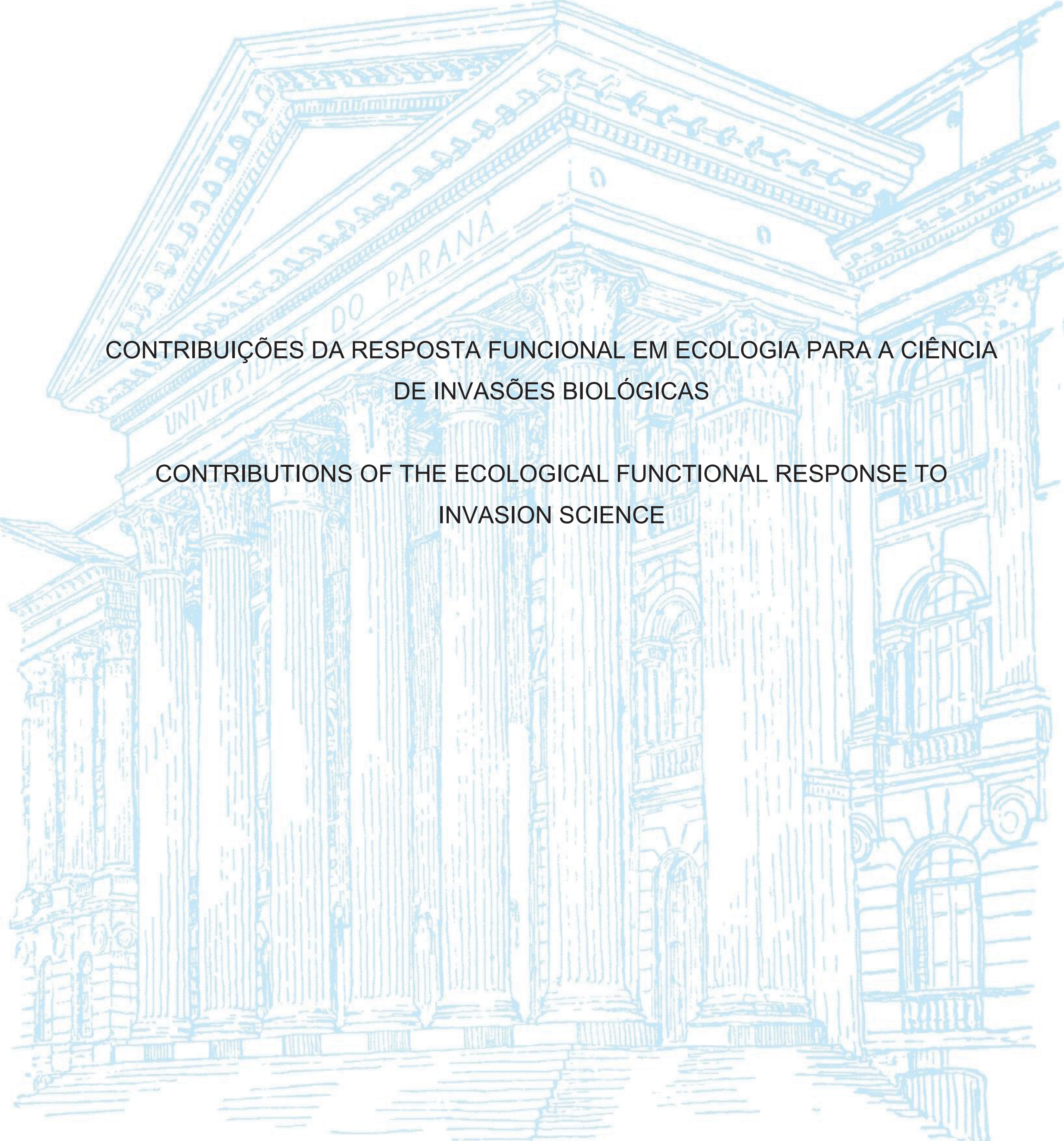
UNIVERSIDADE FEDERAL DO PARANÁ

LARISSA FARIA



CONTRIBUIÇÕES DA RESPOSTA FUNCIONAL EM ECOLOGIA PARA A CIÊNCIA DE INVASÕES BIOLÓGICAS

CONTRIBUTIONS OF THE ECOLOGICAL FUNCTIONAL RESPONSE TO INVASION SCIENCE

CURITIBA
2024

LARISSA FARIA

CONTRIBUIÇÕES DA RESPOSTA FUNCIONAL EM ECOLOGIA PARA A CIÊNCIA DE INVASÕES BIOLÓGICAS

CONTRIBUTIONS OF THE ECOLOGICAL FUNCTIONAL RESPONSE TO INVASION SCIENCE

Tese apresentada ao curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutora em Ecologia e Conservação.

Orientador: Prof. Dr. Jean Ricardo Simões Vitule

CURITIBA
2024

DADOS INTERNACIONAIS DE CATALOGAÇÃO NA PUBLICAÇÃO (CIP)
UNIVERSIDADE FEDERAL DO PARANÁ
SISTEMA DE BIBLIOTECAS – BIBLIOTECA DE CIÊNCIAS BIOLÓGICAS

Faria, Larissa
Contribuições da resposta funcional em ecologia para a ciência de invasões biológicas / Larissa Faria. – Curitiba, 2024.
1 recurso on-line : PDF.

Tese (Doutorado) – Universidade Federal do Paraná, Setor de Ciências Biológicas, Programa de Pós-Graduação em Ecologia e Conservação.
Orientador: Prof. Dr. Jean Ricardo Simões Vitule.

1. Avaliação de risco e de impacto. 2. Ecologia de invasões. 3. Interações tróficas. 4. Revisão quantitativa. 5. Risco de predação. I. Vitule, Jean Ricardo Simões. II. Universidade Federal do Paraná. Setor de Ciências Biológicas. Programa de Pós-Graduação em Ecologia e Conservação. III. Título.

Bibliotecária: Camila de Souza Dorneles CRB-9/2056

MINISTÉRIO DA EDUCAÇÃO
SETOR DE CIÊNCIAS BIOLÓGICAS
UNIVERSIDADE FEDERAL DO PARANÁ
PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO
PROGRAMA DE PÓS-GRADUAÇÃO ECOLOGIA E
CONSERVAÇÃO - 40001016048P6

TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná foram convocados para realizar a arguição da tese de Doutorado de **LARISSA FARIA** intitulada: **CONTRIBUIÇÕES DA RESPOSTA FUNCIONAL EM ECOLOGIA PARA A CIÊNCIA DE INVASÕES BIOLÓGICAS/ CONTRIBUTIONS OF THE ECOLOGICAL FUNCTIONAL RESPONSE TO INVASION SCIENCE**, que após terem inquirido a aluna e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de doutora está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

CURITIBA, 25 de Março de 2024.

Assinatura Eletrônica
25/03/2024 14:18:12.0
JEAN RICARDO SIMÕES VITULE
Presidente da Banca Examinadora

Assinatura Eletrônica
25/03/2024 19:58:04.0
CAROLINA ARRUDA DE OLIVEIRA FREIRE
Avaliador Externo (UNIVERSIDADE FEDERAL DO PARANÁ)

Assinatura Eletrônica
28/03/2024 06:40:29.0
ANA CLARA SAMPAIO FRANCO
Avaliador Externo (UNIVERSITAT DE GIRONA (ESPANHA))

Assinatura Eletrônica
26/03/2024 14:41:28.0
JOSIE SOUTH
Avaliador Externo (UNIVERSITY OF LEEDS)

ACKNOWLEDGEMENTS

A doctoral thesis has only one author, but it is certainly the result of collaboration and support from many people. Below, I hope to do justice to all those who in some way helped in my four-year-long endeavour to produce this final piece of work.

First, I want to thank my advisor Professor Jean Vitule, who constantly pushed me to believe in my capacity to get things done. Thank you for all your support and openness to discuss science with me. I am also extremely fortunate to have shared this period with such an amazing and collaborative team of graduate students in the Ecology and Conservation Lab (LEC). Thank you very much Laís, Natali, Juliani, Zinho and Thiago for being the best support network I could ask for. I hope we can work together again in the future. I am also grateful to all those who were part of LEC and contributed to this thesis directly or indirectly.

A special thanks to the Universidade Federal do Paraná for having me for four more years during my doctoral education. I will always appreciate and defend the high-quality public education offered by the oldest Brazilian university. Likewise, I want to thank the Programa de Pós-Graduação em Ecologia e Conservação, represented by all its excellent professors who inspire and motivate us, especially Professor Viviane Prodocimo who generously shared her lab space and experience with me. I would also like to thank Juliana Leão for always being available when (many) doubts arose regarding the graduation process throughout these years.

I am very grateful to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES for funding the scholarship that allowed me to dedicate myself to research (Finance Code 001). I thank Professor Jonathan Jeschke and the Freie Universität Berlin, and the Fundação da Universidade Federal do Paraná – FUNPAR for funding the publication costs of the published papers. I am also very indebted to the Fulbright Commission in Brazil which made possible the dream of developing part of my research project overseas, through the Doctoral Dissertation Research Award. A warm thanks to Carolina Martins, who so kindly assisted all awardees during this frightening but exciting process, and to all my fellow Fulbrighters for always being there to help each other. You guys are amazing!

I cannot help but thank Professor Julian Olden who so promptly agreed to advise me during my stay in the US. Thank you for always being available to discuss my research ideas and embracing the challenge of field sampling and experiments in such a short time. You will always be an example for me. I appreciate all the support received from the School of Aquatic and Fishery Sciences of the University of Washington that made my research project possible. I also thank my lab mates there, Rachel, Jess, Emily, Gio, Claire, and Brielle, who not only helped me to assemble all the experimental arenas and collect crayfish but also welcomed me very well in Seattle. Likewise, I will be forever grateful to Beka Stiling and her lovely family for hosting me and my husband on our first days in the US. We will never forget that!

I feel very privileged to have had the opportunity to work with an extraordinary team of researchers in two of the papers that compose this thesis. Thank you very much to Dr Ross Cuthbert, Dr James Dickey, Professor Jonathan Jeschke, Professor Anthony Ricciardi, and Professor Jamie Dick for accepting my invitation to collaborate. It was an honour to have you as co-authors, and I learned a lot from your ideas and contributions. Likewise, I appreciate the time spent by the examination board to evaluate and contribute to this work. Thank you, Dr Ana Clara Franco, Professor Josie South, Professor Carolina Freire, and Professor Rosana Rocha. I am a big fan of your work and I feel very honoured to have you in this important stage of my scientific training.

Finally, I want to thank my friends and family who continuously supported me during this time. I could not have made it here without you all. Especially, thanks to my wonderful mother Adriane who one more time encouraged me to accept the challenge of living in a different country, and to my loved husband Alexandre who has left everything aside to accompany me in this adventure. Thank you for listening to me speaking infinite times about non-native species and how they can be “bad” (not to mention all the complaints about the arduous process of pursuing a PhD). I love you both very much, thank you for everything!

Here again we are reminded that in nature nothing exists alone.
(Rachel Carson, 1962, *Silent Spring*)

Having recently passed the great age of biogeography, we will have entered
the age *after* biogeography, in that virtually everything will live virtually everywhere,
though the list of species that constitute “everything” will be small. (…)
My label for that place, that time, that apparently unavoidable prospect, is the
Planet of Weeds. Its main consoling felicity, as far as I can imagine, is that there will
be no shortage of crows. (David Quammen, 1996, *The Planet of Weeds*)

RESUMO

Invasões biológicas são uma das principais causas de perda de diversidade global e o número de espécies introduzidas tende a continuar aumentando. Devido a dependência do contexto no processo de invasão, prever quais espécies não-nativas (ENN) irão causar mais impacto para priorizar investimentos de manejo e detecção rápida torna-se um desafio. A resposta funcional (RF) – a relação entre a taxa de consumo e a disponibilidade de recursos – foi proposta como uma metodologia universal para quantificar e prever o impacto de espécies invasoras. Essa tese tem como objetivo investigar a contribuição da abordagem de RF para a ciência de invasões, através de revisão sistemática, meta-análise e abordagem experimental. A revisão sistemática foi conduzida para entender o estado-da-arte do uso de experimentos de RF na pesquisa sobre invasões biológicas. Um total de 120 artigos foram incluídos, revelando vieses para estudos conduzidos no Hemisfério Norte investigando interações predador-presa em ambientes de água doce, principalmente com invertebrados e peixes como consumidores. Entretanto, essa abordagem tem um amplo potencial de aplicação na ciência de invasões podendo ser usada para testar as principais hipóteses deste campo de pesquisa. A meta-análise foi realizada utilizando dados de taxa de ataque e taxa máxima de consumo, de um subconjunto de estudos que compararam a RF de espécies nativas e ENN usando o mesmo recurso. O principal objetivo foi testar a hipótese de que ENN são mais eficientes em consumir recursos do que espécies nativas troficamente análogas. Ao todo, 125 tamanhos de efeito foram calculados como o log da razão de resposta dos parâmetros de RF da ENN e sua nativa análoga. Em geral, consumidores não-nativos apresentam taxas máximas de consumo superiores corroborando a hipótese inicial; porém, não há diferença significativa nas taxas de ataque. Por fim, a revisão evidenciou que a RF é classicamente aplicada para quantificar os efeitos consumíveis de ENN. Contudo, efeitos não-letais de predadores (i.e., ecologia do medo) podem ser tão cruciais quanto os efeitos consumíveis, resultando em cascatas tróficas. Assim, a abordagem de RF foi aplicada para investigar experimentalmente os efeitos não-letais de uma das 100 piores espécies invasoras do mundo, o peixe predador de topo black bass (*Micropterus salmoides*), nas taxas de consumo de consumidores intermediários: uma espécie nativa e três ENN de lagostins. Os lagostins foram expostos ao tratamento com pistas químicas do predador ou ao tratamento controle enquanto predavam caramujos. Verificou-se que as taxas de consumo foram menores quando as pistas químicas do predador estavam presentes, exceto para o lagostim nativo em que os parâmetros não diferiram. Isso demonstra que os efeitos não consumíveis das ENN também devem ser considerados na previsão de seus impactos, com potenciais aplicações no manejo de populações invasoras. Por fim, conclui-se que a abordagem de RF tem um amplo potencial de contribuição para o campo da ciência de invasões, podendo ser utilizada para quantificar o impacto de ENN, testar hipóteses de ecologia de invasões, prever em quais contextos bióticos e abióticos os impactos de ENN serão mais pronunciados e fornecer soluções para o manejo.

Palavras-chave: avaliação de risco e de impacto; ecologia de invasões; interações tróficas; revisão quantitativa; risco de predação.

