14, 0.63)	0.24 ± 0.41 (0.47, 1.20)	0.29 ± 0.36 (-0.27, 1.13)	0.20 ± 0.42 (-0.54, 1.19)
Cover of grass (>30cm tall)	-0.05 ± 0.33 (-0.76, 0.60)	0.17 ± 0.42 (-0.51, 1.21)	-0.01 ± 0.37 (-0.81, 0.77)	-0.11 ± 0.27 (-0.72, 0.37)	0.12 ± 0.34 (-0.48, 0.92)
Cover of rocks and stones	-0.38 ± 0.14 (-0.66, -0.10)	-0.08 ± 0.54 (01.27, 1.02)	-0.12 ± 0.42 (-1.11, 0.60)	0.00 ± 0.26 (-0.54, 0.55)	0.07 ± 0.33 (-0.58, 0.81)
Cover of human structures	-0.62 ± 0.26 (-1.14, -0.11)	1.17 ± 1.24 (-0.26, 4.07)	-0.21 ± 0.41 (-1.22, 0.45)	0.18 ± 0.32 (-0.38, 0.93)	0.01 ± 0.34 (-0.73, 0.68)

Table 6.1. Posterior coefficient estimates (median ± standard error, and 95% Credible Intervals) of the mixture Poisson-Binomial abundance models for five species of alien reptiles on Christmas Island.

Discussion

We have developed and tested a reliable early detection framework using the case study of alien reptiles on Christmas Island. In the process, we have identified important challenges for the implementation of early detection programs, mostly as a consequence of the large surveying efforts required to confidently declare absence (Figs. 6.4-6.6). Our research has highlighted two crucial issues that need to be explicitly considered at the beginning of the planning process. First, we found important differences in the probability of individual detection of alien reptiles (Table 6.1), a result of crucial relevance for implementing a successful program because the effort to be deployed will vary depending on the estimated baseline detection probabilities. In order to properly address such differences, we recommend that environmental managers base their decisions on the surveying effort required for confirming the absence of the species with the smallest detection probability (thus, ensuring that other more detectable species will also be detected). Second, the amount of effort necessary to confirm absence depends on the prior beliefs, knowledge, and confidence of environmental managers regarding the presence of new alien species. These prior beliefs should be justified and communicated properly before the surveys commence, producing transparent decisions about the survey effort to be undertaken (Canessa et al. 2016; Groves and Game 2016).

Our results show that alien reptiles are difficult to detect in the wild with estimates varying widely across the five species surveyed, and with mean posterior estimates < 0.33 in all but one case (common house gecko during night time surveys; Table 6.1). Our results are in agreement with previous evidence showing that reptiles are difficult to detect in the field during survey activities (Kéry 2002; Christy et al. 2010; Durso et al. 2011; McDiarmid et al. 2011; Sewell et al. 2012; Lardner et al. 2015; Rodda et al. 2015). In the context of alien reptile management, it is of particular concern that the posterior estimates of the probability of individual detection of wolf snakes were very low (mean < 0.04; Table 6.1). This is very unfortunate because alien snakes are, amongst all the alien reptiles, the worst threats to native species in the recipient communities (Dorcas et al. 2012; Kraus 2015; Silva-Rocha et al. 2015). Our posterior estimate of the detection probability of wolf snakes was very similar to that reported for other snakes in places around the world and surveyed using different techniques (Kéry 2002; Christy et al. 2010; Durso et al. 2011; Sewell et al. 2012; Durso and Seigel 2015), suggesting that regardless of the location, species and surveying method, snakes are very difficult to detect in the field. Preventing the establishment of alien snakes via early detection activities therefore requires considerable surveying efforts to declare absence confidently.

The estimates of the surveying effort necessary to confirm absence were influenced by the prior probability of absence, which in turn depends on the beliefs, knowledge, and confidence of the environmental managers planning and conducting the early detection surveys (Ramsey et al. 2011; Guillera-Arroita et al. 2015). Here, we have adopted a scenario simulation approach to illustrate the impact of different prior beliefs on the estimated surveying efforts (Groves and Game 2016). It is likely that there will be some information available on the likelihood that a new alien reptile has been introduced, for example from observations provided by citizen science or the application of transport pressure models to estimate probabilities of introduction (Gallo and Waitt 2011; Yemshanov et al. 2015). These data can be integrated with methods, such as the Delphi method, to elicit managers' beliefs and expert knowledge to construct proper prior probabilities of absence, $P(A^{-})$ in equation (4) (Choy et al. 2009; Burgman et al. 2011).

The combination of our survey methods and quantitative framework provides a flexible yet reliable support framework for planning and undertaking early detection programs for alien reptiles. Our framework can be further extended to support decision-making by estimating 'stopping rules' for setting thresholds for the probability of absence to inform optimal timing to stop survey efforts (Regan et al. 2006; Guillera-Arroita et al. 2014a). Moreover, estimating baseline probabilities of detection do not necessarily need to rely on the surveying methods described and used here. For example, eDNA and meta-barcoding techniques can provide complementary or alternative methods for estimating probabilities of detection (Piaggio et al. 2014; Davy et al. 2015); nonetheless, even those alternative techniques are not exempt of requiring quantitative methods such as those developed here to inform management actions (Roussel et al. 2015; Guillera-Arroita et al. 2017).

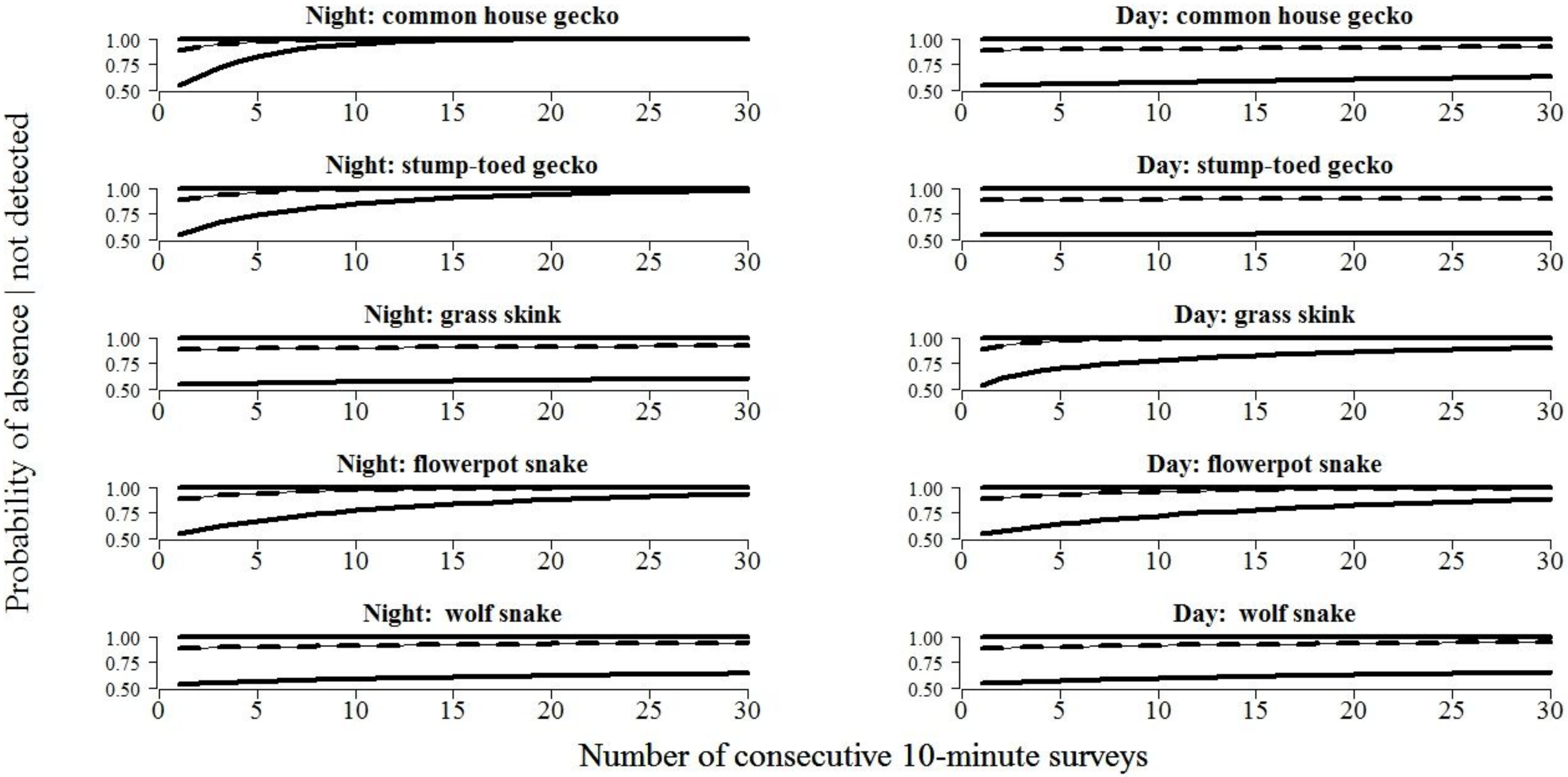


Fig. 6.4. Estimates of the probability of absence of five alien reptile species in a surveillance site, given that no individual is detected during the survey occasions for Scenario 1 (strong belief that new alien reptiles are absent). The median (dashed lines) and 95% Credible Intervals (solid lines) were obtained from one million draws of equation (6.5).

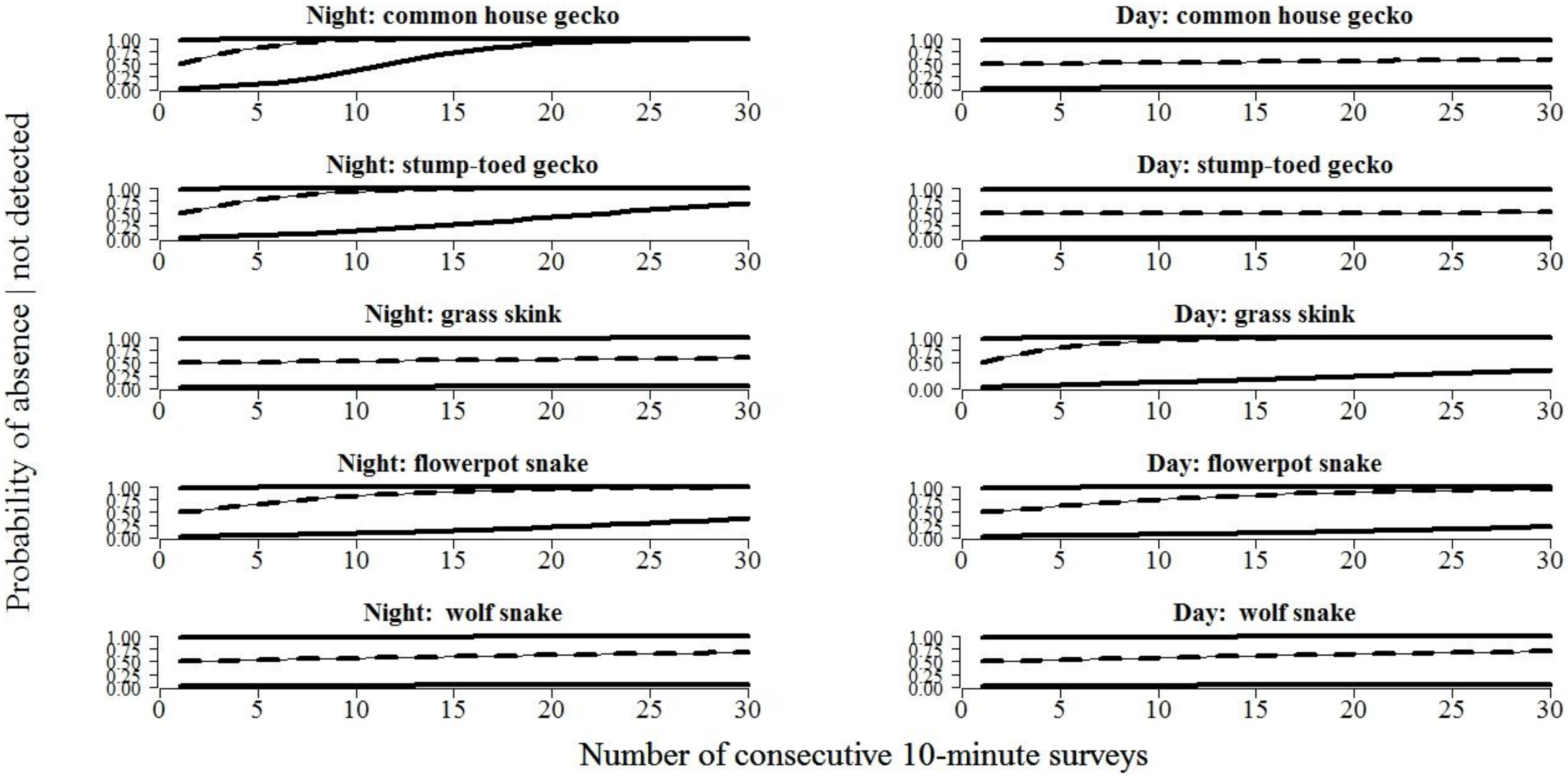


Fig. 6.5. Estimates of the probability of absence of five alien reptile species in a surveillance site, given that no individual is detected during the survey occasions for Scenario 2 (no strong belief in the presence or absence of new alien reptiles). The median (dashed lines) and 95% Credible Intervals (solid lines) were obtained from one million draws of equation (6.5).