ABSTRACT

Biological invasions are among the leading causes of global biodiversity loss, and the number of introduced species tends only to grow in the future. Due to the context-dependency of the invasion process, predicting which non-native species (NNS) will cause more impact to prioritize investments for their management and rapid detection becomes a challenge. The functional response (FR) – the relationship between consumption rate and resource availability – has been proposed as a universal methodology for quantifying and predicting invasive species impacts. This thesis aimed to investigate the contribution of the FR approach to the invasion science, through a systematic review, meta-analysis, and experimental approach. The systematic review was conducted to understand the state-of-the-art of using FR experiments in invasion science research. A total of 120 papers were included in the review, revealing biases for studies conducted in the Northern Hemisphere investigating predator-prey interactions in freshwater habitats, mainly using invertebrates and fish as consumers. However, this methodology has broad potential application in invasion science and can be used to test major hypotheses in this research field. The meta-analysis was conducted using data of FR parameters' attack rate and maximum feeding rate from a subset of studies that compared FRs of native and NNS towards the same resource type. The main aim was to test the hypothesis that NNS are generally more efficient in consuming resources than trophically analogous native species. A total of 125 effect sizes were calculated as the log response ratio of FR parameters from the NNS and its native analogue. Overall, non-native consumers have higher maximum feeding rates than their native counterparts corroborating the hypothesis; however, there is no significant difference regarding attack rates. Finally, the review evidenced that FR is classically applied to quantify the consumptive effects of NNS. Nevertheless, non-lethal effects of predators (i.e., ecology of fear) can be as crucial as consumptive effects, resulting in trophic cascades. Thus, the comparative FR approach was applied to experimentally investigate the non-lethal effects of one of the 100 world's worst invasive species, the top predator fish largemouth bass (*Micropterus salmoides*), on consumption rates of intermediate consumers: a native and three NNS of crayfish. Crayfish were exposed to either predator cue treatment or control while preying on snails. Consumption rates were lower when predator chemical cues were present, except for the native crayfish where FR parameters did not differ between the treatment and the control. This demonstrates that non-consumptive effects of NNS should also be considered when predicting their impacts, with potential applications for the management of invasive populations. To conclude, the FR approach has a wide range of contributions to invasion science as it can be used to quantify NNS impacts, test hypotheses in invasion ecology, predict which biotic and abiotic contexts can magnify NNS impacts and provide insights for management.

Keywords: invasion ecology; predation risk; risk and impact assessments; quantitative review; trophic interactions.

PREFÁCIO

Antes de apresentar formalmente os resultados da minha pesquisa de doutorado, peço licença para compartilhar um pouco da minha perspectiva pessoal sobre esta jornada acadêmica que está se encerrando agora.

Minha história com a ciência de invasões começou ainda na graduação, em algumas disciplinas que cursei e posteriormente, no projeto de verão que desenvolvi durante meu intercâmbio acadêmico na Inglaterra pelo programa Ciência sem Fronteiras, e na minha monografia. Mas foi no mestrado que eu me deparei com o conceito de resposta funcional. Um colega de laboratório me indicou a leitura de um artigo[1] enquanto eu ainda estava pensando em que projeto queria desenvolver durante aqueles dois anos. Podemos dizer que foi amor à primeira vista quando se trata de ciência? Na hora que terminei de ler o artigo eu sabia que queria aplicar aquela metodologia tão interessante para quantificar o impacto de espécies invasoras na minha dissertação. E foi assim que nasceu meu primeiro artigo publicado como primeira autora[2].

PREFACE

Before formally presenting the results of my doctoral research, I ask permission to share a bit of a personal perspective on this academic journey that is being concluded now.

My story with invasion science began during my undergraduate years, in some classes I took and later, in the summer project I developed during my academic exchange in England through the Science without Borders programme and in my bachelor's final project. But it was during my master's degree that I came across the concept of functional response. A lab mate recommended me a paper[1] to read while I was still thinking about what project I wanted to develop during those two years. Can we say it was love at first sight when it comes to science? By the time I finished reading the paper, I knew I wanted to apply that interesting methodology to quantify the impact of invasive species on my master's dissertation. And that was how my first publication as first author was born[2].

---

[1] Dick, J. T. A. et al. (2014). Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biological Invasions, 16(4), 735–753.

[2] Faria, L., Alexander, M. E., & Vitule, J. R. S. (2019). Assessing the impacts of the introduced channel catfish *Ictalurus punctatus* using the comparative functional response approach. Fisheries Management and Ecology, 26(6), 570–577.

Assim que ingressei no doutorado, no início de 2020, eu tinha certeza de que queria me aprofundar mais neste tema. Então, decidi fazer uma ampla revisão sobre o tópico, tentando capturar todas as possibilidades da metodologia para então aplicá-la de maneiras ainda pouco exploradas, principalmente no Brasil. O plano da revisão funcionou, porém, com a explosão do novo coronavírus, a parte aplicada foi prejudicada pelas dificuldades impostas por uma pandemia (universidade fechada, distanciamento social, etc., vocês sabem!).

Com o cronograma já um pouco apertado, começamos a coleta de peixes para os experimentos apenas após todos estarem vacinados contra a covid-19, no início de 2022. Foi na mesma época em que surgiu a oportunidade de realizar parte da pesquisa nos Estados Unidos através de uma bolsa concedida pela Comissão Fulbright. Sendo assim, adaptamos a parte experimental para essa nova perspectiva. A ideia era comparar a resposta funcional de uma população naturalizada nos EUA do black bass, uma das 100 piores espécies invasoras no mundo, com uma população invasora no Brasil. Entretanto, diferenças nas normas de comitê de ética nos dois países fizeram com que só fosse possível realizar metade desse plano.

As soon as I started my doctorate at the beginning of 2020, I was sure that I wanted to delve deeper into this subject. So, I decided to do a broad review on the topic, trying to capture all the possibilities of the methodology and then apply it in ways that were still little explored, especially in Brazil. The review plan worked, however, with the explosion of the new coronavirus, the applied part was hampered by the difficulties imposed by a pandemic (closed university, social distancing, etc., you know!).

With the schedule already tight, we started collecting fish for experiments only after everyone was vaccinated against covid-19, in early 2022. At the same time, the opportunity to carry out part of the research in the United States through a scholarship awarded by the Fulbright Commission came up. Therefore, we adapted the experimental part to this new perspective. The idea was to compare the functional response of a North American naturalised population of largemouth bass, one of the 100 worst world invasive species, with that of an invasive population in Brazil. However, differences in ethics committee standards in Brazil and the USA resulted in just half of this plan being possible.

Os experimentos foram conduzidos no Brasil conforme planejado, porém, chegando na University of Washington descobri que não conseguiríamos a aprovação do projeto pelo comitê de ética da Universidade, pois lá eles têm regras mais rígidas para experimentos em que a morte de vertebrados é esperada – no nosso caso, devido à predação pelo black bass. Mais uma vez os planos tiveram de mudar. Como as restrições não se aplicavam a invertebrados, mudamos o nosso modelo experimental para lagostins predando caramujos, investigando o efeito indireto do black bass, e assim, tentando preencher uma das lacunas observadas na revisão.

Como vocês podem perceber, o projeto inicial do meu doutorado mudou muito ao longo desses quatro anos. E assim aconteceu comigo também. Sinto que amadureci muito nesse período, tanto pessoalmente – com uma pandemia e uma mudança de país (e de estado civil!) no meio do percurso – como cientificamente também. A sensação nesta reta final é de dever cumprido. Pode soar clichê, mas já começo até a sentir saudades de tudo que vivi nesses últimos quatro anos e, com certeza, muitos momentos ficarão guardados com carinho na minha memória.

The experiments were conducted in Brazil as planned, however, upon arriving at the University of Washington, I found out that the project would not get the approvement from the University's ethics committee, as they have stricter rules for experiments in which the death of vertebrates is expected – in our case, due to predation by largemouth bass. Once again plans had to change. As the restrictions did not apply to invertebrates, we changed our experimental model to crayfish preying on snails while investigating the indirect effect of largemouth bass, thus attempting to fill one of the gaps noted in the review.

As you can see, the initial project of my doctorate changed a lot over these four years. And so did I. I feel like I've grown a lot during this period, both personally – with a pandemic and a change of country (and marital status!) along the way – and scientifically as well. The feeling in this final stretch is one of accomplishment. It may sound cliché, but I'm already missing everything I've experienced in these last four years and many moments will certainly be kept fondly in my memory.

Foram tantas leituras, planilhas, fórmulas, códigos, idas ao laboratório em finais de semana e feriados para cuidar dos bichos, passeios de barco para coletar peixes e lagostins, aulas online, reuniões online, apresentações, e claro, muitos surtos! Devo confessar que quando terminei o mestrado não imaginei que um dia estaria aqui escrevendo esse texto, prestes a concluir o doutorado. Mas que bom que estou! Espero que essa tese inspire você, leitor, que está com dúvidas sobre seguir a carreira acadêmica, ou que já está nesse barco se perguntando se vai dar conta de tudo. Meu conselho para você é aquele que eu sempre dou a mim mesma: só vai! Ou como diria a nossa querida Dory[3]: “Continue a nadar, continue a nadar...”.

There was so much reading, spreadsheets, formulas, coding, trips to the lab on weekends and holidays for animal caring, boat trips to collect fish and crayfish, online classes, online meetings, talks, and, of course, many mental breakdowns! I must confess that when I finished my master's degree, I didn't imagine I would be here writing this text one day, about to complete my doctorate. But how glad I am now! I hope this thesis inspires you, reader, who is questioning yourself about pursuing an academic career, or who is already on this boat wondering if you will manage everything. My advice to you is the one I always give myself: go for it! Or as our beloved Dory would say[3]: “Just keep swimming, just keep swimming...".

---

[3] Personagem de “Procurando Nemo” (Pixar Animation Studios, 2003).

[3] “Finding Nemo” character (Pixar Animation Studios, 2003).

CONTENTS

PRESENTATION

This presentation aims to provide some context and historical perspective for the thesis. Here, I discuss the relationship between invasion science and functional response and how they are related to my research. In the following chapters, I will delve deeper into important concepts in the introduction section of each paper.

INVASION SCIENCE: WHERE ARE WE STANDING NOW?

Since the 19th century, the phenomenon of biological invasions has been observed by prominent naturalists such as Charles Darwin (Ludsin & Wolfe, 2001; Richardson & Pyšek, 2008). Indeed, the movement of species outside their native geographic range initiated as soon as humans started to travel around the world (Simberloff & Rejmanek, 2011). When a species is introduced into a new geographic location, intentionally or not, through human activities, it is considered non-native (Lockwood et al., 2007). Darwin (1859) speculated about which factors determine the naturalisation of non-native species (NNS) in a new environment and their possible impacts on the naïve native biota in several passages of his book '*On the Origin of Species*' (Simberloff & Rejmanek, 2011) and in his annotations aboard the Beagle's expedition – later edited in a book by R. D. Keynes (2001). Despite these very early and insightful observations, biological invasions were not explicitly studied as a human alteration on the planet until the middle of the 20th century.

Invasion science as a systematic discipline has emerged only recently, and the book '*The Ecology of Invasions by Animals and Plants*' by Charles Elton (1958) is claimed as its foundation (Ricciardi & MacIsaac, 2008; Simberloff, 2011). However, even after the book's publication, studies about invasive species and their consequences were not highly produced until the mid-1990s (Richardson & Pyšek, 2008; Simberloff, 2011). Only after the establishment of an international programme on invasion ecology, the Scientific Committee on Problems of the Environment (SCOPE), intensive research on biological invasions in many parts of the world started (Richardson & Pyšek, 2007; Simberloff, 2011). Since then, it has emerged as a multi-disciplinary field with many hypotheses being proposed to explain why and how NNS are successful and impactful, yet the pressing issue remains the lack of a strong predictive framework (Enders et al., 2020; Heger et al., 2013; Ricciardi et al., 2021).

Our ability to predict NNS' success and impacts is challenged by the context-dependency of the biological invasion process (Catford et al., 2022; Kumschick et al., 2015; Novoa et al., 2020; Thomsen et al., 2011). Many factors are at play when one species is moved from its native distribution to a new region, such as how many individuals are transported and whether they are healthy or not (Lockwood et al., 2007). Likewise, characteristics of the new environment, such as temperature, resource availability and the resident species, will strongly influence its probability of surviving, establishing a new population and spreading (Pyšek et al., 2020). Still, the impacts of non-native populations can vary in space and time (Jeschke et al., 2014; Strayer et al., 2006) and indirectly affect the resident community through non-consumptive interactions, for instance when native prey needs to keep vigilance for predators instead of foraging (Preisser et al., 2005; Sih et al., 2010). All of this complicates the much-needed capacity to predict which NNS will be more impactful to prioritise their management, particularly in a globalised world where rates of new introductions are constantly increasing (Hulme, 2021; Ricciardi et al., 2013; Seebens et al., 2021; Simberloff et al., 2013).

A NNS can cause impacts at any ecological level, ranging from genes to entire ecosystems (Parker et al., 1999; Ricciardi et al., 2013). The impact of a NNS has initially been described as the final stage in the invasion process (i.e. transport, establishment, spread, impact) (Catford et al., 2009; Lockwood et al., 2007) however, it is now presumed that it can happen at any stage since the introduction, being usually defined as a measurable change in the invaded ecosystem (Blackburn et al., 2011; Jeschke et al., 2014; Ricciardi et al., 2013). The first attempt to create a predictive metric of invasion impacts recognised three factors that might play a role in the overall impact of a NNS: the total area occupied, their abundance and some individual measure of impact, or the *per capita* effect (Parker et al., 1999). After that, other frameworks were proposed, usually with *per capita* effect as a central factor determining impact (Thomsen et al., 2011). Conversely, while quantifying the abundance and the area occupied by a species are somewhat straightforward (although not always feasible), it is less clear how the *per capita* effect of a species should be measured (Parker et al., 1999; Thomsen et al., 2011).

Non-native species have been perceived as more efficient consumers compared to native species (Funk & Vitousek, 2007; Morrison & Hay, 2011; Paolucci et al., 2013; Salo et al., 2007). Indeed, many hypotheses in invasion science that intended to explain the success and impacts of NNS are linked to their efficiency in consuming available resources (Catford et al., 2009; Ricciardi et al., 2013). It can be assumed then that impactful NNS will be those with higher consumption rates, being this rate a proxy of their impact (Dick et al., 2014). Under this context, the classical ecological concept of functional response – the increase in consumption as a function of the availability of resources, was proposed as a universal method for quantifying *per capita* effects of NNS (Dick et al., 2014, 2017).