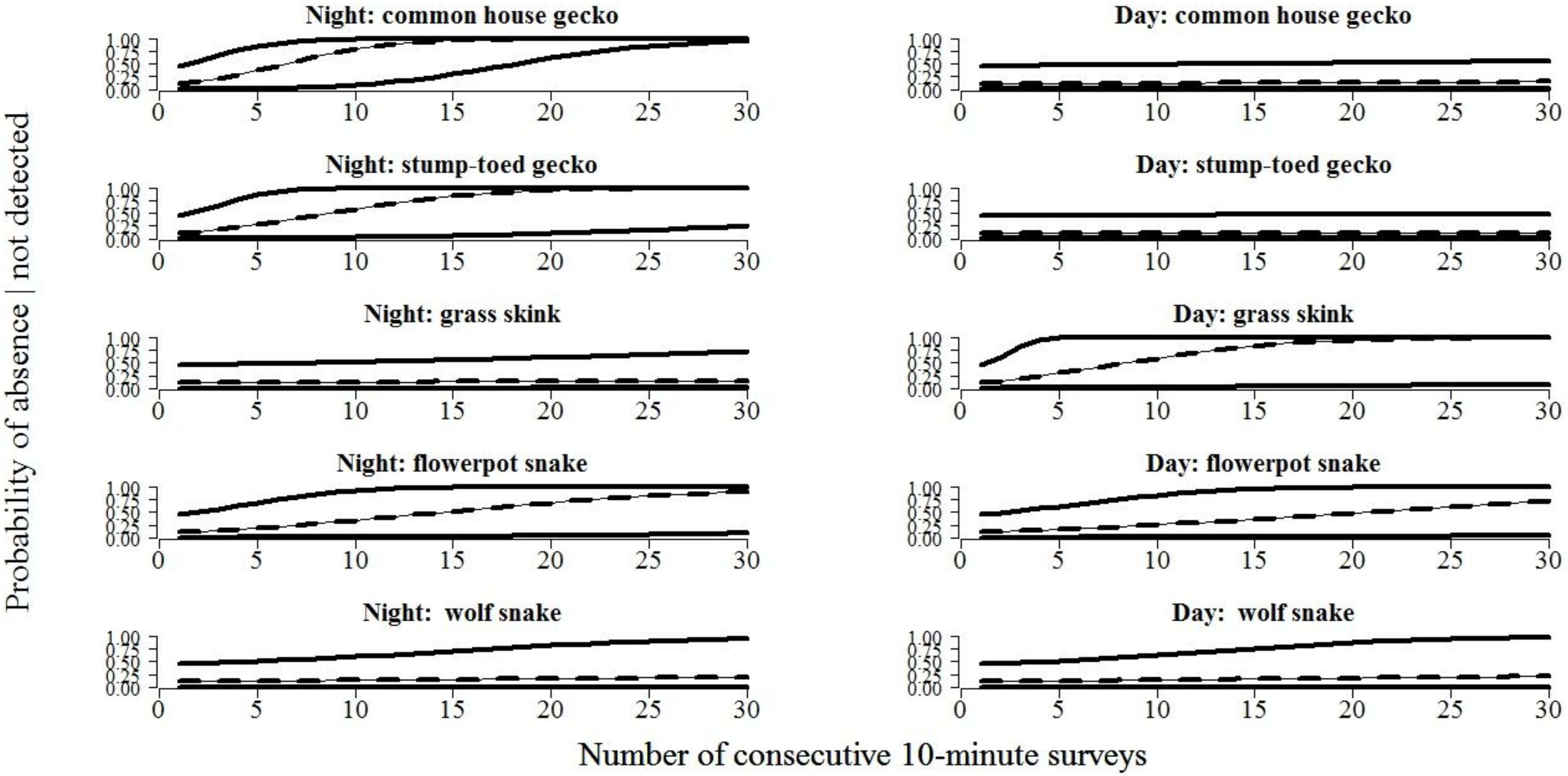


Fig. 6.6. Estimates of the probability of absence of five alien reptile species in a surveillance site, given that no individual is detected during the survey occasions for Scenario 3 (strong belief that new alien reptiles are present). The median (dashed lines) and 95% Credible Intervals (solid lines) were obtained from one million draws of equation (6.5).

We are aware of the potentially overwhelming task of designing and conducting early detection surveys for alien species. In particular, the decision to survey multiple sites (i.e., choosing how many sites to survey) around areas of greatest incursion risk is also a non-trivial task that will multiply the necessary surveying effort, and has been considered elsewhere (Brockerhoff et al. 2006; Yemshanov et al. 2015). Even so, we want to encourage ecologists, invasion biologists, environmental managers, and decision-makers to advance to a stage where early detection programs are planned and implemented on the field and not just recognised in publications. The scientific knowledge to underpin robust early detection programs is already well developed, and it is time that early detection programs become a widespread approach in the toolbox for managing alien species.

Chapter 7. General Discussion

Alien species are a product of human activities (Wilson et al. 2009; Wilson et al. 2016), and changes in human activities through time have resulted in the emergence of novel transport pathways. These novel pathways provide an opportunity to transport a different pool of alien vertebrates compared to historical times; particularly before the scientific-technical and digital revolution starting in the 1970s (see Chapter 5). Potential future shifts in the importance of transport pathways will challenge existing capacities for dealing with the environmental, social and economic problematic of alien vertebrates (Hulme 2009; Simpson and Srinivasan 2014; Hulme 2015; Early et al. 2016; Turbelin et al. 2016).

In this thesis, I have used the conceptual framework provided by the first three stages of the invasion pathway (transport, introduction and establishment; see Fig. 1.2 in the General Introduction), to understand and inform preventive measures for three groups of emergent alien vertebrates: amphibians (Chapter 2), reptiles (Chapters 3, 4 and 6), and fishes (Chapter 5). My research has provided insights into the importance and risks of transport, introduction, and establishment posed by different pathways transporting alien species of the three vertebrate groups. In the next pages, I discuss the broad implications of my findings and their relevance for policy and the management of alien vertebrates, both in Australia and globally.

Transport Pathways for Alien Amphibians, Reptiles, and Fishes

My research on alien amphibians, reptiles, and fishes identified a number of different transport pathways in Australia (Fig. 7.1). Three pathways were exclusive to alien fishes (acclimatisation, aquaculture and international legal trade), whereas alien amphibians and reptiles have also been recorded as unintentionally transported in Australia. The Eastern mosquitofish (*Gambusia hoolbrooki*) and the Cane toad (*Rhinella marina*) were transported in the past for biocontrol purposes (Pyke 2008; Shine 2010), but this transport pathway is no longer active in Australia for any species of the three groups studied here. Critically, my research revealed that the pathways differ in their importance. In this aspect, the deeper insights came from the research on alien amphibians (Chapter 2) and fishes (Chapter 5). Most of the alien amphibians in Australia have been transported for trade (71 out of 109 species; 65.1%), compared to species arriving as stowaways (38 species; 34.9%). In the case of alien fishes, the major pathways have been acclimatisation (pre-1970; 64%: 9 out of 14 established alien fishes in this period) and the ornamental fish trade (post-1970; 68% out of the 31 species established).

The scheme in Fig. 7.1 provides a snapshot of transport pathways for the three groups, but the importance of each pathway has changed over time as demonstrated in Chapter 5; regarding the temporal dynamics of alien fish richness in Australia. Previous research has also highlighted the swift changes that can occur in the importance of transport pathways, including in Australia (Blackburn et al. 2009; Kraus 2009; Henderson et al. 2011; Hulme 2015). For most of the alien vertebrate groups, the existing evidence supports a pivotal role of the legal and illegal wildlife trade (i.e., reptile and amphibian pets and ornamental aquarium fishes) as a primary source of alien species nowadays. Perhaps the best studied vertebrate taxa are alien birds, with an early emphasis by acclimatisation societies attempting to establish alien birds (1800s to early 20th century). This has subsequently changed to the current context where most of the new introductions are a consequence of escapes or releases of pet birds (Lever 1992; Blackburn et al. 2009; Su et al. 2016; Vall-llosera and Cassey 2017a). The changes in the importance of different transport pathways for alien fishes in Australia (Chapter 5) is remarkably similar to the global pattern for alien birds. Early during the European colonisation and settlement in Australia, there were pushes by acclimatisation societies for intentionally establishing alien fishes such as European carp (*Cyprinus carpio*), but this pathway lost importance in modern times in relation to the a dominance of alien ornamental fishes (Chapter 5).

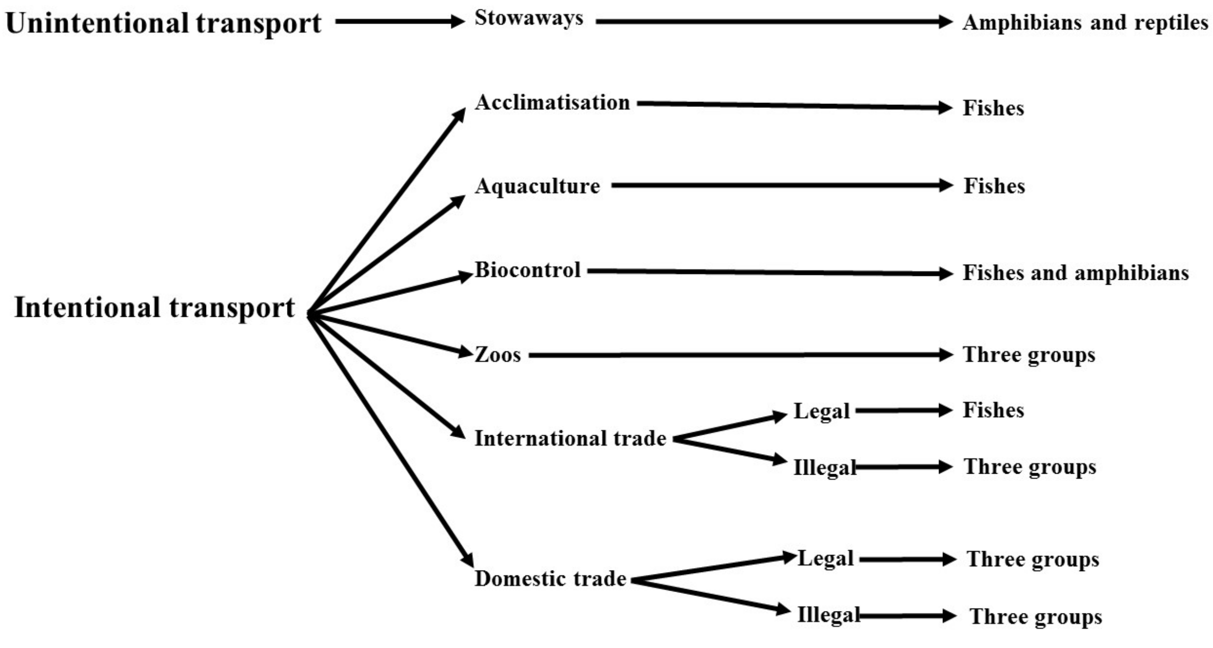


Fig. 7.1. Proposed classification of transport pathways for alien amphibians, reptiles, and fishes in Australia. This classification has been derived from the results exposed in this thesis.