FUNCTIONAL RESPONSE: A PROMISING TOOL FOR INVASION SCIENCE

The first model used to explain population dynamics governed by consumption was proposed by two independent researchers in the early 1920s and is known as the Lotka-Volterra model (Begon et al., 2006). This seminal model assumed that a consumer's consumption rate would be constant, proportionally increasing as the availability of resources increased. However, this assumption is quite unrealistic since consumers eventually become satiated, besides being limited by the time needed to pursue and consume each item (Gotelli, 2008). Therefore, the consumption rate must be affected by the availability of resources in a density-dependent manner (Solomon, 1949). Based on this, Solomon defined the term functional response (FR) for the first time as:

> "there must be a *functional* response to (say) an increase in the host density, because of the increased availability of victims: as host density rises, each enemy will attack more host individuals, or it will attack a fixed number more rapidly." (Solomon, 1949, p. 16).

Afterwards, the term was used again only ten years later by Holling when describing the three basic FR types (Holling, 1959a) and the equation that depicts consumption rate as a function of resource density, known as the disc equation (Holling, 1959b). Since then, the concept has been used in classical ecological studies, once the FR type can determine if a consumer will stabilise or destabilise population dynamics (Begon et al., 2006; Gotelli, 2008; Juliano, 2001).

The FR was applied in the invasion context only in the early 2000s to estimate the predatory impact of non-native crustaceans such as amphipods and copepods (Bollache et al., 2008; Hooff & Bollens, 2004). These initial studies were followed by many others (e.g. Alexander et al., 2012, 2013; Dick et al., 2010, 2013; Twardochleb et al., 2012) sparking an interest in the approach that culminated in its proposal as a universal proxy of *per capita* effects to predict the ecological impacts of invasions, as discussed in the first chapter of this thesis. The reasoning is that higher FRs are observed for NNS with known field impacts relative to trophically analogous native species; hence, it could be used to predict impact (Dick et al., 2014). At the time, however, there were just a few studies employing this approach and the authors encouraged more research encompassing different taxa and populations to verify its utility (Dick et al., 2014), which are here explored in the first and second chapters.

A key advantage of using the comparative FR approach is the possibility of including different biotic and abiotic features in laboratory experiments to deal with the context-dependency of the invasion process and provide more realistic assessments (Dick et al., 2014, 2017). Indeed, the FR is not a fixed trait of a species but may vary with different factors such as habitat complexity, presence of alternative resources, temperature, consumer health, and so on (DeLong, 2021; Dick et al., 2014; Holling, 1959). All these factors can be incorporated into FR studies to account for relevant features of the invaded system, as presented here in the third chapter, or to investigate possible synergistic effects of NNS and other drivers of global change, such as habitat degradation and climate change (e.g. South et al., 2017).

Another feature of the approach is the chance of testing classical hypotheses in invasion science. For instance, the Biotic Resistance hypothesis predicts that more diverse assemblages will be less prone to the introduction and impacts of NNS due to more antagonistic interactions (Elton, 1958; Jeschke, 2014; Jeschke et al., 2012). In this case, the FR could be used to measure if the consumption rates of native consumers towards non-native prey will be enough to control them. Similarly, the Ecological Naïveté hypothesis which predicts that prey without previous experience with a novel predator will be more susceptible to their negative effects (Cox & Lima, 2006; Saul & Jeschke, 2015), can be tested by comparing the FR of a co-evolved predator and an introduced NNS towards the same prey. In the same vein, the classical Enemy Release hypothesis and correlates (e.g. Enemy of my Enemy and Evolution of Increased Competitive Ability), can be verified by testing the effect of enemies such as parasites or top predators in the FR of non-native consumers, once the success and impacts of NNS can be correlated to the lack of a natural enemy in the invaded community (Colautti et al., 2004; Jeschke, 2014; Jeschke et al., 2012; Keane & Crawley, 2002). These and other hypotheses in invasion science can be tested using the FR approach (Saul et al. 2013; Saul & Jeschke, 2015), and the first chapter provides suggestions of how it could be done.

Despite being a promising method for quantifying and predicting NNS impacts while dealing with the context-dependency of invasions, it has been argued that scaling up *per capita* effects measured as FRs in the laboratory to field conditions might not be realistic (Griffen, 2021; Griffen et al., 2020). These arguments are based generally on the simplistic setups of experiments, e.g. offering just one resource type while consumers may forage on a range of them, the confined configuration of experiments that do not allow prey to escape or ignoring other interactions occurring at the same time as intra- and inter-specific competition (Landi et al., 2022). Indeed, these critics (discussed in detail in the first chapter) will apply to any experiment that needs to simplify the reality observed in nature to understand a specific facet without a myriad of confounding factors. However, being aware of these limitations is key to refine the method and move forward.

OBJECTIVES

Since its recent proposal, the comparative FR approach has not been critically reviewed and applications are mainly limited to single resource-consumption interactions. Therefore, the general aim of this thesis is to investigate the overall contributions of the classical FR ecological concept to the invasion science field. To this end, the thesis is structured into three chapters presented as papers, starting from a holistic view to a more practical and applied approach.

The first chapter aims to delineate the status of the FR approach in invasion science, through a systematic review. Specific objectives were to review which types of studies are being conducted in the field and to identify gaps, biases, and sub-explored pathways to move forward.

The second chapter aims to check if the underlying assumption NNS have higher FRs than their native counterparts is verified. A meta-analysis of comparative FR studies was performed with the specific objectives of testing if NNS are more efficient in consuming resources compared to trophically analogous native species and under which conditions this pattern emerges. With that, the comparative FR approach is critically reviewed as a useful rapid assessment tool to predict the impacts of invasions.

Finally, the third chapter explores experimentally other potential applications of the method, such as revealing indirect effects of NNS. This chapter aims to investigate how a broader biological context can be incorporated into NNS impact prediction. Therefore, comparative FR experiments were conducted considering the predation risk imposed by a non-native top predator on the consumption rate of native and non-native intermediate consumers. The specific objectives were to examine if the non-lethal effects of NNS can influence the FR of lower trophic levels and demonstrate the approach's utility in providing more realistic assessments.

1 THE RISE OF THE FUNCTIONAL RESPONSE IN INVASION SCIENCE: A SYSTEMATIC REVIEW

This paper is the result of a collaboration with a team of invasion scientists experienced with the comparative functional response approach and is already published in NeoBiota. The initial idea was conceived by me and my advisor Professor Jean Vitule, with later inputs from all the other authors. I performed the collection and analysis of data and wrote the initial draft. All authors revised the manuscript. The supplementary material of this paper can be found in Appendix 1.

Published as[1]: Faria, L., Cuthbert, R. N., Dickey, J. W. E., Jeschke, J. M., Ricciardi, A., Dick, J. T. A., & Vitule, J. R. S. (2023). The rise of the Functional Response in invasion science: a systematic review. *NeoBiota*, *85*, 43–79. https://doi.org/10.3897/neobiota.85.98902

Abstract

Predicting which non-native species will negatively impact biodiversity is a longstanding research priority. The Functional Response (FR; resource use in relation to availability) is a classical ecological concept that has been increasingly applied to quantify, assess and compare ecological impacts of non-native species. Despite this recent growth, an overview of applications and knowledge gaps across relevant contexts is currently lacking. We conducted a systematic review using a combination of terms regarding FR and invasion science to synthesise scientific studies that apply the FR approach in the field and to suggest new areas where it could have valuable applications. Trends of publications using FR in invasion science and publications about FR in general were compared through the Activity Index. Data were extracted from papers to reveal temporal, bibliographic, and geographic trends, patterns in study attributes such as type of interaction and habitat investigated, taxonomic groups used, and context-dependencies assessed. In total, 120 papers were included in the review. We identified substantial unevenness in the reporting of FRs in invasion science, despite a rapidly growing number of studies. To date, research has been geographically skewed towards North America and Europe, as well as towards predator-prey interactions in freshwater habitats. Most studies have focused on a few species of invertebrates and fishes. Species origin, life stage, environmental temperature and habitat complexity were the most frequently considered context-dependencies. We conclude that while the FR approach has thus far been narrowly

---

applied, it has broad potential application in invasion science and can be used to test major hypotheses in this research field.

Keywords: ecological impact prediction, hypothesis testing, invasive alien species, resource use, risk assessment, trophic interactions

1.1 INTRODUCTION

With rates and effects of biological invasions magnifying worldwide (Pyšek et al. 2020, Diagne et al. 2021, Seebens et al. 2021), predicting and quantifying which non-native species (NNS) will have the greatest impacts has become a research priority, especially in the face of ongoing anthropogenic environmental change (Kumschick et al. 2015, Ricciardi et al. 2021). Invasion science has been slow to develop predictive approaches that explain and forecast the negative ecological impacts of existing invasive and emerging NNS under relevant contexts (Dick et al. 2017a). This hampers management prioritisation towards the most damaging species across invasion stages (Robertson et al. 2020). Moreover, research has been highly uneven across taxa, trophic groups, regions and forms of impact (Pyšek et al. 2008, Bellard and Jeschke 2016, Braga et al. 2017, Crystal-Ornelas and Lockwood 2020), possibly reflecting the lack of standardised and broadly applicable methods (but see Dick et al. 2014, 2017a).

The rapid exploitation of resources (e.g. food, water, space, nutrients) is considered a characteristic trait of high-impact invasive consumers (Johnson et al. 2008, Morrison and Hay 2011, Ricciardi et al. 2013). It has been hypothesized that the most ecologically disruptive NNS typically exploit resources more efficiently than other resident species (Funk and Vitousek 2007, Ricciardi et al. 2013). On this basis, a valuable and still largely underexploited approach to quantify and compare NNS ecological impact is the classical Functional Response (*sensu* Solomon 1949, Holling 1959), the relationship between resource availability and resource consumption rate. In addition to being employed in studying predator-prey dynamics (e.g. Sinclair et al. 1990, Eby et al. 1995, Heikinheimo 2001), the Functional Response (FR) has also been used to evaluate the efficacy of biological control agents towards target organisms (van Driesche and Bellows 1996, Madadi et al. 2011), sport fish-angler interactions (Johnson and Carpenter 1994, Yodzis 1994, Eggleston et al. 2003), and impacts of human hunting on wildlife conservation (Sinclair et al. 1998, Swanepoel et al. 2015). Over the past decade, the FR has been applied to predict and quantify NNS impacts on native populations and communities (Dick et al. 2014, 2017a).

The Functional Response has been broadly characterised into linear (Type I), hyperbolic (Type II), sigmoidal (Type III), or dome-shaped (sometimes called Type IV) curves (Jeschke et al. 2004). As many invasion hypotheses are centred on trophic interactions (Catford et al. 2009, Ricciardi et al. 2013, Enders et al. 2020), FRs can be useful in hypothesis testing and measuring trophic impacts of non-native consumers (Dick et al. 2014). Indeed, as all living organisms use resources, there is no limit taxonomically or trophically to the use of FRs, and hence it could be a unifying method across all NNS (Dick et al. 2017a). Furthermore, the type of FR mediates impact; for example, predators exhibiting Type II FRs are deemed to be more destabilising to resource populations than those exhibiting Type III FRs, owing to high proportional feeding rates at low resource densities and a concomitant lack of low-density refugia for prey (Murdoch and Oaten 1975).

The comparative FR approach has been grounded in relative pairwise comparisons of native and NNS under standardised conditions, or by comparison of the same NNS under different contexts when trophic analogues are absent, normally in controlled laboratory environments (but see Smout et al. 2013, Goss-Custard et al. 2006 for field-derived FRs). By carefully matching comparator species according to size, sex, life stage, and other variables, a balanced comparison of *per capita* impacts is sought, usually in terms of consumer attack rates, handling times, maximum feeding rates, and combinations of such parameters (Cuthbert et al. 2019b), acknowledging NNS impacts relative to native consumers or different contexts. Critically, NNS with a higher magnitude FR, characterised by greater search efficiencies and/or shorter handling times (depending on the FR shape), are predicted to have greater *per capita* ecological impacts than trophically analogous native species with lower magnitude FRs (Fig. 1). Across studies, there is a tight corroboration of these experimentally derived patterns with actual impacts recorded in the field (Dick et al. 2017a). Indeed, the FR could be considered a universal *per capita* measure for consumptive effects within the classical Parker-Lonsdale impact equation which defines that the total impact of a given NNS is the product of its abundance, range, and *per capita* effect (Parker et al. 1999, Dickey et al. 2020).

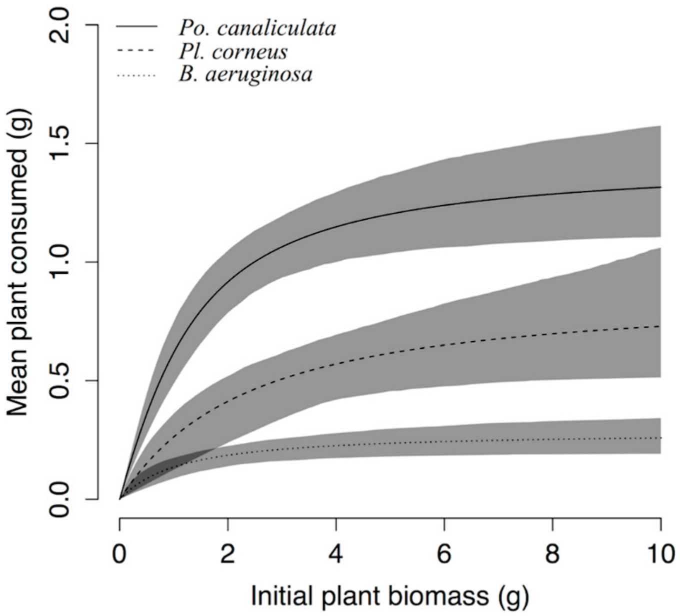


Figure 1. Functional Responses of known impactful invasive non-native species (NNS) are often higher when compared to those of native or non-invasive NNS trophic analogues, as shown for aquatic snails: the invasive NNS *Pomacea canaliculata*, the non-invasive NNS *Planorbarius corneus*, and the native *Bellamya aeruginosa* feeding on four locally occurring plant species in China. Reproduced from Xu et al. (2016).