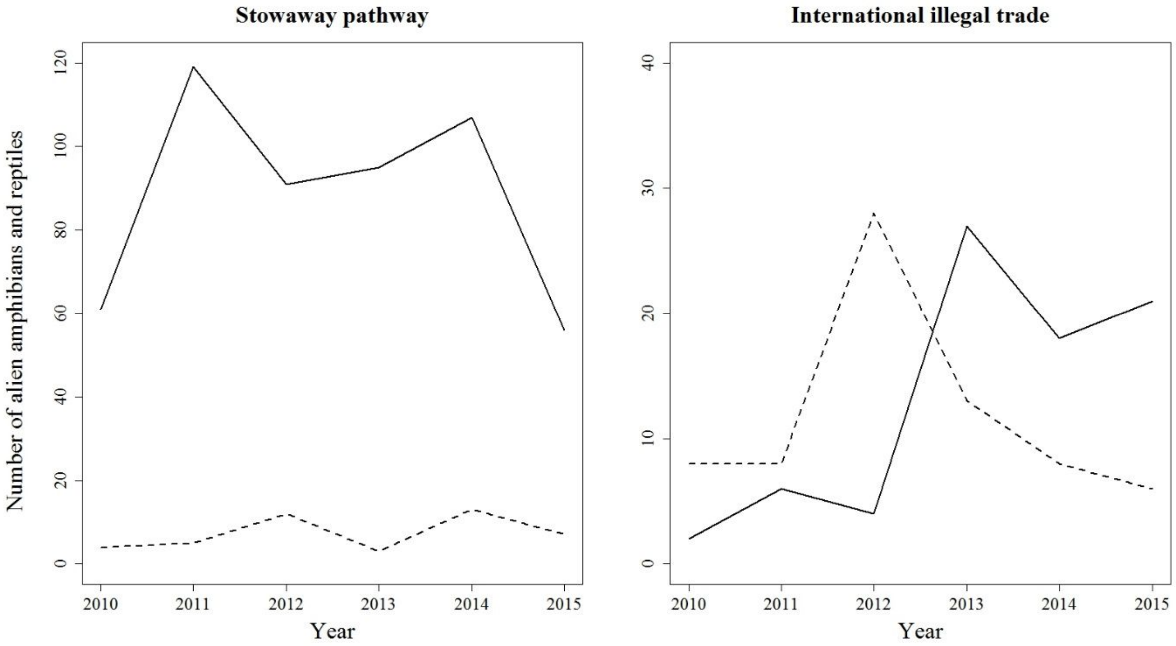


Fig. 7.2. Recent trends in the numbers of alien amphibian and reptile individuals intercepted by border authorities (solid line) and detected at large by authorities in Australia (dashed line) for two main transport pathways. Data compiled by the Intergovernmental Invasive Plants and Animals Committee, http://www.agriculture.gov.au/pests-diseases-weeds/pest-animals-and-weeds/invasive/ipac.

Recent trends in the numbers of alien amphibians and reptiles intercepted by authorities and detected at large in Australia (2010-2015; Fig. 7.2) do not seem to reveal any clear patterns, although the five-year period is insufficient for drawing sound conclusions. This was clearly not the case before 2010; for the period 1999-2010, Henderson et al. (2011) found a positive increase in the number of alien amphibians and reptiles reported in Australia. A longer time series of the monetary value of two pathways for alien fishes (AUD, 1988-2011), showed a steady growth in ornamental and aquaculture fish production and imports in Australia (Fig. 1.1 in the General Introduction).

It is important to realise that transporting high numbers of species do not necessarily equate to higher risks regarding the likelihood of establishment success. The analyses of the relationship between the global trade in Nearctic turtles and their transit through the stages of introduction to establishment in novel localities (Chapter 3) illustrated the complexity of the connection between the quantities traded (number of turtles imported per country) and the end result of successful establishment. The total number of slider turtles imported to a country did not influence the probability of establishment success of the species. Instead, the models found propagule numbers, measured as the minimum number of releases per country

(Lockwood et al. 2005; Blackburn et al. 2015), as a fundamental driver. The relationship between numbers traded and establishment success was indirect: numbers traded drive the probability of introduction, which in turn means increasing propagule numbers leading to higher probabilities of establishment success. Moreover, it is apparent that not all species in a pathway present the same risks. The whole-pathway analysis developed in Chapter 4 indicated that the illegal trade in alien reptiles poses a potential risk. However, examining each of the 28 illegal reptile species showed a wide variation in the estimated probabilities of establishment success (mean estimates ranging from 0.24 to 0.71 for the scenario with a moderate propagule number = 3; see Fig. 4.3 in Chapter 4).

Efficacy in Managing New and Emergent Alien Vertebrates: An Overview

The diversity of transport pathways has resulted in the existence of a range of management strategies, some of them tackling more than one pathway at once, and implemented simultaneously (Table 7.1). Achieving an integrated approach for managing alien vertebrates would benefit from considering how all the strategies fit together. In this situation, it seems appropriate to assess the capacities of management strategies in preventing alien species rather than concentrating on transport pathways (Game et al. 2013; Groves and Game 2016). An overview of management strategies used for preventing alien species in Australia may potentially produce timely lessons of relevance for other regions designing and implementing preventive policies (Genovesi et al. 2015; Lodge et al. 2016; Turbelin et al. 2016).

I have summarised the major management strategies recognised during the conduct of my own research, obtaining five broad categories that I examine in the light of my results (Table 7.1). In most of the cases, the strategies manage more than one transport pathway and potential impacts of alien vertebrates, and may act complementarily in reducing risks. For example, compulsory species-based risk assessments for the importation of alien species may be viewed as a first step to preventing alien species in Australia (banning those deemed too risky), supplemented with quarantine screening of those specimens from species that are indeed allowed for importation (Whittington and Chong 2007).

Most of the management strategies employed for preventing the introduction and establishment of alien amphibians, reptiles, and fishes can be assessed as being moderately or highly effective by themselves (i.e., independently of each other) based on the results presented in this thesis and additional scientific publications on alien birds and fishes (Table 7.1). The recent trends plotted in Fig. 7.2 suggest that management strategies for alien amphibians and reptiles transported as stowaways have had a consistent high efficacy in intercepting animals and preventing them from escaping into the wild. On the other hand, the number of alien amphibians and reptiles intercepted from the illegal international trade has increased recently, with a concomitant decrease in the number of animals found at large (Fig. 7.2), suggesting an improvement in the performance of the relevant management strategies. Nonetheless, the performance of management strategies varies across alien taxa and states. For example, border and on-shore biosecurity activities in Australia reduced the risk of introduction of alien ranaviruses in the country substantially (García-Díaz et al. 2016b). In contrast, a number of studies have demonstrated that border biosecurity activities have been ineffective in intercepting alien insects in Australia and Europe (Bacon et al. 2012; Caley et al. 2015; Faulkner et al. 2016). Similarly, not all states within Australia are equally willing to manage new alien vertebrates, with some states investing more resources in policing potentially risky pathways (see Chapter 4 for the case of the illegal alien reptiles).

It is clear that there is a strong emphasis on managing pathways that transport alien vertebrates from overseas. Domestic pathways (i.e., within Australia), on the other hand, tend to be scarcely regulated, if managed at all (Table 7.1), with the exception of the states of Western Australia and Tasmania that manage their own borders. This attention to alien species is not fully warranted by the results presented here. The majority of transported alien amphibians are domestic exotics (66% of 97 species; Chapter 2), and the probability of establishment success of domestic reptiles does not differ from that of alien reptiles (widely overlapping posterior intercepts for alien and domestics; Fig. 4.2 in Chapter 4). A convoluted wildlife licensing system enforced at the both federal and state levels drives the availability and abundance of vertebrate species in the domestic legal trade (Chapter 2) (Vall-llosera and Cassey 2017b), but it seldom considers the role of the domestic trade as a fundamental pathway for alien vertebrates.

Despite the preventive efforts and the seeming efficacy of on-shore biosecurity activities in intercepting alien vertebrates (García-Díaz et al. 2016b), there had been alien amphibians and fishes from overseas establishing in the wild in Australia in modern times (Lintermans 2004; Morgan et al. 2004; Tingley et al. 2014). There may even exist an ‘establishment debt’, where some alien species have not yet established because they have not had sufficient time to form a self-sustaining population since they were introduced (Crooks 2005; Faulkner et al. 2016; Rouget et al. 2016). On-shore management strategies and activities may need to be reviewed to assess their early detection and rapid response capabilities.

Strategies	Examples of activities	Pathway(s) targeted	Impact(s) targeted	Efficacy	References
Species-specific risk assessments	Standardised risk assessments for the importation of alien amphibians and reptiles	1. Legal international trade 2. Zoos	All	High	Bomford et al. (2005); Whittington and Chong (2007); Deveney and Beyer (2014); Cassey and Hogg (2015); Lodge et al. (2016); Chapters 3 and 4
Quarantine	Compulsory quarantine screening of imported live animals	1. Legal international trade 2. Zoos	Diseases Parasites	Moderate	Whittington and Chong (2007); Becker et al. (2014); Rimmer et al. (2015); García-Díaz et al. (2016b)
Border biosecurity	Inspection of international incoming goods and commodities	1. Stowaways 2. Illegal international trade	All	High	Hyatt et al. (2002); García-Díaz et al. (2016b); Chapter 4
On-shore biosecurity	Public awareness campaigns Early detection of new alien species Inspection of interstate incoming goods and commodities	1. Stowaways 2. Legal international trade 3. Illegal international trade 4. Legal domestic trade 5. Illegal domestic trade	All	Moderate	Tingley et al. (2014); García-Díaz et al. (2016b); Vall-llosera et al. (2016); Chapters 2, 4 and 6
Wildlife licensing	Permits and licences regulating the interstate trade in live animals	1. Legal domestic trade	Pest potential	Low	Vall-llosera and Cassey (2017b); Chapters 2 and 4

Table 7.1. Summary of the main current management strategies and examples of activities and their efficacy in preventing alien amphibians, reptiles, and fishes in Australia. These strategies target different transport pathways (see Fig. 7.1) and impacts. Potential impacts were classified following the approach of Clout and Williams (2009) for providing a simplified guide of impacts targeted: (i) pest potential: including the impacts ‘competition’, ‘predation’, and ‘hybridisation’ from the classification system of Blackburn et al. (2014); (ii) diseases: alien species are diseases or vectors for diseases; (iii) parasites: alien species are parasites or vectors for parasites. Efficacy was evaluated using a simple ranking to facilitate its quick interpretation (Groves and Game 2016): low, moderate, and high. The supporting references are not meant to be an exhaustive list, but provide support for the interpretations made in the Table. Note that three pathways for alien fishes, acclimatisation, biocontrol and aquaculture, are not included in the Table either because they are no longer active (biocontrol) or because they are poorly regulated as a source of alien species, or are even actively promoted (acclimatisation via stocking of alien fishes and aquaculture).

Recommendations for Improving the Efficacy of Preventive Strategies

The outlook in the previous section highlighted some areas where there is room for improvement, which may prove essential for successfully facing the threats and risks posed by emergent alien vertebrates (Simpson and Srinivasan 2014; Early et al. 2016). Proposals for potential improvements have been detailed in each Chapter of the thesis, so here I focus on more general issues not deeply discussed in previous chapters.

At the level of the design, planning, and implementation of policies and management strategies for preventing alien vertebrates, it is important to address the elephant in the room: the largely neglected issue of the domestic legal trade, a pathway contributing a substantial share of the alien vertebrates (Chapters 2 and 4). Applying the same principles of species-based risk assessments used for managing international imports can also provide a basis for regulating the domestic trade, which can be embedded within the existing system of wildlife licensing (Chapter 2)(Vall-llosera and Cassey 2017b). Preventive strategies such as banning the trade in one species might be difficult to justify and may meet with social resistance (Smith et al. 2009; Perry and Farmer 2011). In this situation, better reporting of the costs and benefits produced by alien vertebrates is paramount (Williamson et al. 2011; Leung et al. 2014; Hoffmann and Broadhurst 2016). The costs and benefits can be fed into cost-benefit analyses for assessing management and policing alternatives (e.g., prohibition versus eradication if established), and for supporting the delivery of policies based on the expected benefits (Hammitt 2013; Keller and Springborn 2013; Lodge et al. 2016). The comparison of the costs incurred by different management strategies for slider turtles shown in the General Introduction (Fig. 1.3) is an excellent example of the interest of using expenditures in justifying preferred management strategies.

In the arena of species and pathway profiling, there is a need for further research into the drivers and dynamics of most of the pathways. Future research may address, amongst other things, the differences in the tendencies for the different pathways and taxa, and potentially adopting the concept of leading indicators from economics and policy making (Gyomai and Guidetti 2012; Barber 2015), which would likely help in recognising emergent pathways before they become a source of new alien vertebrates. Across pathways and taxa, additional research would clarify the risks posed by each pathway, a fundamental step towards managing transport pathways (McGeoch et al. 2015; Saul et al. 2016). The risk posed by a pathway is compounded by the risks of the individual species transported, the abundance of each species in the pathway, and the social dimension of the pathway (i.e., the behaviour of humans). A full understanding of transport pathways would require uncovering the incentives and motivations of people shaping and driving the pathway (Daly and Morton 2006; Van Wilgen et al. 2010; Colléony et al. 2016; Vaz et al. 2017), as suggested in Chapter 4 for the illegal trade in reptiles. An outstanding repercussion of the results of my research on alien fishes is that the application of species-based risk assessments should be adaptive whenever possible (Linkov et al. 2006; Groves and Game 2016; Salafsky et al. 2016). This will ensure that potential changes in the covariates influencing alien species richness due to shifts in transport pathways are properly accounted fo in the assessments (Chapter 5). Otherwise, species-based risk assessments may produce biased risk estimates.

The indirect influence of numbers of animals traded or imported on the probability of establishment success (Chapter 3)(Gertzen et al. 2008; Van Wilgen et al. 2010; Bradie and Leung 2015; Su et al. 2016), raises the interesting question of whether imposing a quota, or a cap, on numbers may be a potentially sensible alternative to full species' bans. It is a research path worth exploring in further detail, although it might prove controversial given the experience with wildlife harvesting quotas (Mysterud 2011; Perry and Farmer 2011; Di Minin et al. 2016; Ripple et al. 2016). The quantitative models developed in Chapter 3 offer a robust starting point for conducting research in this direction.

In this thesis, I have developed a quantitative approach for the early detection of alien species, which I tested using the case study of alien reptiles in Christmas Island (Chapter 6). These results demonstrate that implementing early detection activities would be a very challenging task as a consequence of the necessary surveying efforts required to declare absence of new alien species confidently. However, early detection is critical to trigger rapid responses and thus a fundamental pillar of an integrative approach for ensuring that no new alien species become established (Simpson et al. 2009; Bylemans et al. 2016; Lodge et al. 2016; US Department of the Interior 2016). The collaboration and awareness of the general public are invaluable in reporting the presence of new alien species to authorities, and it is important to strive to involve citizen science better in alien species management (Gallo and Waitt 2011; Moorhouse et al. 2016). In any case, being proactive in managing new alien species by conducting structured early detection activities in sites identified to have a high likelihood of a new incursion would represent an important leap forward compared to the haphazard tactics that characterise most of early detection programs in the world. Using the early detection framework developed here, or incorporating some of its elements into other early detection protocols, would deliver a reliable approach for implementing early detection activities.

It is important to stress that the overarching goal of alien species management is to mitigate or avoid their potential ecological, economic and social impacts (Woodford et al. 2016; Russell and Blackburn 2017). Some management approaches recommend the prohibition of new alien species likely to have large impacts and allow those for which there is no, or weak, evidence of potential negative impacts (Tollington et al. 2015). The current state of knowledge does not permit drawing clear quantitative generalisations of the drivers of the importance of potential impacts across environments, taxa, and geographic regions (Ricciardi and Simberloff 2009; Ricciardi et al. 2013; Blackburn et al. 2014; Jeschke et al. 2014). Moreover, there is scarce information available on the impacts, if any, produced by the vast majority of alien vertebrates (Cucherousset and Olden 2011; Blackburn et al. 2014; Kraus 2015; Evans et al. 2016; Measey et al. 2016). The knowledge gap of the impacts produced by most alien vertebrates undermine the applicability of assessing potential impacts. Much more research is needed on this front to obtain predictions that can be appended to assessments of establishment risk.

Conclusion

Shifts in the importance of transport pathways are changing the number and taxonomy of alien vertebrates being moved around the world. This is particularly well reflected in the current importance of the wildlife trade and the unintentional movement of stowaways as the main transport pathways for alien vertebrates, compared to the previous role played by acclimatisation societies in spreading alien species worldwide. Alien vertebrates are critical drivers of biodiversity loss worldwide, and there is a persistent need for understanding the factors underlying biological invasions and how to combat their current and future potential impacts. In this thesis, I have applied quantitative methods to the comparative analysis of the features driving the transport, introduction, and establishment of three groups of emergent alien vertebrates: amphibians, reptiles, and fishes. The analyses have been conducted in the general context of assessing pathways of transport, a major objective of preventing the establishment of new alien species. Additionally, I have developed approaches to support evidence-based management activities for alien species.

Despite the global political trend leaning towards regionalism rather than globalisation, it can be expected that the number of alien vertebrates transported will continue to grow, posing a severe challenge to their successful management. In my research, I have provided critical knowledge and novel analytical tools for informing the management of alien vertebrates, highlighting the relevance of understanding and investigating transport pathways and the crucial role of propagule pressure in explaining the establishment success of alien species. I have focussed on particular case studies throughout this thesis, but the methods developed and the broad conclusions reached are expected to be of relevance to decision makers, researchers, and field operatives involved in managing and studying biological invasions. It is fundamental that we collaborate across disciplines and groups of interest to produce and translate research into evidence-based policies and best management practices for alien vertebrates. The future of biodiversity may depend on it.

Appendix 1. Supplementary material to Chapter 2.

1.1. Geographical Origin of Transported and Introduced Amphibians in Australia.

Worldwide maps (size of the squares of the grid: 10º x 10º) based on the latitudinal and longitudinal mid-points of the native range of transported and introduced amphibians in Australia.

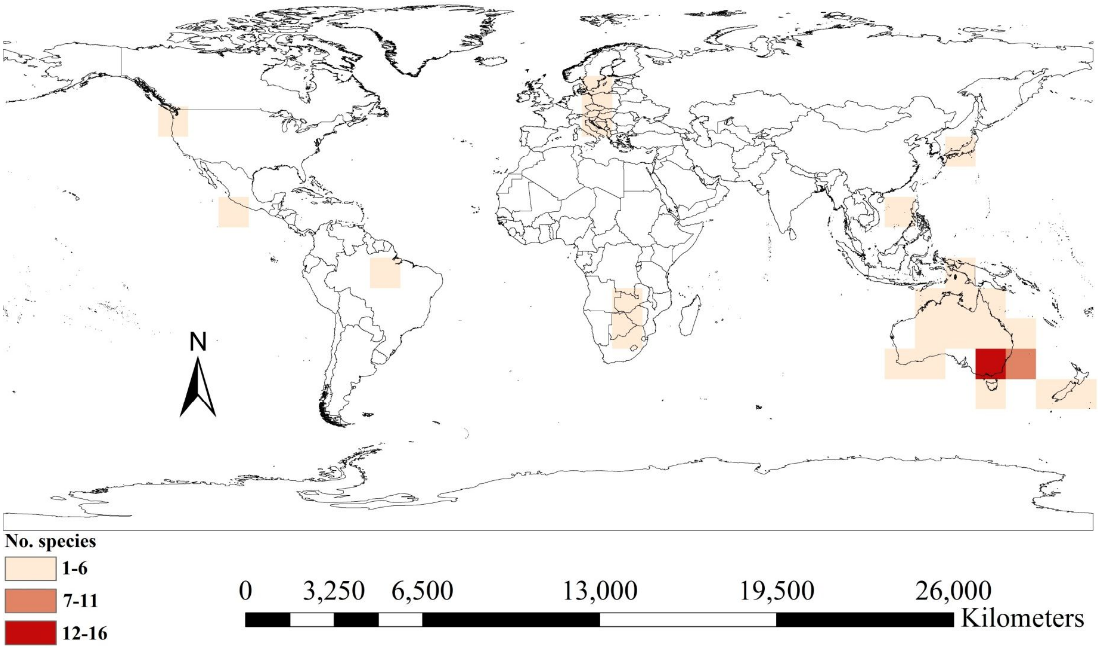


Fig. A.1.1. Species richness based on the geographical origin of amphibians transported for trade (n=71).

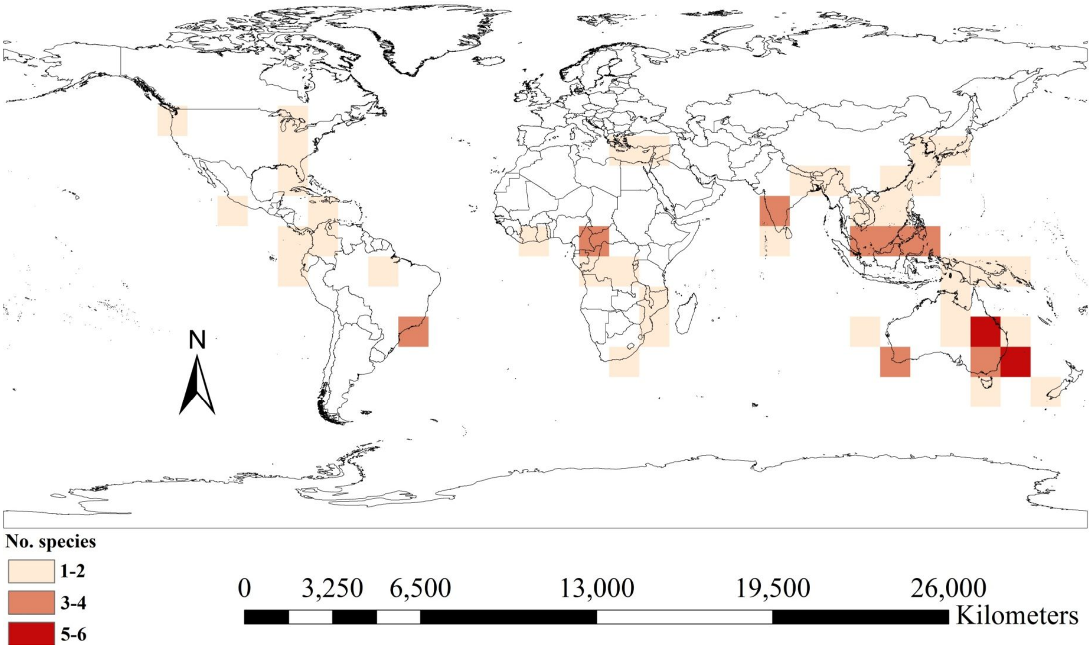


Fig. A.1.2. Species richness based on the geographical origin of amphibians transported as stowaway (n=38).