A species FR is not a fixed trait and, like NNS impacts, can vary across myriad biotic and abiotic contexts. The advantage of FRs is that these context-dependencies can be incorporated into experimental designs to provide more realistic assessments while isolating the variables of interest (Dick et al. 2017a, 2017b, Penk et al. 2017), and help to understand how NNS impacts relate to physical habitat conditions (i.e. the Environmental Matching hypothesis; Iacarella et al. 2015a). Nevertheless, although context-dependent variation remains a challenge for reliably predicting NNS impacts, the malleability of the FR approach makes it an excellent tool to explicitly incorporate and test context-dependencies. Given ongoing climate and land-use changes, for example, it is relevant to test variation in FRs under different temperatures (Englund et al. 2011, Uiterwaal and DeLong 2020) or related abiotic variables to understand how impacts of NNS may be altered. Furthermore, FRs can be combined with different levels of habitat complexity, a feature that may have direct implications on the type of FR and thus on resource population stability (Toscano and Griffen 2013, Murray et al. 2016, Kalinkat et al. 2023). Biotic contexts, such as organism life stage, multiple predator effects or higher-order predator presence, can also be useful to understand impacts, considering that consumers may not forage alone in nature (Smout et al. 2010, Ball et al. 2015, Médoc and Spataro 2015).

The FR measures individual *per capita* effects and then can be scaled with the numbers of individual consumers to derive a measure of overall impact (i.e. Total Response = Functional Response x Numerical Response; Holling 1959), as has been done with biological control (e.g. killing rate *per* individual agent x number of agents) and fisheries assessments (e.g. overall offtake rates by predators). The Relative Impact Potential (RIP) metric integrates numerical responses (consumer population change) or their proxies — such as field abundances or other population-level metrics (Dick et al. 2017b, Dickey et al. 2020) — to reveal overall expected field impacts of novel NNS. Further advances to this approach have amalgamated different parameters of the FR to streamline impact comparisons (e.g. the Functional Response Ratio, FRR; Cuthbert et al. 2019a) and integrated measures of propagule pressure that combine impact with risk assessment (Dickey et al. 2022). Moreover, GIRAE (Generalised Impact = Range size × Abundance × *per*-unit Effect) has been recently developed as a tool to predict *per capita* ecological and economic effects of NNS based on available data, again stemming from the Parker-Lonsdale impact equation (Latombe et al. 2022).

There are some important criticisms to the comparative FR approach related to its generalization and the potentially unrealistic nature of the experiments. Vonesh et al. (2017) argues that if consumers used in trials have different ecological parameters beyond those estimated in experiments, the comparison of their FRs has less ecological meaning. Specifically, two consumers may differ in their mortality rate when resources are absent (background mortality) and also on the proportion of resource consumed that is effectively converted into increasing the abundance of the consumer (conversion efficiency), which can substantially influence consumer effects on resource dynamics in the long-term (Landi et al. 2022). Likewise, Griffen (2021) points out that the comparative FR approach is only useful if species respond similarly to the artificial conditions and techniques employed, and that directly scaling FRs measured on individuals to entire populations could yield misleading results. However, previous syntheses of the limited number of FRs available in the context of invasion impacts attest to its high potential to explain and predict impact (Dick et al. 2017b).

Despite the rapidly increasing use of the FR approach in invasion science, we still lack a synthesis of its application in this field that could reveal knowledge gaps to be addressed and avenues for future improvement. Currently, studies are potentially disparate across different life stages of the same organism, taxonomic groups, trophic groups, environments, and geographic regions, meaning likely unevenness in the testing of the approach in different study systems, and in turn frustrating the holistic assessment of its efficacy. Therefore, this timely systematic review of studies to date aims to synthesise the available scientific literature that applies the FR approach in invasion science to elucidate potential shortcomings that can be addressed in future work to improve the representativeness and the explanatory and predictive capacities of the method.

1.2 METHODS

1.2.1 Literature search and screening

We performed a literature search in January 2021 using the Web of Science database (WoS). The following combination of search terms was used: TOPIC = (“*functional response**”) AND (*invasive* OR *invader* OR *introduced* OR *alien* OR *exotic* OR *non-native* OR *nonnative* OR *non-indigenous*). We limited our search to papers published up to 2020. After the removal of duplicates, publications were evaluated by their title and abstract in the first screening, and through full reading in the second screening (Supplementary material, Fig. S1). Papers were excluded if they:

(i) did not conduct classical FR experiments (i.e. application of FR in mathematical models; using only a single resource density; did not estimate the parameters; did not model the type of curve; strictly investigated feeding preference);

(ii) were observational studies (the initial densities and the consumption were not controlled, only estimated);

(iii) did not use NNS in the experiments, either as a consumer or as a resource, or the NNS was only indirectly related (effect of their presence in the FR of a native species, for example);

(iv) were in other languages than English;

(v) were book chapters or other types of documents that did not present original data.

Despite the comparative FR approach being the reason that sparked interest in applying FR in invasion science, we found a variety of study frameworks beyond explicit native versus NNS comparisons. While all of these studies were included because they met the above criteria, they are not comparative *per se*. Thus, the term “FR approach” is used here to refer to any study in our review (i.e. that used a NNS as a consumer or resource in FR experiments), whereas the “comparative FR approach” refers only to those that clearly make a comparison between native and NNS.

1.2.2 Data extraction and publication trends

Data were extracted through a full reading of the papers selected in the second screening (a list of the data extracted from each study is available in Supplementary material, Table S1). To compare the trend of publications using FR in invasion science with publications concerning FR in general, a new search in the WoS database was performed using only the search term TOPIC = (*functional response**), again up to 2020. The results were then filtered through the WoS website, as follows:

(i) the *Research Area* filter was used to refine the search for ecological studies and to exclude mathematical modelling studies (corresponding to the first and second steps in our original search);

(ii) the *Languages* filter was used to select only English papers (corresponding to the fourth step in our original search);

(iii) the *Document Types* filter was used to exclude reviews and book chapters (corresponding to the fifth step of the original search).

To make this comparison between FR publications in invasion science and in general, we calculated the Activity Index (AI) (Caliman et al. 2010, Evangelista et al. 2014):

$$AI = \left(\frac{CY}{CT}\right)\Big/\left(\frac{TY}{TT}\right)$$

where CY is the number of papers using FR in invasion science published in a given year; CT is the total number of papers using FR in invasion science published in all years; TY is the number of papers on FR in general published in a given year; and TT is the number of papers on FR in general published for all of the years studied.

Considering this, AI = 1 indicates that papers on FR in invasion science were published at the same relative rate as those in the overall literature (in our case, publications that used FR in studies other than invasion science); AI > 1 indicates that papers on FR in invasion science were published at a higher relative rate compared to the overall literature; and AI < 1 indicates that papers on FR in invasion science were published at a relatively lower frequency compared to the overall literature. Due to the low number of papers that used FR in invasion science until the 1990s, we analysed the AI for the last 30 years. Journal trends were also analysed as an absolute and weighted number of publications *per* journal (Supplementary material 3).

1.2.3 Study attributes

Papers were classified into three categories regarding their main aims: biological control, biotic resistance, or impact assessment. Papers about biological control tested the efficiency of a native or NNS as a biological control agent of a pest using FR experiments. Papers classified as biotic resistance tested the ability of a native consumer to consume a non-native resource. On the other hand, impact assessment papers used FR to predict or evaluate the effect of NNS as consumers or resources in different contexts. The type of interaction, whether predator-prey, host-parasitoid, herbivore-plant, filter-feeding, or plant-nutrient was recorded according to the authors' classification. Finally, the habitat where the experiment was performed was classified into freshwater, marine/brackish water, or terrestrial according to the methods described in each paper and the country where the study was conducted was recorded to identify geographic trends of FRs in invasion science.

A Pearson's chi-squared test of homogeneity was used to test if the frequency of studies was evenly distributed across the different types of interaction and habitats investigated. A chi-square test of independence was used to test for independence between these attributes and the study category (biological control, biotic resistance, or impact assessment).

1.2.4 Taxonomic trends

The Latin names of the species used in the FR experiments were recorded. Some studies did not identify the consumer/resource to the species level, so we used the most specific classification given (whether family or genus). Some studies used more than one species in each case, so the number of species exceeded the number of studies. Each species used in the studies, whether as a consumer or as a resource, was classified into its corresponding coarse taxonomic group following Pyšek et al. (2008). A chi-square test of homogeneity was used to verify if the frequency of studies was evenly distributed through the taxonomic groups used, both as consumer and resource.

The origin of the species used as consumer and resource was defined according to the authors' own classification. Species classified as adventive, alien, exotic, immigrant, imported, invader, invasive, introduced, naturalised, non-indigenous, non-native, or novel, were considered here as "non-native" in origin. For species classified as pests, we checked their origin in the literature. Species described as endemic, indigenous, native, or natural were considered "native" in origin. When the origin of the species was not clearly stated in the text, the classification was searched elsewhere or considered as "non-identified" when it was not possible to confirm.

1.2.5 Context-dependencies and FR types

A single study can perform more than one FR experiment under different contexts. Here, we recorded the number of different contexts used, as well as whether they are biotic (such as life stage, starvation period, and sex) or abiotic (for example, temperature and habitat complexity), and which treatments were tested within each context (a list of treatments for each context is available at the Supplementary material, Table S2).

For each FR experiment, the FR type was identified through the text, tables, or figures according to the authors' classification. If the paper did not explicitly classify into one of the FR types, it was identified by the equation used to model the curve. For example, Rogers' random predator equation and Holling's disc equation were considered Type II FR, whereas Hassell's equation was considered Type III. Pearson's chi-squared tests of independence were used to test for independence between the FR curve type and the type of interaction, or the habitat studied. All analyses were performed in R v. 4.1.0 (R Core Team 2021), considering a significance level of alpha = 0.05.

1.3 RESULTS

1.3.1 Literature search and screening

The search yielded 785 documents and the first screening through title and abstract was more conservative, so all potentially relevant papers were selected for the next step, totalling 175 papers. The second screening through full-text reading resulted in 120 papers included in the systematic review (Fig. S1; the list of all references included in the systematic review is available in Supplementary material).

1.3.2 Publication trends

The first paper published in our survey of FRs in invasion science dates from 1966; however, this study investigated a non-native consumer FR without clearly aiming to assess impacts or test invasion hypotheses. Likewise, publications were generally rare (i.e. one or none *per* year) and strictly related to biological control until 2003 (Fig. 2A). The relative frequency of studies using FR in the context of invasion science only surpassed those of FR in general in 2014, corroborating the growth in the AI (Fig. 2B). Journal trends are presented in the Supplementary material (Fig. S2).

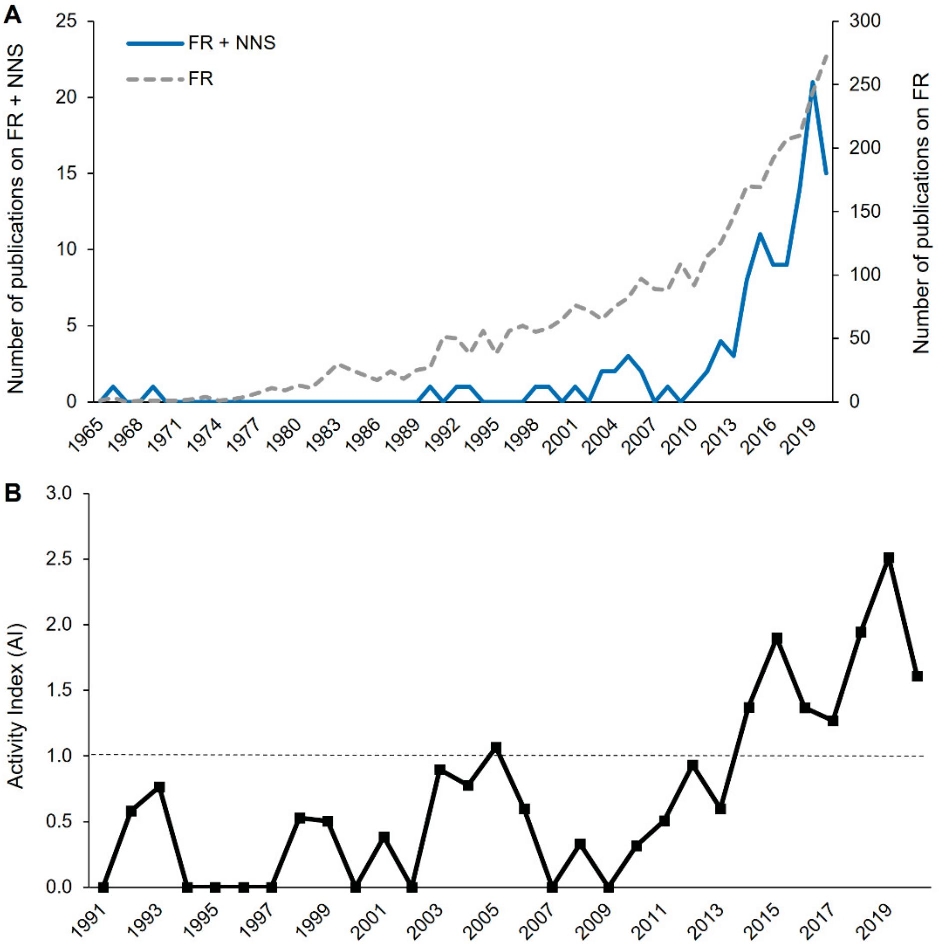


Figure 2. Temporal trends of papers using Functional Response in invasion science (i.e. FR + NNS) and Functional Response in general (FR). **A** number of published papers *per* year (please note the different scale on the right) **B** the Activity Index (AI) in research output that used Functional Response in the context of invasion science relative to all studies about Functional Response in general in the same period.

1.3.3 Study attributes

Most of the studies were classified as impact assessment (62.5%), whereas 28.3% were categorised as biological control and 9.2% as biotic resistance. Studies investigating predator-prey interactions were by far the most common (76.7%), followed by host-parasitoid interactions (12.5%), herbivory (5.8%), and filter-feeding (4.2%), while plant-nutrient interactions were the least studied (0.8%). Therefore, the distribution of studies according to the type of interaction was not homogeneous (χ^2 = 245.2, df = 4, n = 120, $p < 0.001$), with predator-prey interactions predominantly featuring in impact assessment studies, and all studies of host-parasitoid interactions classified as biological control (χ^2 = 47.1, df = 8, n = 120, $p < 0.001$; Fig. 3). There are also significant differences regarding the type of habitat, as almost half of the studies featured freshwater environments (50.8%), followed by terrestrial (35.8%) and marine/brackish water (13.3%) ($\chi^2 = 25.7$, df = 2, n =120, $p < 0.001$). Most studies in the terrestrial environment were those classified as biological control (79%), whereas all the freshwater studies were classified as impact assessment or biotic resistance, and hence these two variables were not independent ($\chi^2 = 92.8$, df = 4, n = 120, $p < 0.001$; Fig. 3). Regarding geographic trends, most studies were conducted in the UK (n = 35), followed by USA (n = 20), Canada (n = 13), and China (n = 8). Six papers were conducted in more than one country and thus were counted more than once. Striking gaps in FR reporting from NNS were found across much of Asia, Africa, Eastern Europe, and South America (Fig. 4).