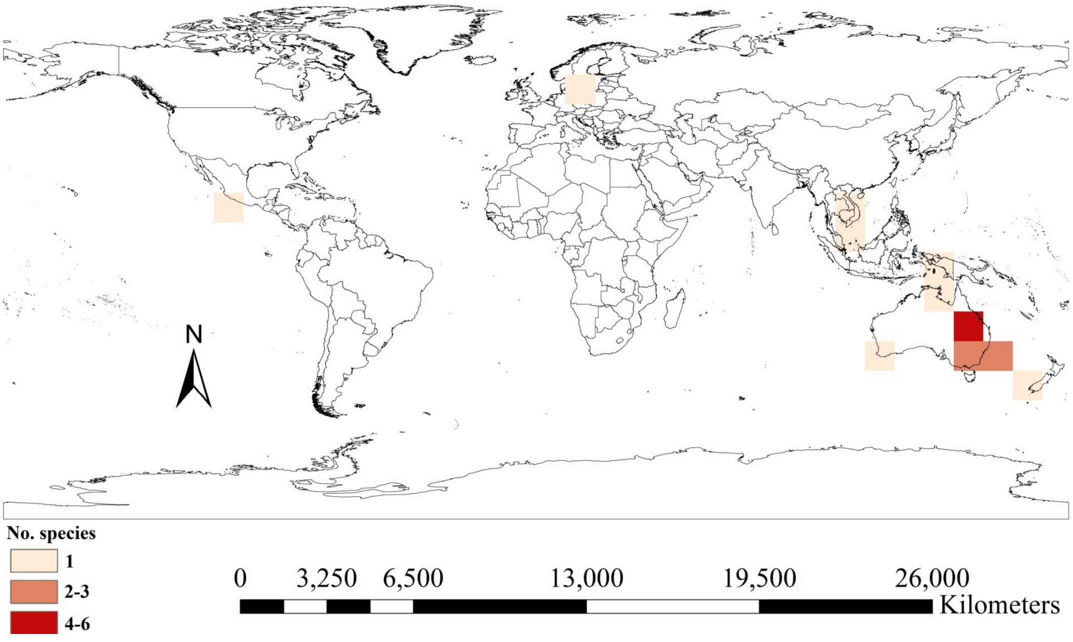


Fig. A.1.3. Species richness based on the geographical origin of introduced amphibians (n=19).

1.2. Coefficient Estimates for the Best Fitted GLMMs for Transported Amphibians to or Within Australia.

	Estimate ± standard error	**Bias**	**95% Confidence Intervals**
Intercepts-family specific			
Ambystomatidae	-3.99 ± 3.97	-2.67	-5.28, 3.56
Cryptobranchidae	-6.44 ± 7.67	-5.35	-5.90, 6.08
Dendrobatidae	-2.69 ± 7.64	-5.71	-10.13, 2.51
Dicroglosidae	-0.84 ± 8.63	-8.25	-9.12, -4.56
Hylidae	-7.78 ± 8.70	-7.17	-16.31, -3.23
Leiopelmatidae	-6.33 ± 8.99	-8.47	-9.06, -2.85
Microhylidae	-7.75 ± 8.72	-7.85	-12.33, -3.33
Myobatrachidae	-7.66 ± 8.67	-7.29	-14.49, -2.48
Pipidae	-6.83 ± 8.72	-7.19	-12.35, -1.39
Ranidae	-6.63 ± 9.02	-6.59	-9.84, -3.56
Rhacophoridae	-6.27 ± 7.71	-5.52	-13.35, -5.96
Salamandridae	-5.44 ± 13.24	-5.46	-15.03, -2.13
Area	0.34 ± 2.11	0.35	0.09, 0.49
Longitude	0.04 ± 0.23	0.04	0.03, 0.05

Table A.1.1. Coefficient estimates for the best fitted generalized linear mixed model for amphibians transported for trade. Structure of the best fitted model: logit(transport probability) ~ [Family] + log10(Area) + Longitude ([Family]: random factor). Estimates were obtained by means of 1000 bootstrapped runs of the model. Biases represent the difference between bootstrap and sample estimates.

	Estimate ± standard error	**Bias**	**95% Confidence Intervals**
Intercepts-family specific			
Bufonidae	-3.59 ± 6.63	-1.99	-5.40, -.176
Dendrobatidae	-3.64 ± 3.98	-0.96	-6.55, -2.00
Dicroglosidae	-3.64 ± 4.09	-1.23	-5.96, -1.70
Hylidae	-3.64 ± 4.24	-1.24	-6.35, -1.83
Microhylidae	-3.63 ± 3.15	-0.69	-6.76, -1.56
Myobatrachidae	-3.64 ± 3.94	-0.53	-7.99, -1.01
Pelobatidae	-3.63 ± 4.09	-1.07	-6.43, -2.02
Pipidae	-3.63 ± 4.22	-1.16	-6.26, -1.87
Ranidae	-3.64 ± 5.20	-1.34	-6.39, -1.68
Rhacophoridae	-3.64 ± 3.61	-1.08	-6.21, -1.86
Salamandridae	-3.63 ± 2.50	-0.94	-6.48, -2.04
Area	1.40 ± 0.69	0.34	0.84, 1.99

Table A.1.2. Coefficient estimates for the best fitted generalized linear mixed model for amphibians transported as stowaway. Structure of the best fitted model: logit(transport probability) ~ [Family] + log10(Area) ([Family]: random factor). Estimates were obtained by means of 1000 bootstrapped runs of the model.

Appendix 2. Supplementary material to Chapter 3.

2.1. Genus-level Phylogenetic Relationships of Nearctic Turtles

The phylogeny of turtles was obtained from Guillon et al. (2012)(downloaded from TreeBase: http://treebase.org/). We selected a representative species for each of the genera of exported turtles. We obtained the final genus-level phylogeny by dropping all the other tips of the original tree of Guillon et al. (2012). This procedure was conducted using the function drop.tip in the R package ape (Paradis et al. 2004; Paradis 2011; R Development Core Team 2015). The phylogeny obtained after pruning the tree is presented in Figure A.2.1.

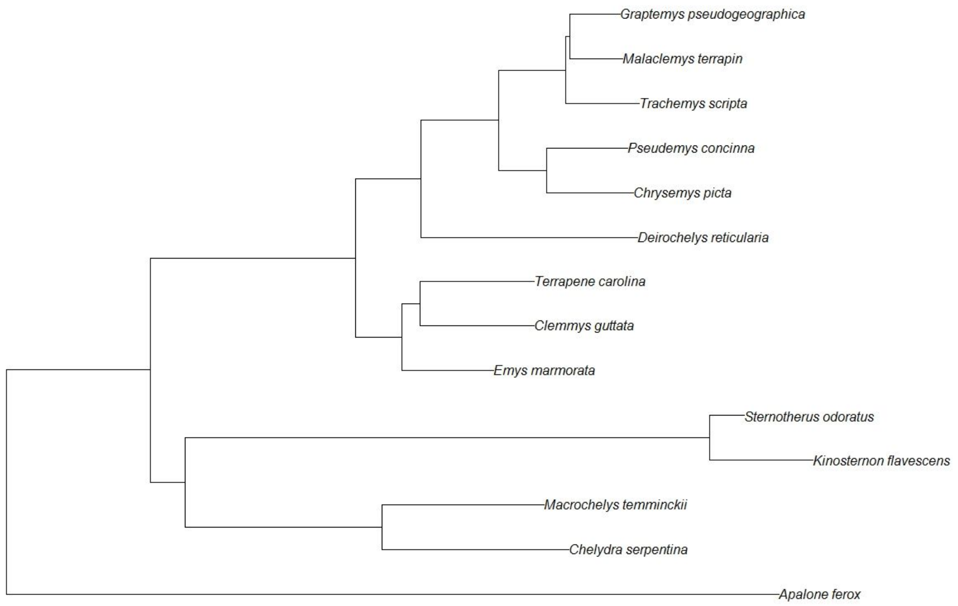


Fig. A.2.1. Phylogeny of Nearctic turtles used to inform the models of probability of introduction.

2.2. Ambient Temperatures and Survival of Slider Turtles

We calculated the proportion of 2.5º x 2.5º cells whose ambient temperatures would permit the survival of slider turtles (*Trachemys scripta*) by assuming that every cell with a temperature within the physiological limits of the species would permit their survival (Kearney and Porter 2009; Araújo et al. 2013; Ceia-Hasse et al. 2014)(Fig. S2). The physiological limits were defined as the critical thermal maxima and minima (when the locomotion of the species becomes disorganized): 42º and 1.8ºC, respectively (Hutchison et al. 1966b; Ernst and Lovich 2009).

We utilized two ambient temperatures: the maximum temperature of the warmest month and the minimum temperature of the coldest month. We selected these two covariates because there is evidence that extreme temperatures strongly affect the survival of slider turtles (Bodie et al. 2000; Ernst and Lovich 2009). We downloaded 2.5º x 2.5º gridded worldwide layers for these temperatures from WorldClim: http://www.worldclim.org/current (Hijmans et al. 2005). We then assigned a 1 (or 0) value to each cell within (or outside) the temperature limits, and we repeated this procedure for the two grids independently (Fig. A.2.2). We merged both grids to obtain an unique grid representing the cells whose ambient temperatures were within the physiological limits imposed by the critical temperatures (Fig. A.2.2). This means that if, for example, a cell can support the presence of the species based on the critical maximum, but not based on the critical minimum, then the final value is a 0 (the cell cannot support the species). Finally, we calculated the proportion of cells in a jurisdiction that had ambient temperatures within these limits. We used the proportion of cells in our models for predicting the establishment success of slider turtles. We conducted all of the spatial analyses in packages raster (http://cran.r-project.org/web/packages/raster) and rgdal (http://cran.r-project.org/web/packages/rgdal/) for R (R Development Core Team 2015), and in Arc GIS 10.0 (ESRI, Redland, CA, USA).

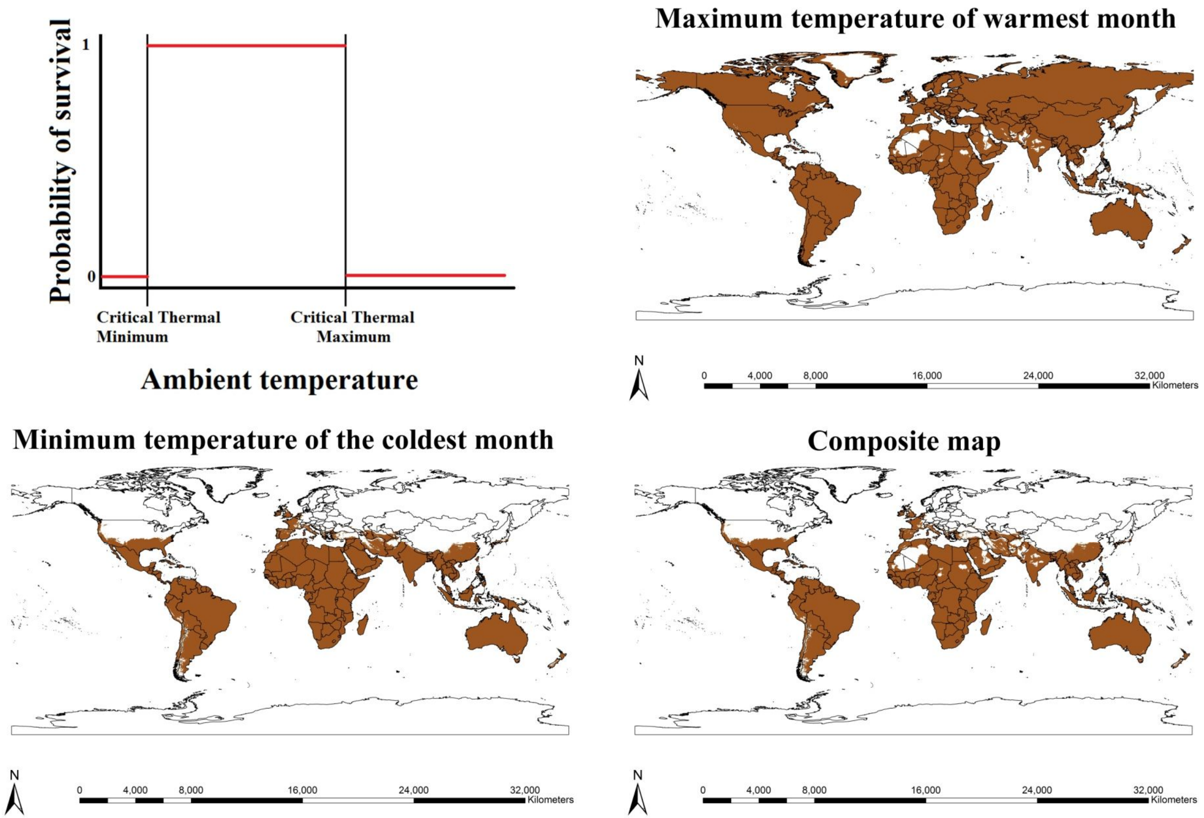
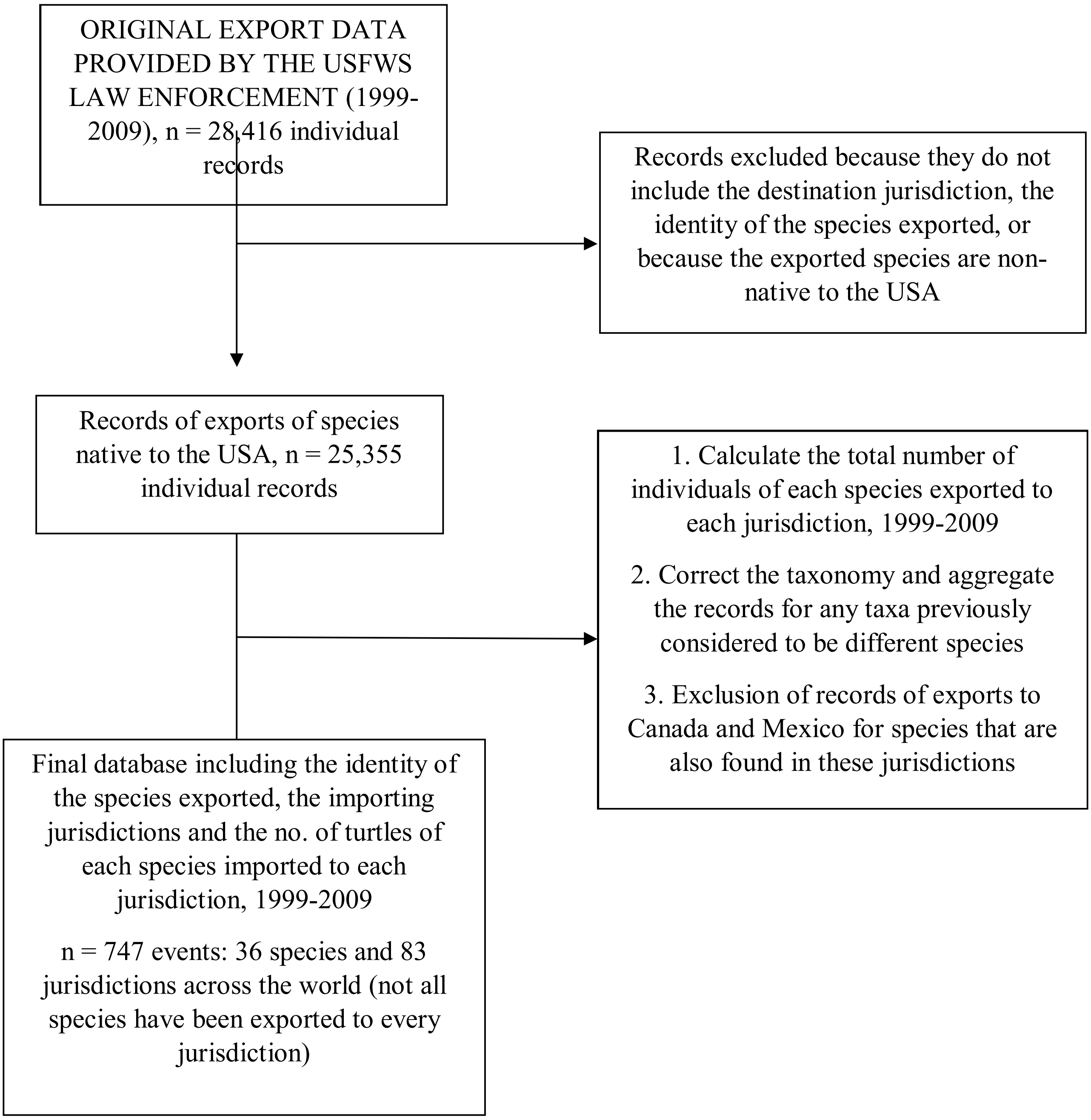


Fig. A.2.2. Graphical representation of the conceptual framework for linking the probability of survival of slider turtles to the ambient temperatures, and procedures for locating the cells within a jurisdiction that fall within the limits imposed by the critical thermal values. Brown colour indicates the regions, for each grid, where the ambient temperatures fall within the ranges marked by the critical thermal temperatures. The composite map was obtained after merging the other two maps.

2.3. Flowchart Showing the Procedures Used to Filter the Database of Freshwater Turtle Exports.



2.4. Posterior Probabilities of Models and Coefficient Estimates

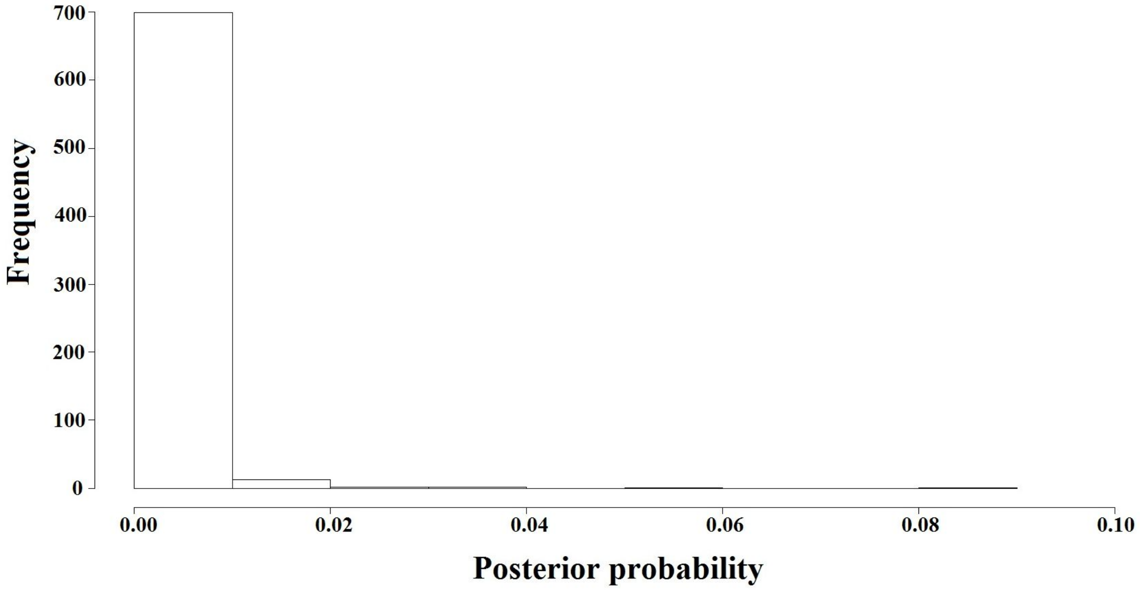


Fig. A.2.4.1. Histogram of the distribution of the posterior probabilities of models for the recorded introduction of Nearctic turtles.

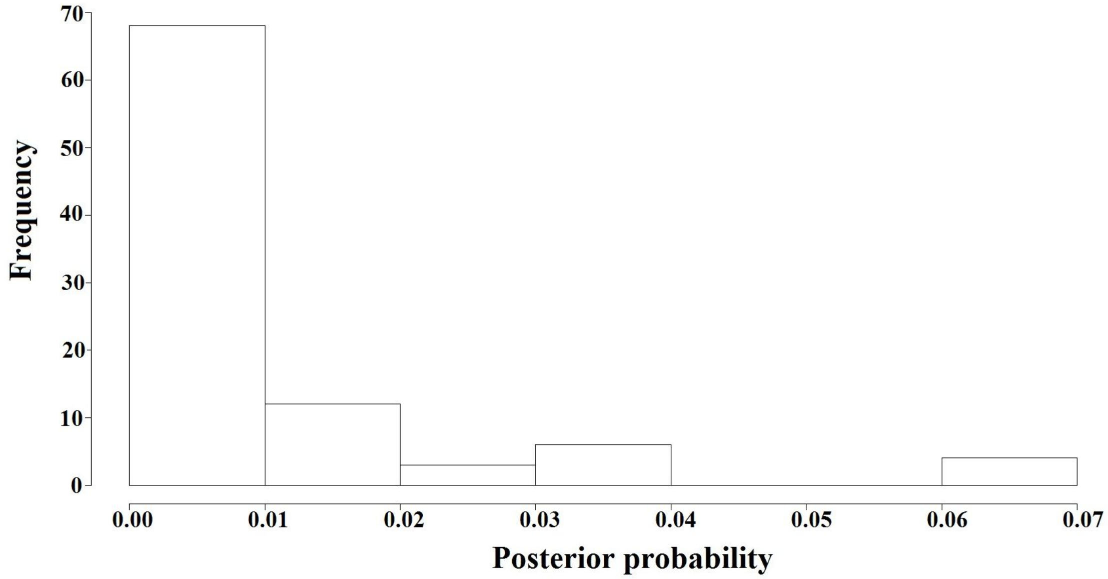


Fig. A.2.4.2. Histogram of the distribution of the posterior probabilities of models for the recorded establishment success of slider turtles.

	Median ± standard deviation	**97.5% HPDI**
Introduction		
Genus-specific intercepts		
Apalone	-1.83 ± 1.02	(-3.93, 0.07)
Chelydra	-0.25 ± 1.10	(-2.46, 1.91)
Chrysemys	-0.83 ± 0.94	(-2.74, 0.98)
Clemmys	-1.66 ± 1.10	(-4.03, 0.24)
Deirochelys	-1.27 ± 1.14	(-3.77, 0.72)
Emys	-1.83 ± 1.49	(-5.35, 0.51)
Graptemys	-1.15 ± 1.02	(-3.27, 0.68)
Kinosternon	-2.01 ± 1.00	(-4.13, -0.17)
Macrochelys	-0.50 ± 1.24	(-3.03, 1.86)
Malaclemys	-1.51 ± 1.19	(-4.30, 0.42)
Pseudemys	-1.62 ± 0.99	(-3.71, 0.15)
Sternotherus	-2.75 ± 1.00	(-5.01, -1.11)
Terrapene	-1.02 ± 1.25	(-3.73, 1.20)
Trachemys	0.96 ± 0.92	(-0.70, 2.94)
Slope of $\log_{10}$(no. turtles imported)	0.47 ± 0.14	(0.19, 0.76)
Slope of $\log_{10}$(age at maturity)	-2.42 ± 0.96	(-4.24, -0.48)
Detection		
Intercept	-0.19 ± 1.17	(-1.62, 3.04)
Slope of $\log_{10}$(no. GBIF records + 1)	1.30 ± 1.40	(0.32, 5.51)

Table A.24.1. Logit-scale posterior coefficient estimates of the top ranked model for the recorded introduction of Nearctic turtles.

Appendix 3. Supplementary material to Chapter 4.