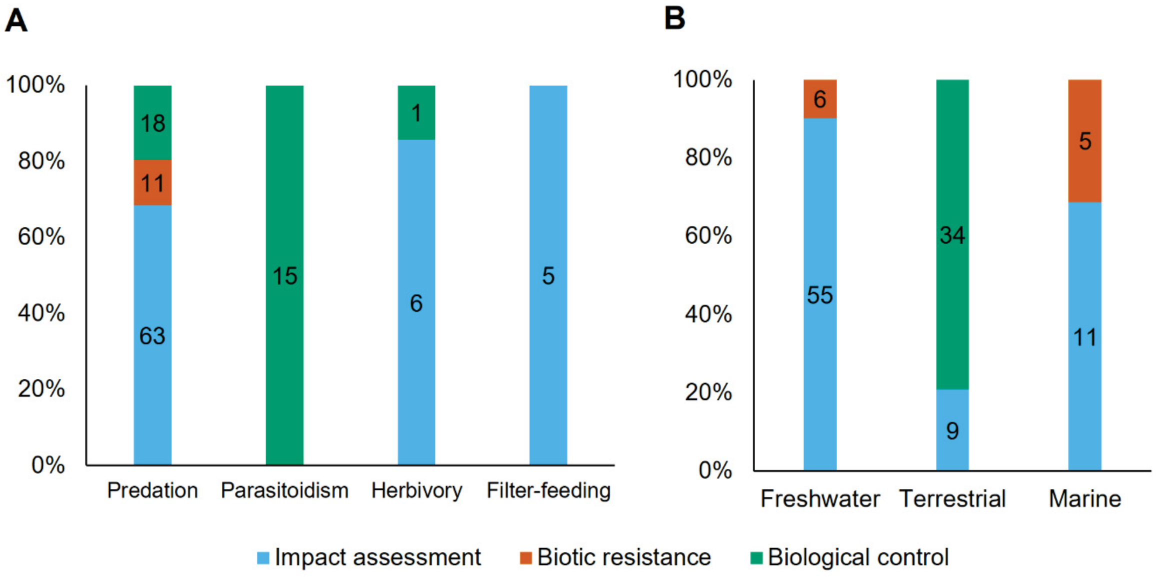


Figure 3. The proportion of studies *per* category. **A** regarding type of interaction **B** regarding habitat type. The numbers inside the bars indicate the total number of papers. The plant-nutrient interaction type was omitted in plot **A** to facilitate visualisation (only one study in the freshwater environment).

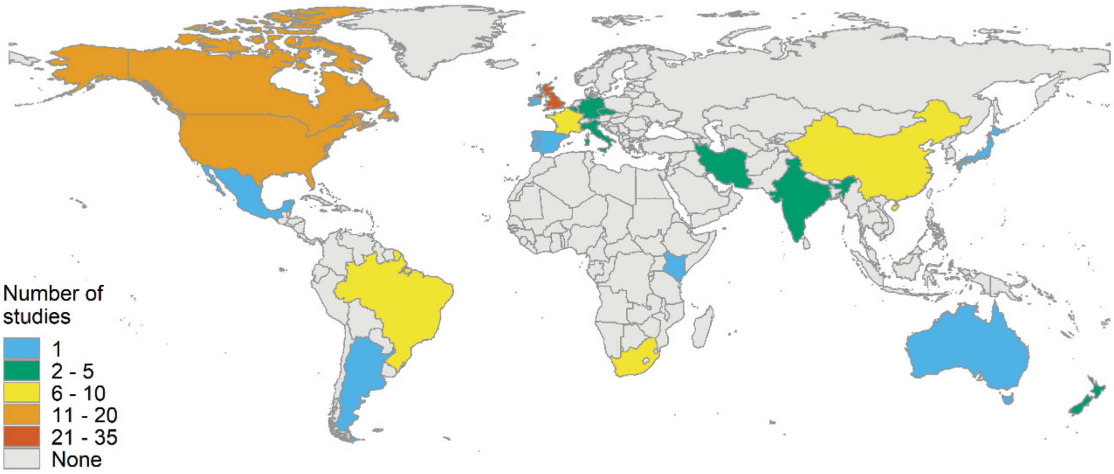


Figure 4. World map showing the number of studies conducted *per* country included in this review. Antarctica is omitted from the map but there are no studies conducted in this region.

1.3.4 Taxonomic trends

In general, insects and crustaceans were the most studied taxonomic groups, both as consumers (χ^2 = 98.1, df = 7, n = 122, $p < 0.001$) and as resource (χ^2 = 176.5, df = 7, n = 134, $p < 0.001$), followed by fish and molluscs as consumers and resources, respectively (Fig. 5). Yet within crustaceans, gammarids (Gammaridae) comprised almost half (49%) of the studies using a crustacean as a consumer. Among biological control studies in the terrestrial habitat, investigations of host-parasitoid interactions were most common and always used insects as study species. Regarding impact assessment and biotic resistance studies, most investigations were related to predator-prey interactions, mainly using crustaceans and fish.

As some studies used more than one species as a consumer and/or resource, a total of 249 species were used in the FR experiments. Some species were used both as a consumer and as a resource, resulting in 147 species used as consumers and 112 as resources. Regarding consumer species, *Gammarus pulex* (Amphipoda: Gammaridae) (n = 15 studies) was most frequently used, followed by *Dikerogammarus villosus* (Amphipoda: Gammaridae) (n = 8), *Gammarus duebeni celticus* (Amphipoda: Gammaridae) (n = 6), and *Hemimysis anomala* (Mysida: Mysidae) and *Neogobius melanostomus* (Perciformes: Gobiidae), which were both used in five studies each. All other species were used in fewer than five studies. The species most commonly used as a resource was also *G. pulex* (n = 9), followed by *Daphnia magna* (Diplostraca: Daphniidae) (n = 8), and *Asellus aquaticus* (Isopoda: Asellidae) and *Tuta absoluta* (Lepidoptera: Gelechiidae), which were both used in five studies each. All other species used as a resource were employed in fewer than five studies. In 22 studies, the resource was not identified at the species level, with Chironomidae larvae being most frequently employed (n = 14).

Most studies used non-native consumers (39.2%), or compared native and non-native consumers (38.3%), whereas 22.5% used a native consumer only. Regarding the resources, the greatest number of studies used only non-native resources (40.7%), whereas 18.6% of studies used native resources and 17.8% compared native and NNS. For some studies, it was not possible to identify the origin of the resource used, either in the text or in other sources (22.9%).

1.3.5 Context-dependencies and FR types

Most studies (81.7%) considered context-dependency in their experimental design by modelling the FR under different biotic and abiotic treatments. From these, the majority tested biotic contexts (65.7%), followed by studies testing different abiotic contexts (20.2%), while just 14.1% used both biotic and abiotic treatments. Each study used from one to four different treatments, and because of that, the 120 papers yielded data from 735 FR curves. Among the biotic contexts, the most frequently used were consumer or resource origin (i.e. native or non-native), and life stage (Fig. 6). Regarding abiotic contexts, the most frequently tested were temperature and habitat complexity (Fig. 6).

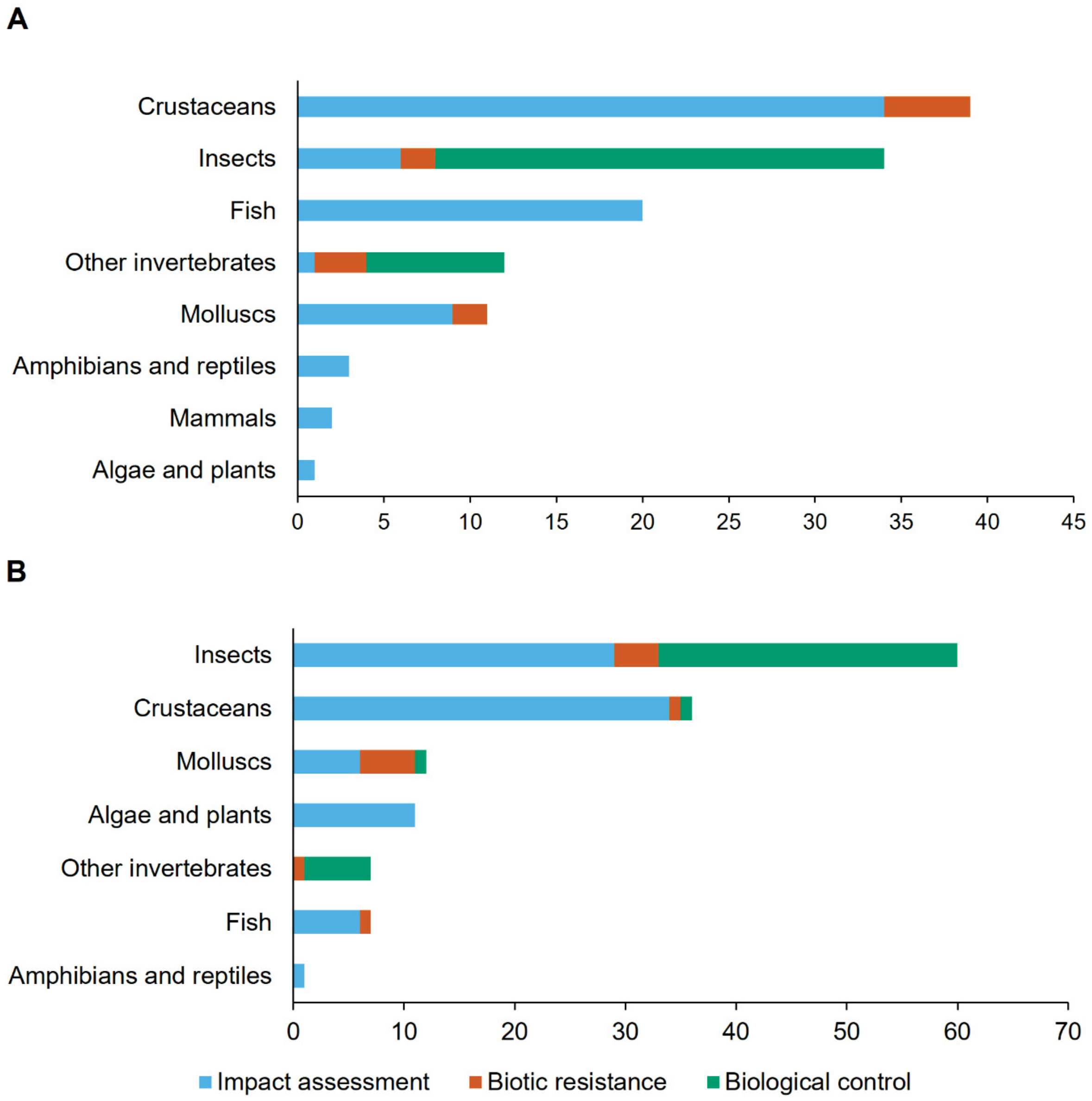


Figure 5. Frequency of studies for each taxonomic group considering the different study categories. **A** regarding the consumer used **B** regarding the resource used. Studies that used species from different taxonomic groups were counted once for each case.

Most of the 735 FR curves recorded were classified by the study as Type II (87.7%). Those classified as Type III accounted for 7% of the FR curves, and only 25 (3.4%) were classified as Type I. One study classified the curve as Type IV, whereas four studies did not clearly define the FR type in the text or figures, nor the type of equation used to model the FR. The type of interaction and the FR type are not independent, as Type II FRs were more common for all types of interaction except filter-feeding (χ^2 = 243.3, df = 6, n = 717, $p < 0.001$). Type II was also the most common type of FR regardless of the type of habitat studied (χ^2 = 33.2, df = 4, n = 717, $p < 0.001$).

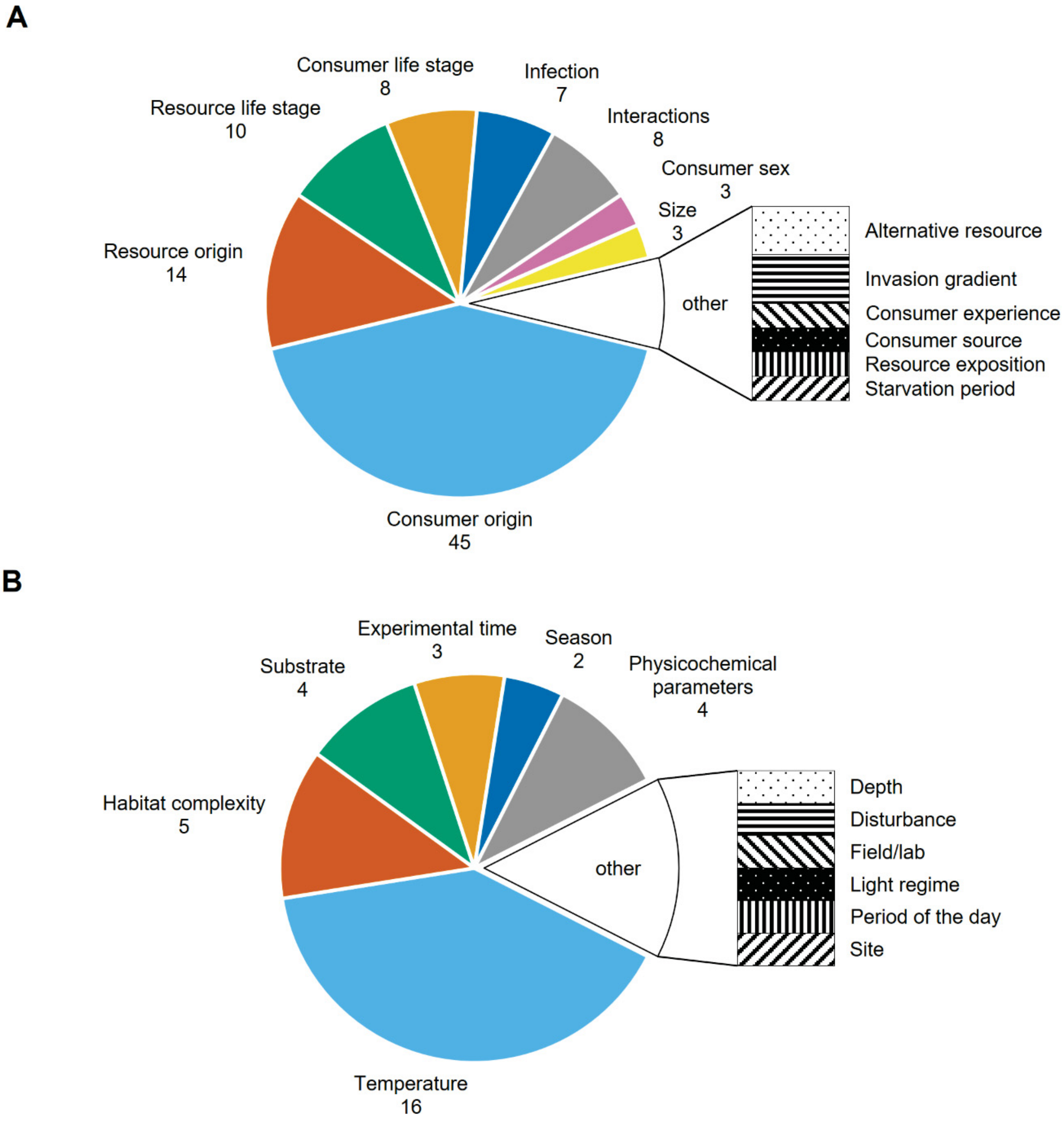


Figure 6. Different contexts used in experiments of the studies which derived Functional Responses under more than one treatment. **A** regarding biotic contexts **B** regarding abiotic contexts. For biotic contexts, treatments used in two or fewer studies (alternative resource 2, invasion gradient 2, consumer experience 1, consumer source 1, resource exposition 1, and starvation period 1) were included in "other". For abiotic contexts, treatments used in only one study (depth, disturbance, field versus laboratory, light regime, period of the day, and site) were included in "other".