3.1. Data Sources

Covariate	**Definition**	**Data sources**
Propagule number	Minimum number of independent release events	See data accessibility statement
Body length	Average adult body length (cm) Turtles: carapace length Squamates: snout-vent length	Gans (1969-2010); Shine (1998); Boback and Guyer (2003); Wilson (2003); Cogger (2014); Myers et al. (2014); Das (2015)
Fecundity per breeding season	Number of eggs per clutch (oviparous species) Number of juveniles born per season (viviparous)	Gans (1969-2010); Shine (1998); Wilson (2003); Myers et al. (2014); (Das 2015); Macdonald (2015)
Number of congeneric species	Total number of species of the same genus present in Australia	Uetz and Hošek (2013); Cogger (2014)
Preferred body temperature	Average body temperature during activity bouts (° C)	Brattstrom (1965); (Hutchison et al. 1966a); Light et al. (1966); McGinnis and Moore (1969); Webb and Johnson (1972); (Otis 1973); Johnson (1975); Feder and Feder (1981); Shine and Lambeck (1985); Bennett and John-Alder (1986); (Ellis and Chappell 1987); Brown and Brooks (1991); Pianka (1994); Manning and Grigg (1997); Bedford and Christian (1998); Roark and Dorcas (2000); Seebacher et al. (2004); Ikeuchi et al. (2005); Seebacher (2005); Chen and Lue (2008); Roe et al. (2008); Clusella-Trullas et al. (2011); McConnachie et al. (2011); Meiri et al. (2013)
Area	Area of the region, km^2 / 10,000	http://www.ga.gov.au/scientific-topics/national-location-information/dimensions/area-of-australia-states-and-territories

Table A.3.1. Definition and information sources for the six covariates included in the regularised Bayesian logistic regression for modelling the establishment success of introduced reptiles in Australia and external Territories. Preferred body temperature was not a covariate in the model, but rather was used to calculate the absolute Thermal Safety Margin. However, as there were missing data for body temperatures (15 species with missing data), we illustrate here the distribution for the species for which we had data and which we used for the Bayesian imputation procedures.

3.2. Supplementary Methods

Procedures for calculating the absolute Temperature Safety Margin (aTSM) for models of establishment success of alien reptiles in Australia and external Territories, and for alien species illegally traded in the country.

The climate in the recipient location, or its match to the climate in the native range, is frequently found to be a correlate of establishment success for introduced reptiles (Bomford et al. 2009b; Van Wilgen et al. 2009; Fujisaki et al. 2010; Van Wilgen and Richardson 2012; Mahoney et al. 2014). The relationship between individual reptiles and the surrounding environment can be examined by measuring body and environmental temperatures, which in turn can provide mechanistic insights into the thermal niche of the species (Clusella-Trullas et al. 2011; Araújo et al. 2013; Ceia-Hasse et al. 2014). Following and Clusella-Trullas et al. (2011), we estimated the absolute Temperature Safety Margin (aTSM) as the absolute difference between the introduced reptile species' preferred body temperature and the median average temperature of the warmest quarter in the region of introduction. We used the temperature of the warmest quarter because it is the period when reptiles are most active, and when ambient temperatures will likely have the greatest influence on ecological behaviour (Clusella-Trullas et al. 2011).

Values for the aTSM index provide a mechanistic explanation for the interplay between body and environmental temperatures in an establishment success framework because aTSM values close to zero indicates that the species is living in an approximately optimal environment whereas aTSM values far from zero indicate sub-optimal conditions (Deutsch et al. 2008). Therefore, we expect that aTSM values closer to zero will favour establishment success. We obtained data on median average temperatures of the warmest quarter (bio10; 30' resolution, 1961-1990) for mainland Australia and each of the external island territories from the CliMond database (Kriticos et al. 2012). The data available on the geographical location of alien reptile releases indicates that species were mainly released in urban and peri-urban areas in Australia and the external Territories (Smith 1988; Maryan 2001; Clemann 2005; Burgin 2006; McKay and Horner 2007; Hoskin 2011). In order to account for the characteristics of the release sites, we have calculated median average temperatures of the warmest quarter in an area defined within 50 kilometres of the boundaries of the towns and cities in mainland Australia and the external Territories. The digital map of the boundaries of cities and towns in Australia was obtained from the Australian Bureau of Statistics (http://goo.gl/WO7s3T). Following the procedures described, the calculated median temperatures were 24.5 ºC for mainland Australia, 26.19 º for Christmas Island, 27.14 º for Cocos (Keeling) Islands, 22.13 º for Lord Howe Island, and 21.72 º for Norfolk Island.

Following Clusella-Trullas et al. (2011) we estimated the preferred body temperature as the average body temperature of the species measured during activity bouts in the field. We found no information on the preferred body temperature for 15 species (six turtles and nine squamates). For these species, we used Bayesian missing data imputation to estimate the missing data for preferred temperatures, assuming that the data were missing at random (Gelman et al. 2013). Bayesian imputation involves specifying a distribution of the covariate with missing data. In our case, we did this independently for turtles and squamates, given the differences among the preferred body temperatures for the two groups (over 5º C of difference; Table 1). For the turtles, we assumed that preferred body temperatures (in ºC) follow a Normal distribution, ~ N(mean, variance) with mean ~ N(26.2, 10) and variance ~ U(0, 1000). The values for the mean of the Normal distribution for the preferred temperatures were estimated from the values obtained from calculating this parameter for those species for which we had preferred body temperature information, whereas the variance component was set to be a uniform distribution bounded by 0 and 1000 to allow exploration by the imputation procedures of a wide parameter space for the missing data for preferred body temperatures. This means, for instance, that 26.2ºC is the average body temperature reported for the turtle and tortoise species for which we found information. We proceeded in a similar manner for squamates, but in this case, the value for the mean was drawn from ~ N(31.7, 10). Values were drawn from the estimates obtained from the species for which we had data (47 species). Once we had calculated and imputed missing body temperature values, we calculated aTSM values for each species by region record as the absolute difference between body temperature and the median average temperature of the warmest quarter.

In the case of the illegally traded species, there were missing data on preferred body temperatures for ten species of illegal squamates (35.7% of all illegally traded species; 37% of the illegally traded squamates). We employed the same Bayesian missing data imputation methods described before, but the mean value for the imputation was drawn from ~ N(29.8, 10). The value 29.8ºC is the average body temperature reported for the pool of Squamate species composed of the illegally traded species and the introduced into Australia for which we had information on body temperatures (18 and 47 species, respectively). We considered this approach to be more representative of the distribution of preferred body temperatures rather than only the distribution of body temperatures for the 17 species illegally traded for which we had data. Given that the data for illegal trade only occurred in mainland Australia, we have only used the median temperature for mainland Australia (24.5 º) for calculating the aTSM for illegally trades reptiles.

We are aware that our approach to climate matching is different from that used in previous research on alien reptiles, which was mainly based on estimating indices of similarity between the climate in the introduced and the native range (Bomford et al. 2009b; Van Wilgen et al. 2009; Fujisaki et al. 2010; Van Wilgen and Richardson 2012; Mahoney et al. 2014). However, recent research has demonstrated that alien reptiles expand or shift their climatic niches in the invasive range compared with the native range, leading to underestimations in the estimated potential climatic suitability of invasive ranges (Rodrigues et al. 2016; Tingley et al. 2016b). Ideally, this shortcoming would be overcome by using mechanistic biophysical niche models developed for ectotherms, but these models are data-intensive (Kearney and Porter 2009; Guisan et al. 2013; Walker et al. 2015), and there is no sufficient information for populating them for every alien species introduced in Australia and the external Territories. We are also aware of the use of species' critical thermal maximum and minimum temperatures (CTs) to define thermal niches and environmentally suitable habitats (Clusella-Trullas et al. 2011; Araújo et al. 2013), and we have applied this approach before for modelling the establishment success of alien turtles (García-Díaz et al. 2015). We conducted a comprehensive search for CTs of the alien reptile species in Australia and external Territories, but the data available was scarce and would require us to use Bayesian missing data imputation for much of the pool of alien reptiles. We consider that the benefit that would be achieved in terms of a potentially better delineation of thermal niches do not trump the costs in terms of data accuracy that would be incurred by inputting such a large amount of data. Therefore, we used aTSM values to approximate the physiological mechanisms of the thermal niche of alien reptiles.

3.3. Supplementary Results

	Mean	**95% Credible Intervals**
Intercept (Testudines)	0.08	(-0.17, 1.08)
Intercept (Squamata)	0.03	(-0.29, 0.55)
Intercept (Alien)	0.05	(-0.40, 1.32)
Intercept (Domestic exotics)	0.19	(-0.14, 2.43)
Intercept (Mainland)	0.06	(-0.35, 1.21)
Intercept (Island)	0.14	(-0.21, 2.27)
Log_{10} Propagule number	3.33	(0.48, 6.96)
Log_{10} Body length	-0.77	(-2.70, 0.49)
Squared Fecundity per breeding season	0.46	(-0.22, 1.42)
Absolute Thermal Safety Margin	0.05	(-0.17, 0.26)
$\text{Log}_{10}(+1)$ number of congeneric species	0.13	(-0.89, 1.20)
Log_{10} $\text{Km}^2/10{,}000$	-0.83	(-1.50, -0.33)
Rho (orders)	0.02	(-0.99, 0.99)
Rho (domestic and alien)	0.03	(-0.99, 0.99)
Rho (mainland and island)	0.02	(-0.99, 0.99)

Table A.3.1. Posterior coefficient estimates obtained from the model for the establishment success of introduced reptiles in Australia and external Territories. Estimates were obtained by means of 3 chains each with 810,000 iterations, discarding the first 400,000 iterations, and a thinning of five. Rho are the correlation coefficients between the groups in the intercepts.

Species	**Low propagule number**	**Moderate propagule number**	**High propagule number**
Chelydra serpentina	0.55 (0.03, 0.99)	0.71 (0.08, 0.99)	0.80 (0.13, 1.00)
Acrantophis dumerili	01.8 (0.02, 0.44)	0.41 (0.10, 0.77)	0.62 (0.16, 0.97)
Bitis arietans	0.30 (0.05, 0.67)	0.56 (0.16, 0.94)	0.73 (0.22, 0.99)
Bitis gabonica	0.30 (0.04, 0.72)	0.56 (0.12, 0.95)	0.71 (0.18, 0.99)
Boaedon fuliginosus	0.14 (0.02, 0.36)	0.35 (0.08, 0.73)	0.55 (0.12, 0.96)
Cerastes cerastes	0.22 (0.06, 0.45)	0.49 (0.18, 0.83)	0.68 (0.24, 0.98)
Coelognathus helenus	0.14 (0.01, 0.36)	0.33 (0.07, 0.69)	0.54 (0.13, 0.93)
Corallus caninus	0.14 (0.01, 0.38)	0.34 (0.07, 0.69)	0.55 (0.13, 0.94)
Crotalus durissus	0.11 (0.01, 0.34)	0.28 (0.04, 0.68)	0.48 (0.08, 0.93)
Daboia russelii	0.28 (0.04, 0.66)	0.54 (0.13, 0.94)	0.71 (0.19, 0.99)
Epicrates cenchria	0.17 (0.02, 0.44)	0.34 (0.09, 0.76)	0.60 (0.14, 0.96)
Eublepharis macularius	0.14 (0.03, 0.31)	0.35 (0.13, 0.68)	0.57 (0.16, 0.95)
Eunectes notaeus	0.31 (0.05, 0.72)	0.57 (0.14, 0.94)	0.73 (0.21, 0.99)
Hemitheconyx caudicinctus	0.16 (0.04, 0.35)	0.40 (0.13, 0.78)	0.60 (0.17, 0.97)
Heterodon nasicus	0.20 (0.04, 0.42)	0.45 (0.19, 0.73)	0.66 (0.26, 0.96)
Lampropeltis alterna	0.13 (0.01, 0.35)	0.32 (0.07, 0.68)	0.52 (0.11, 0.94)
Lampropeltis getula	0.13 (0.01, 0.36)	0.32 (0.07, 0.69)	0.54 (0.12, 0.94)
Lampropeltis triangulum	0.14 (0.02, 0.36)	0.35 (0.09, 0.72)	0.56 (0.14, 0.95)
Lichanura trivirgata	0.14 (0.01, 0.35)	0.33 (0.09, 0.64)	0.55 (0.16, 0.92)
Micruroides euryxanthus	0.10 (0.00, 0.37)	0.24 (0.01, 0.65)	0.42 (0.04, 0.90)
Naja kaouthia	0.24 (0.04, 0.56)	0.50 (0.13, 0.89)	0.68 (0.19, 0.99)
Naja siamensis	0.19 (0.03, 0.44)	0.44 (0.13, 0.79)	0.64 (0.18, 0.97)
Pantherophis obsoletus	0.18 (0.03, 0.42)	0.43 (0.14, 0.78)	0.63 (0.19, 0.97)
Pituophis catenifer	0.15 (0.02, 0.39)	0.37 (0.09, 0.74)	0.58 (0.14, 0.96)
Python bivittatus	0.33 (0.05, 0.72)	0.59 (0.16, 0.94)	0.75 (0.25, 0.99)
Python regius	0.14 (0.01, 0.35)	0.34 (0.10, 0.64)	0.56 (0.17, 0.93)
Thamnophis sirtalis	0.23 (0.03, 0.58)	0.48 (0.10, 0.91)	0.66 (0.15, 0.99)
Vipera latastei	0.15 (0.03, 0.36)	0.38 (0.12, 0.69)	0.60 (0.18, 0.95)

Table A.3.2. Posterior predicted probability of establishment success (mean and 95% Credible Intervals) in mainland Australia of 28 species of alien reptiles under three scenarios for propagule number (number of release events: low=1, moderate=3, and high=7). These estimates were obtained by using the regularised Bayesian logistic model for the establishment success of alien reptiles in Australia to screen the 28 species of alien reptiles. Individuals of these species have been seized or intercepted as illegal pets in the State of Victoria (1999-2012). Estimates were obtained by means of 3 chains each with 810,000 iterations, discarding the first 400,000 iterations and a thinning of five.