1.4 DISCUSSION

The Functional Response can be applied broadly to any consumer-resource interaction, despite being classically used to understand how predation affects population dynamics (Jeschke et al. 2004). In recent years, this concept has gained attention due to its application in fields beyond population ecology, biological control, fisheries management and in particular, invasion science (Ricciardi et al. 2021).

However, the rapidly growing number of invasion science studies that use FR have done so in environmentally, geographically and taxonomically restricted applications, thus impeding large-scale quantitative comparisons and tests of hypotheses across different contexts. There is a conspicuous bias in the geographic distribution of studies, reflecting a common trend in invasion science (Pyšek et al. 2008, Bellard and Jeschke 2016). A limitation of our review is that we only searched for publications in English (Angulo et al. 2021); if we had included grey literature or used other repositories, we may have further broadened the geographic distribution of the reviewed papers. Nevertheless, we found that FR research has been geographically skewed towards North America and Europe (especially the United Kingdom), where research capacities are comparatively high, as well as towards predator-prey interactions in freshwater habitats, with a paucity of terrestrial and marine studies and other trophic and taxonomic groups. In turn, most studies have focused on a few species of crustaceans, insects, molluscs, and fishes, and considered origin, life stage, temperature, and habitat complexity as principal context-dependencies.

Despite rapid growth in the FR approach in the last decade, the first study investigating the FR of a NNS (Mook and Davies 1966) was published only seven years after the seminal paper about FR by Holling (1959). The Activity Index (AI) showed that, after 2014, papers using FR in invasion science were published at a higher relative rate compared to the overall literature on FR (i.e. AI >1). This coincides with the publication of a series of seminal papers using FR in the context of invasion science between 2008 and 2014 (e.g. Bollache et al. 2008, Dick et al. 2013a, Alexander et al. 2014), culminating in the first paper formally outlining the use of the comparative FR as a methodology to predict NNS impacts (Dick et al. 2014). This suggests that the papers published in the period and empirical demonstrations of the method (e.g. Alexander et al. 2014) had a substantial impact in the field, generating a ‘boom’ of studies applying the FR approach in impact assessment of NNS, which was claimed to be a method capable of unifying invasion science (Dick et al. 2017a but see Vonesh et al. 2017, Griffen 2021).

Among study types, it was revealed that studies using the FR approach to demonstrate the impact of NNS were more common than those with a biological control focus or investigating biotic resistance. However, it is important to highlight that our search string was focused on invasion science terminology. Despite many pests being NNS, their origin is often disregarded in purely biological control studies, whereas studies that investigate NNS ecological impacts generally clearly state the non-native origin of the species. Therefore, we do not expect to have captured all studies that used FR in the biological control context, largely because of a different terminology (e.g. “pest” or “weed” species). There is also a difference in journals that typically publish these study types. For instance, we found that Biological Invasions and Biological Control were the journals with a higher number of publications of FRs in invasion science; however, the former published proportionally more impact assessment studies than the latter.

We found important biases regarding study attributes, such as the type of interaction and habitat investigated. Studies on the FR of predators are numerous, and this was somewhat expected given that predators are long recognised as damaging NNS (Salo et al. 2007, Paolucci et al. 2013). Also, the general idea of FR was classically applied to understand the effects of predators on prey population dynamics (Holling 1959, Oaten and Murdoch 1975) and in early work concerning FRs in invasion science (Bollache et al. 2008), although FR use was recognised in algal nutrient uptake (e.g. Tilman 1977) and herbivory (e.g. Farnsworth et al. 2002, Gioria and Osborne 2014). Thus, there is a historical bias towards the investigation of predator-prey interactions. This pattern is also found in a global compilation of FR data, where more than 90% of the compiled curves were from predators (FoRAGE database; Uiterwaal et al. 2022). The second most studied type of interaction was host-parasitoid, albeit always in biological control studies. As parasitoids are often specialists, this may explain their application to biological control investigations, mainly when trying to control an introduced pest that is released from its natural enemies in the invaded system (Hassell and Waage 1984). Despite this, it is important to highlight that FRs can be applied to other forms of resource exploitation (including resources other than food), such as plant nutrient uptake, habitat conversion, shelter use, pollination of flowering plants, and so on (Dick et al. 2017a, Dickey et al. 2020). An example of its potential for diverse application is the employment of FRs to quantify the exploitation of invasive macrophyte as case-building material by larval caddisflies (Crane et al. 2021).

Another striking bias is the number of studies performed in the freshwater environment, given that the vast majority of NNS are in terrestrial ecosystems (Cuthbert et al. 2021), and most studies in invasion science focus on the terrestrial realm (Pyšek et al. 2008, Jeschke and Heger 2018). A priori, one might thus assume that there would be more

FR studies of NNS in this realm. One potential driver for this prevalence of freshwater research could be the practicalities of measuring FRs in aquaria, for which methods have been well developed, in addition to the interests of active research groups in the field that use FR. However, experiments can also be easily performed in other environments, as evidenced by similar proportions of FR curves derived for marine, terrestrial and freshwater environments in the FoRAGE database (Uiterwaal et al. 2022), with greater research effort therefore needed to measure FRs of NNS in terrestrial and marine realms. When studying marine organisms, researchers can use artificial seawater in experimental setups similar to those applied in freshwater studies (e.g. Alexander et al. 2015, DeRoy et al. 2020). On the other hand, cages placed in the field can aid in investigating FRs of terrestrial organisms outside of the laboratory. For instance, Norbury and van Overmeire (2019) measured the predation rate of the invasive European hedgehog on native invertebrate prey, placing small cages in pastures of native and non-native vegetation.

The bias in habitat types is also reflected in the taxonomic groups and species used in the experiments. Crustaceans and insects are significantly more employed, not only as resources but also as consumers, a trend also observed in the FoRAGE database (Uiterwaal et al. 2022). Although it is not surprising regarding biological control studies, given that many pests are insects (as well as their respective predators and parasitoids; or weeds with insect agents), it is unexpected in the case of impact assessment and biotic resistance investigations. This may be explained by invertebrates being small-sized and easier to maintain in artificial environments such as laboratories. Additionally, many countries are faced with restrictions on the use of vertebrates in experimental studies, which may bias investigations towards invertebrate interactions. An alternative is to derive FRs using field data for vertebrate taxa (Goss-Custard et al. 2006, Smout et al. 2013) or through the use of quantitative PCR of gut contents. However, even when it is possible to use vertebrates in experiments, a common challenge is the number of organisms needed to perform sufficient replications under an adequate gradient of initial resource densities. Recently, novel approaches have been applied to quantify FR using fewer individuals, such as via measuring time between captures and gut content analysis (Mofu et al. 2019, Coblentz and DeLong 2021) which could allow FR studies to involve more practically challenging taxa (e.g. limited numbers, large-sized, ethically restricted).

The species most commonly used as both a consumer and a resource was *Gammarus pulex*, being already studied in a wide variety of contexts such as infection (Haddaway et al. 2012, Bunke et al. 2019), temperature (Laverty et al. 2017), habitat complexity (Barrios-O’Neill et al. 2015), and substrate (Dodd et al. 2014, Cuthbert et al. 2019b). Moreover, we noticed a similar trend for freshwater crustaceans in general (gammarids, mysids, decapods), which may reflect their prevalence as invasive freshwater species (Gherardi 2007, Strayer 2010), as well as the value of these taxa as model organisms for predator-prey interactions. Several known impactful species, for example the walking catfish (*Clarias batrachus*) and the red imported fire ant (*Solenopsis invicta*), and rapidly spreading NNS such as the striped eel catfish (*Plotosus lineatus*), however, are still entirely understudied regarding their FRs. In particular, we found only one study measuring FRs of invasive plants, but this may relate to differences in terminology in terms of resource acquisition in plants (e.g. “uptake curves”, Rossiter-Rachor et al. 2009; "resource use efficiency", Funk and Vitousek 2007; "nutrient responses", King and Wilson 2006).

Despite the comparison of the FR of non-native and native analogue consumers being proposed as a practical tool to predict and quantify the impacts of NNS, just half (53%) of the impact assessment studies have performed such a comparison. We highlight that the comparative FR approach is a phenomenological rather than a mechanistic method to understand impacts of NNS and should be interpreted relative to native trophic analogue consumers. When native analogues are absent, it can still be used within species as a response to different relevant contexts. For example, four studies compared the FR of the same species from different populations of its native and introduced ranges (Dick et al. 2013a, Howard et al. 2018, Boets et al. 2019, Grimm et al. 2020). Intraspecific inter-population comparisons in disparate geographical regions and eco-evolutionary contexts may help to shed light on the adaptive mechanisms of NNS that make them impactful in their introduced region. Moreover, impact assessments based on estimates from single populations or a single site could be misleading due to context-dependencies (Howard et al. 2018, Boets et al. 2019, Grimm et al. 2020), and further studies comparing multiple populations must be performed to understand sources of variation in *per capita* effects of the same species in different regions.

Indeed, the possibility of incorporating different context-dependencies in FR experiments is taken as one of the main advantages of this methodology in NNS impact prediction (Dick et al. 2014, 2017a). Several different biotic and abiotic variables can influence the FR (Holling 1959), and accordingly many studies use different treatments to simulate more realistic conditions when deriving FR curves for a species. The biotic contexts most investigated were the origin (native or non-native) of the consumer or resource species, which was expected given the studies targeted by this review. Following origin, the second most studied biotic context was the life stage. It is well known that the diet of a given species can change along with its ontogenetic development (Werner and Gilliam 1984) and reproductive cycle (Dalal et al. 2021), influencing the identity and quantity of the resources used. Additionally, the life stage is directly related to size, influencing the FR parameter of handling time and thus the maximum consumption rate (Vucic-Pestic et al. 2010, Barrios-O'Neill et al. 2016).

Ecological interactions such as cannibalism, intra-guild predation, competition, and higher-order predator presence (Paterson et al. 2015, Bunke et al. 2019, DeRoy et al. 2020, Otturi et al. 2020) were among the most highly investigated biotic contexts. These contexts are critical for upscaling interactions to the ecosystem level where, for example, the presence of conspecifics or other species can lead to facilitation or interference (Griffen 2006, Médoc and Spataro 2015, Médoc et al. 2015), in turn directly influencing consumption rates. This is a feature that should be more often incorporated in future FR studies in the context of invasion science to provide realistic assessments (Griffen 2021).

In addition to biotic variables, the most tested abiotic contexts across studies were temperature and habitat complexity. Temperature has well-known effects on metabolism of ectothermic organisms (DeLong et al. 2018), directly influencing consumption rates across species. The general relationships between temperature and the FR parameters attack rate and handling time have become well established (Englund et al. 2011, Uiterwaal and DeLong 2020). They suggest that under future climate warming (IPCC 2021) the negative trophic effects of NNS will be exacerbated (Sorte et al. 2013). Many studies thus tested projected temperatures to better understand the impacts of non-native consumers in this scenario (Pellan et al. 2016, Gebauer et al. 2018, Kemp and Aldridge 2018).

Habitat complexity is also an important abiotic context, given its capability of changing the FR curve type. Complex environments create barriers between the consumer and the resource, particularly at low densities, which favours the observation of a Type III FR; whereas in simpler habitats it is common to observe Type II FRs (Alexander et al. 2012, 2015, Barrios-O'Neill et al. 2015). Furthermore, the simplified habitat of aquaria and cages used in experiments and their limited space intensifies consumer-resource encounters, likely resulting in higher consumption rates than those expected to be observed in natural conditions (Bergström and Englund 2004, Uiterwaal et al. 2019, Griffen 2021). However, rather than trying to derive "true" FRs of species, it is the comparison among species (i.e. relative FRs) that are of interest in this context. Indeed, relative FR values correspond with actual impact in the field; for example, NNS/native species FR disparities explained differential impacts of invasive mysids (Dick et al. 2013b).

From our set of 120 papers, we obtained data from 735 FR curves, with Type II the most commonly reported form, and this is considered the simplest curve to model (Jeschke et al. 2002, 2004). However, it is important to keep in mind that this curve type can again be a result of the simplified arena and limited space used to perform trials, or the absence of alternative resources and thus lack of switching opportunities (Kalinkat et al. 2023). However, we found that studies employing more complex habitats in the experiments do not frequently observe the expected change from Type II to Type III curves. These studies found that the FR magnitude (i.e. the maximum feeding rate) was higher in low complexity environments (Alexander et al. 2015, Norbury and van Overmeire 2019) or that the estimated parameters differed (South et al. 2017). Although Barrios-O'Neill et al. (2015) found subtle changes towards Type III in more complex environments when using a flexible FR model, the same data were also adequately categorised as Type II. This underlines the potential importance of other contexts that modulate FR form, such as prey preferences and switching in environments with diverse prey assemblages (Murdoch 1969, Kalinkat et al. 2023). Typically, FR studies provide only one resource, therefore accentuating impacts and neglecting to consider more complex communities that could influence resource refugia.

The pattern of Type I FR being typical for filter feeders (Jeschke et al. 2004) is often cited in the literature. Surprisingly, we found the most common curve type for filter feeders to be Type III, however this was heavily influenced by a single study which derived 16 FR curves under various treatments, from which 13 were classified as sigmoidal (Marescaux et al. 2016). When this study was excluded, Type I was indeed shown to be most common (10 FR curves from a total of 11) for filter feeders, however not exclusively, with examples encountered for parasitoids (Matadha et al. 2005, Savino et al. 2012, Wang et al. 2020) and predators (Kushner and Hovel 2006, Tilves et al. 2013, Benhadi-Marín et al. 2018, Poley et al. 2018).