Propagule number	Number of species	
	Mean	95% Credible Intervals
1	5.18	(0, 12)
2	9.23	(2, 18)
3	12.42	(4, 22)
4	14.85	(5, 25)
5	16.20	(5, 26)
6	17.57	(6, 27)
7	18.53	(6, 27)
8	19.2	(6, 28)
9	19.95	(7, 28)
10	20.45	(7, 28)
11	20.85	(7, 28)
12	21.35	(7, 28)
13	21.56	(7, 28)
14	21.83	(8, 28)
15	22.09	(8, 28)
16	22.32	(8, 28)
17	22.49	(8, 28)
18	22.66	(8, 28)
19	22.92	(8, 28)
20	23.07	(8, 28)

Table A.3.3. Posterior estimates of the total number of illegally traded alien reptiles in mainland Australia that would likely become established if introduced at various propagule numbers (maximum = 28 species established). These estimates were obtained by using the regularised Bayesian logistic model for the establishment success of alien reptiles in Australia to screen the 28 species of alien reptiles. Individuals of these species have been seized or intercepted as illegal pets in the State of Victoria (1999-2012). Estimates were obtained by means of 3 chains each with 810,000 iterations, discarding the first 400,000 iterations and a thinning of five. Note that, to improve interpretability, propagule number values are not transformed here.

Appendix 4. Supplementary Material to Chapter 5.

4.1. Literature Sources of Distribution Data for Alien Freshwater Fishes in Australian Drainages.

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4.2. Posterior Topographic Division Correlation Matrices.

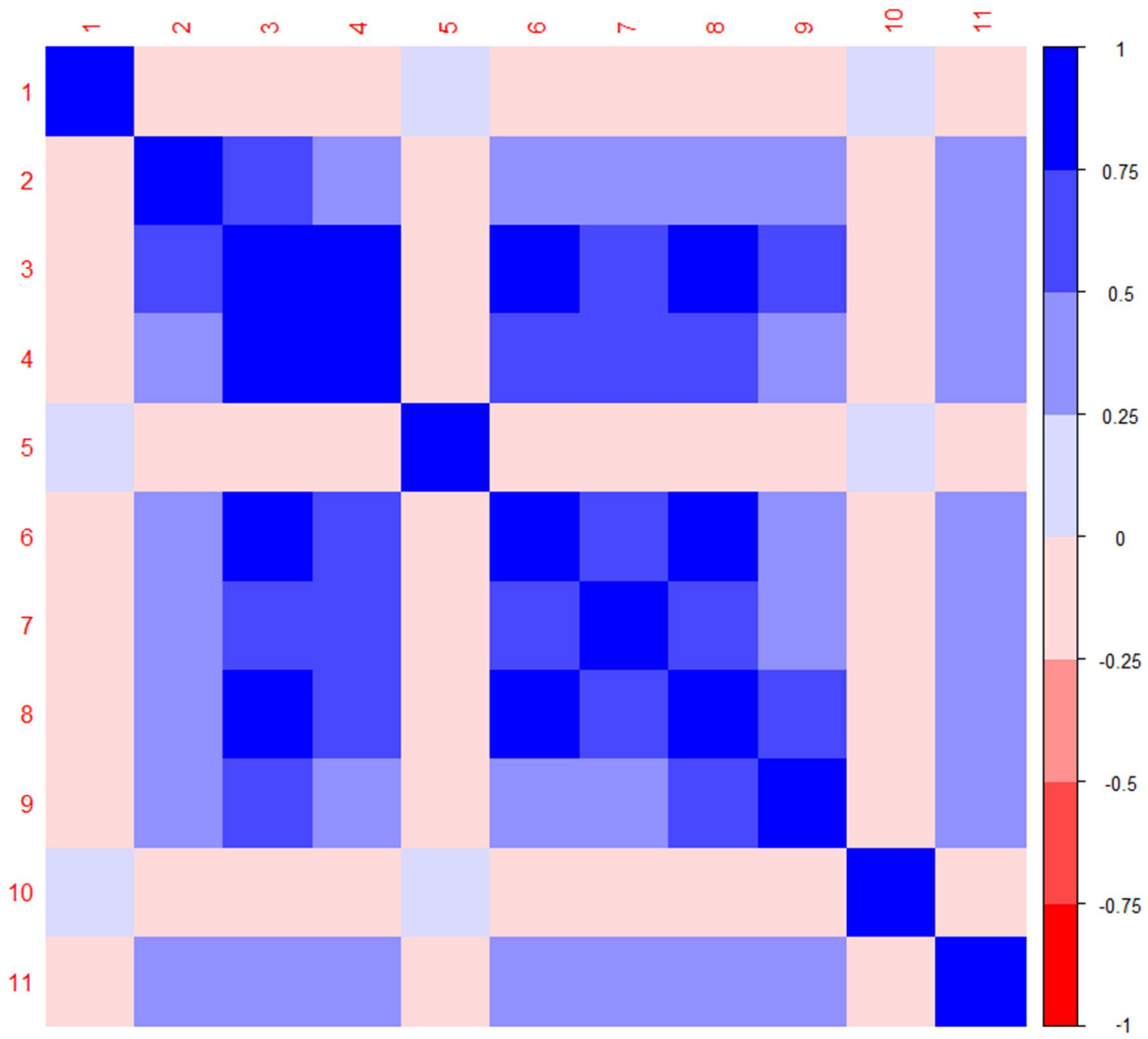

Fig. A.4.1. Mean posterior topographic division correlation matrix of the period pre-1970. Names: 1: Carpentaria Coast; 2: Lake Eyre Basin; 3: Murray-Darling Basin; 4: North-East Coast; 5: Pilbara-Gascoyne; 6: South Australian Gulf; 7: South East Coast (New South Wales); 8: South East Coast (Victoria); 9: South West Coast; 10: Tanami-Timor Sea Coast; 11: Tasmania.

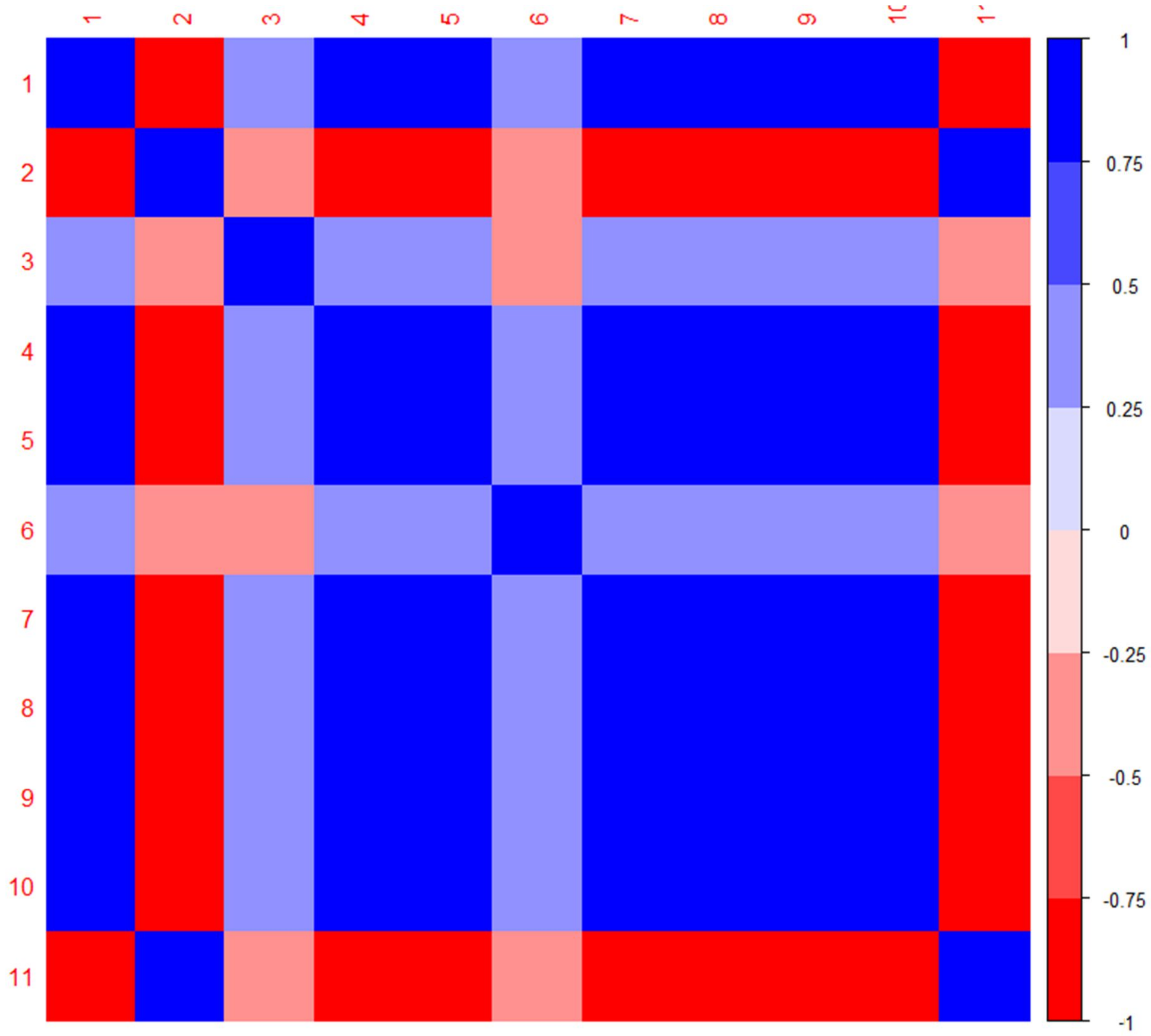

Fig. A.5.2. Mean posterior topographic division correlation matrix of the period post-1970. Names: 1: Carpentaria Coast; 2: Lake Eyre Basin; 3: Murray-Darling Basin; 4: North-East Coast; 5: Pilbara-Gascoyne; 6: South Australian Gulf; 7: South East Coast (New South Wales); 8: South East Coast (Victoria); 9: South West Coast; 10: Tanami-Timor Sea Coast; 11: Tasmania.

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Supplementary Material

List of original peer-reviewed manuscripts published by Pablo García Díaz during his PhD candidature (March-2013 to July-2017):

1. Capinha, C., Seebens, H., Cassey, P., **García-Díaz, P.,** Lenzner, B., Mang, T., Moser, D., Pyšek, P., Scalera, R., Rödder, D., Winter, M., Dullinger, S. & Essl, F. (2017). Diversity, biogeography and the global flows of alien amphibians and reptiles. *Diversity and Distributions*, accepted.

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