Our results highlight some challenges in FR analysis in general. The classification of FR types and the correct estimation of parameters is not trivial and depends on data quality (i.e. enough number of replications and optimised initial resource densities). Indeed, there is still a lot of discussion in the literature around how to achieve a more accurate result based on data from laboratory experiments that are often heteroscedastic (Uszko et al. 2020, Papanikolaou et al. 2021). Flexible or generalised models, where a scaling component q can assume values that range from a strict Type II FR ($q = 0$) gradually to a Type III ($q = 1$) can be useful to avoid a dichotomy among types (e.g. Mistri 2004, Kushner and Hovel 2006, Twardochleb et al. 2012, Joyce et al. 2020). The type of FR can nevertheless provide different information to the parameters in terms of theoretical resource stability implications (i.e. Type II FRs can be more destabilising to low-density resources than Type III FRs), thereby complementing information from FR parameters, which can be incomparable between different FR types and models. However, despite being complementary pieces of information, the magnitude of the FR curve, and therefore its parameters, can be more informative regarding the effect of the consumer on the resource population than the FR type, particularly in impact assessment studies (Boets et al. 2019). Indeed, it has been shown in previous studies that the maximum feeding rate ($1/h$) can predict damaging invaders, which is the rationale to use it as the *per capita* effect within the RIP metric (e.g. Dick et al. 2017b).

1.5 OUTLOOK AND RECOMMENDATIONS

This review shows that the use of FR in invasion science is increasing, particularly since the first paper conceptualising the comparative approach (Dick et al. 2014). Despite the burgeoning number of publications, FR studies are highly variable regarding their approaches, and there are pervasive biases in the geographic regions, taxonomic groups, and habitats being studied. Besides addressing the gaps and biases identified here, we propose other underexploited avenues for futures studies applying the comparative FR approach; some general areas of research as well as examples of hypotheses in invasion science that could be tested are presented in Table 1.

We have four primary recommendations to advance the use of the comparative FR approach in invasion science. First, invasion scientists should keep abreast of developments in the analysis of FR to refine their approaches. Despite the FR being a classical ecological concept, its application is still developing, with new studies proposing best practices, analysis protocols, and how parameters may be accurately estimated and interpreted (Rosenbaum and Rall 2018, Uszko et al. 2020, Novak and Stouffer 2021, Papanikolaou et al. 2021, Giacomini 2022). For example, research is needed to understand how different conversion efficiencies and background mortalities may affect the general pattern of FRs; and if so, how to consider this in the method. As proposed by Landi et al. (2022), short-term FR experiments can be paired with longer consumer growth response experiments, to check if changes in consumer biomass across resource densities are significantly different between consumers.

Second, future studies should embrace the possibility of including context-dependencies to provide more realism to experimental results. For instance, species usually have more than one type of resource available in natural environments and will often not be foraging alone, thus facing competition for resources with conspecifics and other species. The presence of alternative resources leading to prey switching can effectively change the FR curve type (Murdoch 1969), so it is important that we also unravel this during experimental trials. Additionally, we can use FR-based metrics to assess the impacts of NNS through competition for resources (Dickey et al. 2020). Thus, there is an urgent need to include alternative resources, and inter- and intraspecific competition in FR experiments to obtain more accurate and realistic assessments (e.g. Médoc et al. 2015, DeRoy et al. 2020, Otturi et al. 2020). Likewise, the source of the organisms used in the experiments needs attention. Many studies use resources (and even consumers) sourced from artificial suppliers such as aquaculture and pet retailers (e.g. South et al. 2017, 2019, Cuthbert et al. 2019a), but this may bias the results as the species have not coexisted naturally and likely respond differently to those in nature. If we want to understand real ecological impacts, it is fundamental to favour organisms sampled from the natural habitat whenever possible, with a special focus on ecologically relevant resources.

Third, we recommend that future studies use FR-based metrics to improve impact predictions. Given that FR considers only *per capita* effects, consideration of numerical responses or associated proxies could improve predictive efforts (e.g. by accounting for the influence of field abundance or reproductive efforts on impact), such as with the RIP metric (Dick et al. 2017b, Dickey et al. 2020). Differential numerical responses should be addressed in risk assessment studies, given that FRs from NNS and native comparators may often be similar or even greater for natives, but impacts can be explained by the higher abundances of non-natives. In turn, the RIP metric originally considered only the maximum consumption rate of the species, but a more intricate relationship of impact and FR parameters can exist. Given this, a useful metric is the Functional Response Ratio (FRR), which reveals impacts through the ratio between the FR parameters attack rate and handling time (i.e. FRR = a/h), and can be a reliable tool for risk assessment of new NNS (Cuthbert et al. 2019a).

Table 1. Examples of research topics and hypotheses related to non-native species (NNS) that could be explored using the comparative Functional Response (FR) approach. Further relevant hypotheses that could be explored can, for example, be found in Enders et al. (2020) and Daly et al. (2023).

Topic	Application	Key references
Trophic interactions	Classical concepts including prey switching, omnivory, multiple and non-lethal predator effects, interaction strengths, and trophic cascades, can be measured and compared under different experimental contexts using the FR.	Alexander et al. 2012, Barrios-O'Neill et al. 2015, 2016, Iacarella et al. 2018
Non-trophic interactions and behaviour	The effects of key behaviours such as aggression, activity, and boldness can be quantified by the FR, yielding predictive information on NNS success and ecological impacts. Competitive interactions (e.g. of omnivores) can be revealed using combinations of stable isotope metrics to quantify shifts in trophic niche space and comparative FRs to quantify interaction strengths.	Dominguez Almela et al. 2021, McGlade et al. 2022
Ecomorphology and ecophysiology traits related to	As the FR can be a phenomenological approach, integrating ecomorphological traits (e.g. body size, feeding structures), metabolic	Naranjo and Hagler 2001, Taylor and Dunn 2018, Luger et

ecological impacts of NNS	rate measurements, or immunoassay analysis can provide mechanistic explanations for differences in consumption impacts, thus improving predictive capacity.	al. 2020, Giacomini 2022
Spatiotemporal variation in the impacts of NNS	Impact prediction based on estimates from single populations can be misleading if *per capita* effects vary greatly across space and time. Studies comparing variation in FRs across conspecific populations have tested the importance of environmental context and, in some cases, revealed predictable patterns. Largescale geographical comparisons, thus far rare, could test fundamental questions such as whether predation intensity (e.g. attack rate) is higher in the tropics.	Dick et al. 2013b, Iacarella et al. 2015b, a, Howard et al. 2018, Grimm et al. 2020, Freestone et al. 2021
Differential impact of invasive species based on biogeographic origin	In some situations, native species are considered invasives. The FR can be applied to compare the differential impact of NNS, whether invasive or not, to invasive native species.	Valéry et al. 2008, Simberloff et al. 2012, Cunico and Vitule 2014, Xu et al. 2016
How consumer population abundance affects trophic impacts	While the FR considers only *per capita* effects, consideration of numerical responses or associated proxies in combined metrics improve predictive efforts. Furthermore, the FR can be derived under different combinations of consumer density.	Dick et al. 2017b, Iacarella et al. 2018, Dickey et al. 2020
Hypothesis	**Prediction (in italics) and application**	**Key references**
Resource Consumption	*Successful NNS are often more efficient at exploiting key resources than functionally-similar native species.* Invasive and non-invasive NNS and trophically analogous native species could be compared with respect to *per capita* effects related to feeding efficiency and voracity (e.g. attack rate, handling time).	Funk and Vitousek 2007, Johnson et al. 2008, Morrison and Hay 2011, Dick et al. 2013b, Ricciardi et al. 2013, Gioria and Osborne 2014
Biotic Resistance	*Diverse communities of native species (and previously established NNS) inhibit subsequent establishment, population growth, and impacts of subsequently introduced NNS through antagonistic interactions including competition and predation.* FR experiments can be used to measure the magnitude of consumptive effects of native consumers on NNS.	Twardochleb et al. 2012, MacNeil et al. 2013

Invasional Meltdown	*NNS can facilitate one another in various ways to increase colonization success, abundance, or performance, thereby causing an acceleration in the rate of invasion and increasing the likelihood of synergistic impacts.* FR experiments could compare interactions between NNS and native consumer-resource combinations, besides different combinations of NNS to reveal if impacts of co-occurring NNS are additive, antagonistic, or synergistic.	Simberloff and Von Holle 1999, Simberloff 2006a, Braga et al. 2020
Ecological Naïveté	*NNS will be more impactful if the recipient community do not share an eco-evolutionary experience with functionally similar species, being naïve to the novel species*. One can use the FR to test the prediction that prey exposed to novel generalist predators would be more likely to be destabilized by the interaction (i.e. FR Type II, with high maximum feeding rate), compared to prey that have experience with such predators. Similarly, comparisons of conspecific populations of NNS on islands and mainlands could be done to test the related hypothesis of increased susceptibility of prey in insular habitats.	Ebenhard 1988, Cox and Lima 2006, Saul and Jeschke 2015, Anton et al. 2020
Enemy of My Enemy	*A NNS co-evolved enemy has a stronger negative effect on resident native species, thereby reducing biotic resistance.* The effect of parasites on *per capita* effects of NNS and natives could be used to evaluate competitive abilities with and without the presence of natural enemies.	Colautti et al. 2004, Dick et al. 2010, Toscano et al. 2014
Enemy Inversion	*Co-evolved enemies of NNS are less harmful for them in the non-native than in the native range, due to altered biotic and abiotic conditions.* This hypothesis could be tested for predator-prey and herbivore-plant interactions in different biogeographic contexts using comparative FR experiments.	Colautti et al. 2004
Evolution of Increased Competitive Ability	*The release or reduction of enemies that constrain a NNS population or performance in the native range can trigger the evolution of increased competitive traits in the introduced range*. This hypothesis could be tested through a comparison of FR *per capita* effects of conspecific populations in invaded and	Blossey and Nötzold 1995

	native ranges.	
Evolutionary Imbalance	*Successful and more competitive NNS are likely originating from geographic regions of high phylogenetic diversity.* FRs can compare *per capita* effects, and thus competitive abilities, of functionally or phylogenetically similar consumers from regions of contrasting diversity.	Fridley and Sax 2014
Environmental Heterogeneity	*Spatiotemporal heterogeneity creates refugia against the impacts of NNS on native resources, thereby facilitating coexistence*. FR experiments can incorporate multiple levels and types of habitat complexity to compare its effects on trophic impacts of NNS.	Melbourne et al. 2007, Barrios-O'Neill et al. 2014
Environmental Matching	*The impact of a NNS is inversely correlated with the distance of the novel habitat conditions from the species' environmental optimum*. FRs can be used to measure variation in *per capita* effects across physicochemical gradients in the lab and in the field.	Kestrup and Ricciardi 2009, Iacarella and Ricciardi 2015, Iacarella et al. 2015a
Invasion Front	*Individuals at the front of a spreading NNS population have higher resource consumption rates (leading to higher trophic impacts) than those from the well-established core population, owing to selection for reduced intraspecific competition at the core.* The comparative FR approach could be applied to test intraspecific differences in *per capita* effects across an expanding population to account for variation in impact across space and time.	Iacarella et al. 2015b
Taxonomic Distinctiveness	*NNS that belong to taxonomic groups (genera, families) that are not present historically in the invaded community are more likely to cause significant impacts on biodiversity, food webs, or ecosystem processes, owing to novel use of resources (see also Ecological Naïveté hypothesis)*. The comparative FR approach can be used to test differences in the impacts of conspecific NNS populations in invaded communities that contain genera shared with the NSS versus those communities in which the NNS belong	Ricciardi and Atkinson 2004

	to a novel genus.	

Our final recommendation is to unite disparate terminology in animal and plant research on FRs as well as between fields considering NNS (invasion science and biological control), as differences in nomenclature may impede us identifying patterns in NNS resource use among different taxa and study systems. This is an issue faced not only in ecology but in science in general (Hodges 2008, Jeschke et al. 2019), and polysemy may hinder our comprehensive understanding of NNS impacts across different types of interaction, simply because we cannot track relevant studies. For example, we found two papers that used the term "functional response" for assessing growth performance of plants (Radford et al. 2007, Radford 2013), so they did not meet the criteria to be included in our review. However, we may have conversely missed important studies with plants that used different terminology (e.g. uptake curves and nutrient responses).

There is still a long path to establish the comparative FR approach as a potential universal NNS impact assessment tool, but here we have aimed to advance this goal by revealing knowledge gaps and identifying potential fertile ground for research. We advocate that FR-based metrics can be included in official risk assessment protocols adopted by the IUCN, such as the Environmental Impact Classification for Alien Taxa (EICAT). Although useful to categorise species regarding its impacts, EICAT depends solely on invasion history which is not available for all NNS. The incorporation of FR in this analysis would potentially allow proactive rather than reactive management, while supporting white and blacklists of NNS (Simberloff 2006b).

As NNS can cause impact at any moment after introduction before going through the various invasion stages (e.g. Blackburn et al. 2011, Ricciardi et al. 2013), the FR approach can help target which species are more likely to cause harm before they become too entrenched to manage. In this sense, we conclude that the FR approach can also be valuable to disentangle the impacts of NNS from those of native species that eventually behave like invasives (i.e. increase their range and abundance), ultimately unravelling the role of biogeographic origin on consumptive and non-consumptive effects (Richardson and Ricciardi 2013, Simberloff and Vitule 2014).

Acknowledgements

We thank Laís Carneiro for her precious help in making Fig. 4. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. RNC is funded by an Early Career Fellowship from the Leverhulme Trust (ECF-2021-001), JWED is funded by the Alexander von Humboldt Foundation, AR is funded by the Natural Sciences and Engineering Research Council of Canada, and JRSV is funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq – Process numbers 310850/2012-6; 303776/2015-3 and 302367/2018-7).

References

Alexander ME, Dick JTA, O'Connor NE, Haddaway NR, Farnsworth KD (2012) Functional responses of the intertidal amphipod *Echinogammarus marinus*: Effects of prey supply, model selection and habitat complexity. Marine Ecology Progress Series 468: 191–202. https://doi.org/10.3354/meps09978

Alexander ME, Dick JTA, Weyl OLF, Robinson TB, Richardson DM (2014) Existing and emerging high impact invasive species are characterized by higher functional responses than natives. Biology Letters 10(2): 20130946. https://doi.org/10.1098/rsbl.2013.0946

Alexander ME, Kaiser H, Weyl OLF, Dick JTA (2015) Habitat simplification increases the impact of a freshwater invasive fish. Environmental Biology of Fishes 98(2): 477–486. https://doi.org/10.1007/s10641-014-0278-z

Angulo E, Diagne C, Ballesteros-Mejia L, Adamjy T, Ahmed DA, Akulov E, Banerjee AK, Capinha C, Dia CAKM, Dobigny G, Duboscq-Carra VG, Golivets M, Haubrock PJ, Heringer G, Kirichenko N, Kourantidou M, Liu C, Nuñez MA, Renault D, Roiz D, Taheri A, Verbrugge LNH, Watari Y, Xiong W, Courchamp F (2021) Non-English languages enrich scientific knowledge: The example of economic costs of biological invasions. The Science of the Total Environment 775: 144441. https://doi.org/10.1016/j.scitotenv.2020.144441

Anton A, Geraldi NR, Ricciardi A, Dick JTA (2020) Global determinants of prey naiveté to exotic predators. Proceedings of the Royal Society B 287. https://doi.org/10.1098/rspb.2019.2978

Ball SL, Woodcock BA, Potts SG, Heard MS (2015) Size matters: Body size determines functional responses of ground beetle interactions. Basic and Applied Ecology 16(7): 621–628. https://doi.org/10.1016/j.baae.2015.06.001

Barrios-O'Neill D, Dick JTA, Emmerson MC, Ricciardi A, MacIsaac HJ, Alexander ME, Bovy HC (2014) Fortune favours the bold: A higher predator reduces the impact of a native but not an invasive intermediate predator. Journal of Animal Ecology 83(3): 693–701. https://doi.org/10.1111/1365-2656.12155

Barrios-O'Neill D, Dick JTA, Emmerson MC, Ricciardi A, MacIsaac HJ (2015) Predator-free space, functional responses and biological invasions. Functional Ecology 29(3): 377–384. https://doi.org/10.1111/1365-2435.12347

Barrios-O'Neill D, Kelly R, Dick JTA, Ricciardi A, MacIsaac HJ, Emmerson MC (2016) On the context-dependent scaling of consumer feeding rates. Ecology Letters 19(6): 668–678. https://doi.org/10.1111/ele.12605

Bellard C, Jeschke J (2016) A spatial mismatch between invader impacts and research publications. Conservation Biology 30(1): 230–232. https://doi.org/10.1111/cobi.12611

Benhadi-Marín J, Pereira JA, Barreales D, Sousa JP, Santos SAP (2018) A simulation-based method to compare the pest suppression potential of predators: A case study with spiders. Biological Control 123: 87–96. https://doi.org/10.1016/j.biocontrol.2018.05.007

Bergström U, Englund G (2004) Spatial scale, heterogeneity and functional responses. Journal of Animal Ecology 73(3): 487–493. https://doi.org/10.1111/j.0021-8790.2004.00823.x

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26(7): 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: A hypothesis. Journal of Ecology 83(5): 887–889. https://doi.org/10.2307/2261425

Boets P, Laverty C, Fukuda S, Verreycken H, Green K, Britton RJ, Caffrey J, Goethals PLM, Pegg J, Médoc V, Dick JTA (2019) Intra- and intercontinental variation in the functional responses of a high impact alien invasive fish. Biological Invasions 21(5): 1751–1762. https://doi.org/10.1007/s10530-019-01932-y

Bollache L, Dick JTA, Farnsworth KD, Montgomery WI (2008) Comparison of the functional responses of invasive and native amphipods. Biology Letters 4(2): 166–169. https://doi.org/10.1098/rsbl.2007.0554

Braga RR, Gómez-Aparicio L, Heger T, Vitule JRS, Jeschke JM (2017) Structuring evidence for invasional meltdown: Broad support but with biases and gaps. Biological Invasions 20(4): 923–936. https://doi.org/10.1007/s10530-017-1582-2

Braga RR, Ribeiro VM, Padial AA, Thomaz SM, Affonso IP, Wojciechowski J, Ribas LGS, Cunha ER, Tiburcio VG, Vitule JRS (2020) Invasional meltdown: An experimental test and a framework to distinguish synergistic, additive, and antagonistic effects. Hydrobiologia 847(7): 1603–1618. https://doi.org/10.1007/s10750-019-04107-x

Bunke M, Dick JTA, Hatcher MJ, Dunn AM (2019) Parasites influence cannibalistic and predatory interactions within and between native and invasive amphipods. Diseases of Aquatic Organisms 136(1): 79–86. https://doi.org/10.3354/dao03415

Caliman A, Pires AF, Esteves FA, Bozelli RL, Farjalla VF (2010) The prominence of and biases in biodiversity and ecosystem functioning research. Biodiversity and Conservation 19(3): 651–664. https://doi.org/10.1007/s10531-009-9725-0

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity & Distributions 15(1): 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Coblentz KE, DeLong JP (2021) Estimating predator functional responses using the times between prey captures. Ecology 102(4): e03307. https://doi.org/10.1002/ecy.3307

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecology Letters 7(8): 721–733. https://doi.org/10.1111/j.1461-0248.2004.00616.x

Cox JG, Lima SL (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. Trends in Ecology & Evolution 21(12): 674–680. https://doi.org/10.1016/j.tree.2006.07.011

Crane K, Cuthbert RN, Ricciardi A, Kregting L, Coughlan NE, MacIsaac HJ, Reid N, Dick JTA (2021) Gimme shelter: Differential utilisation and propagule creation of invasive macrophytes by native caddisfly larvae. Biological Invasions 23(1): 95–109. https://doi.org/10.1007/s10530-020-02358-7

Crystal-Ornelas R, Lockwood JL (2020) The ‘known unknowns’ of invasive species impact measurement. Biological Invasions 22(4): 1513–1525. https://doi.org/10.1007/s10530-020-02200-0

Cunico AM, Vitule JRS (2014) First records of the European catfish, *Silurus glanis* Linnaeus, 1758 in the Americas (Brazil). BioInvasions Records 3(2): 117–122. https://doi.org/10.3391/bir.2014.3.2.10

Cuthbert RN, Dickey JWE, Coughlan NE, Joyce PWS, Dick JTA (2019a) The Functional Response Ratio (FRR): Advancing comparative metrics for predicting the ecological impacts of invasive alien species. Biological Invasions 21(8): 2543–2547. https://doi.org/10.1007/s10530-019-02002-z

Cuthbert RN, Coughlan NE, Dickey JWE, Rea M, Laverty C, South J, Crane K, McCard M, Dick JTA (2019b) Shell shocked: High potential impacts on native prey by non-native turtles irrespective of benthic habitat context. Aquatic Invasions 14(4): 758–774. https://doi.org/10.3391/ai.2019.14.4.13

Cuthbert RN, Pattison Z, Taylor NG, Verbrugge L, Diagne C, Ahmed DA, Leroy B, Angulo E, Briski E, Capinha C, Catford JA, Dalu T, Essl F, Gozlan RE, Haubrock PJ, Kourantidou M, Kramer AM, Renault D, Wasserman RJ, Courchamp F (2021) Global economic costs of aquatic invasive alien species. The Science of the Total Environment 775: 145238. https://doi.org/10.1016/j.scitotenv.2021.145238

Dalal A, Gallogly J, Cuthbert RN, Laverty C, Dickey JWE, Dick JTA (2021) Ecological impacts of an invasive predator are mediated by the reproductive cycle. Biological Invasions 23(3): 669–675. https://doi.org/10.1007/s10530-020-02414-2

Daly EZ, Chabrerie O, Massol F, Facon B, Hess MCM, Tasiemski A, Grandjean F, Chauvat M, Viard F, Forey E, Folcher L, Buisson E, Boivin T, Baltora-Rosset S, Ulmer R, Gibert P, Thiébaut G, Pantel JH, Heger T, Richardson DM, Renault D (2023) A synthesis of biological invasion hypotheses associated with the introduction–naturalisation–invasion continuum. Oikos 09645. https://doi.org/10.1111/oik.09645

DeLong JP, Bachman G, Gibert JP, Luhring TM, Montooth KL, Neyer A, Reed B (2018) Habitat, latitude and body mass influence the temperature dependence of metabolic rate. Biology Letters 14(8): 20180442. https://doi.org/10.1098/rsbl.2018.0442

DeRoy EM, Scott R, Hussey NE, MacIsaac HJ (2020) Density dependence mediates the ecological impact of an invasive fish. Diversity & Distributions 26(7): 867–880. https://doi.org/10.1111/ddi.13063

Diagne C, Leroy B, Vaissière AC, Gozlan RE, Roiz D, Jarić I, Salles JM, Bradshaw CJA, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. Nature 592(7855): 571–576. https://doi.org/10.1038/s41586-021-03405-6

Dick JTA, Armstrong M, Clarke HC, Farnsworth KD, Hatcher MJ, Ennis M, Kelly A, Dunn AM (2010) Parasitism may enhance rather than reduce the predatory impact of an invader. Biology Letters 6(5): 636–638. https://doi.org/10.1098/rsbl.2010.0171

Dick JTA, Gallagher K, Avlijas S, Clarke HC, Lewis SE, Leung S, Minchin D, Caffrey J, Alexander ME, Maguire C, Harrod C, Reid N, Haddaway NR, Farnsworth KD, Penk M, Ricciardi A (2013a) Ecological impacts of an invasive predator explained and predicted by comparative functional responses. Biological Invasions 15(4): 837–846. https://doi.org/10.1007/s10530-012-0332-8

Dick JTA, Alexander ME, MacNeil C (2013b) Natural born killers: An invasive amphipod is predatory throughout its life-history. Biological Invasions 15(2): 309–313. https://doi.org/10.1007/s10530-012-0287-9

Dick JTA, Alexander ME, Jeschke J, Ricciardi A, MacIsaac HJ, Robinson TB, Kumschick S, Weyl OLF, Dunn AM, Hatcher MJ, Paterson RA, Farnsworth KD, Richardson DM (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biological Invasions 16(4): 735–753. https://doi.org/10.1007/s10530-013-0550-8

Dick JTA, Alexander ME, Ricciardi A, Laverty C, Downey PO, Xu M, Jeschke J, Saul WC, Hill MP, Wasserman R, Barrios-O’Neill D, Weyl OLF, Shaw RH (2017a) Functional responses can unify invasion ecology. Biological Invasions 19(5): 1667–1672. https://doi.org/10.1007/s10530-016-1355-3

Dick JTA, Laverty C, Lennon JJ, Barrios-O’Neill D, Mensink PJ, Britton JR, Médoc V, Boets P, Alexander ME, Taylor NG, Dunn AM, Hatcher MJ, Rosewarne PJ, Crookes S, MacIsaac HJ, Xu M, Ricciardi A, Wasserman RJ, Ellender BR, Weyl OLF, Lucy FE, Banks PB, Dodd JA, MacNeil C, Penk M, Aldridge DC, Caffrey JM (2017b) Invader Relative Impact Potential: A new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. Journal of Applied Ecology 54(4): 1259–1267. https://doi.org/10.1111/1365-2664.12849

Dickey JWE, Cuthbert RN, South J, Britton JR, Caffrey J, Chang X, Crane K, Coughlan NE, Fadaei E, Farnsworth KD, Ismar-Rebitz SMH, Joyce PWS, Julius M, Laverty C, Lucy FE, MacIsaac HJ, McCard M, McGlade CLO, Reid N, Ricciardi A, Wasserman RJ, Weyl OLF, Dick JTA (2020) On the RIP: Using Relative Impact Potential to assess the ecological impacts of invasive alien species. NeoBiota 55: 27–60. https://doi.org/10.3897/neobiota.55.49547

Dickey JWE, Arnott G, McGlade CLO, Moore A, Riddell GE, Dick JTA (2022) Threats at home? Assessing the potential ecological impacts and risks of commonly traded pet fishes. NeoBiota 73: 109–136. https://doi.org/10.3897/neobiota.73.80542

Dodd JA, Dick JTA, Alexander ME, MacNeil C, Dunn AM, Aldridge DC (2014) Predicting the ecological impacts of a new freshwater invader: Functional responses and prey selectivity of the “killer shrimp”, *Dikerogammarus villosus*, compared to the native *Gammarus pulex*. Freshwater Biology 59(2): 337–352. https://doi.org/10.1111/fwb.12268

Dominguez Almela V, South J, Britton JR (2021) Predicting the competitive interactions and trophic niche consequences of a globally invasive fish with threatened native species. Journal of Animal Ecology 90(11): 2651–2662. https://doi.org/10.1111/1365-2656.13571

Ebenhard T (1988) Introduced birds and mammals and their ecological effects. Viltrevy (Stockholm) 13: 1–107. [Swedish Wildlife Research]

Eby LA, Rudstam LG, Kitchell JF (1995) Predator responses to prey population dynamics: An empirical analysis based on Lake Trout growth rates. Canadian Journal of Fisheries and Aquatic Sciences 52(7): 1564–1571. https://doi.org/10.1139/f95-149

Eggleston DB, Johnson EG, Kellison GT, Nadeau DA (2003) Intense removal and non-saturating functional responses by recreational divers on spiny lobster *Panulirus argus*. Marine Ecology Progress Series 257: 197–207. https://doi.org/10.3354/meps257197

Enders M, Havemann F, Ruland F, Bernard-Verdier M, Catford JA, Gómez-Aparicio L, Haider S, Heger T, Kueffer C, Kühn I, Meyerson LA, Musseau C, Novoa A, Ricciardi A, Sagouis A, Schittko C, Strayer DL, Vilà M, Essl F, Hulme PE, van Kleunen M, Kumschick S, Lockwood JL, Mabey AL, McGeoch MA, Palma E, Pyšek P, Saul WC, Yannelli FA, Jeschke JM (2020) A conceptual map of invasion biology: Integrating hypotheses into a consensus network. Global Ecology and Biogeography 29(6): 978–991. https://doi.org/10.1111/geb.13082

Englund G, Öhlund G, Hein CL, Diehl S (2011) Temperature dependence of the functional response. Ecology Letters 14(9): 914–921. https://doi.org/10.1111/j.1461-0248.2011.01661.x

Evangelista HBA, Thomaz SM, Umetsu CA (2014) An analysis of publications on invasive macrophytes in aquatic ecosystems. Aquatic Invasions 9(4): 521–528. https://doi.org/10.3391/ai.2014.9.4.10

Farnsworth KD, Focardi S, Beecham JA (2002) Grassland-herbivore interactions: How do grazers coexist? American Naturalist 159(1): 24–39. https://doi.org/10.1086/324114

Freestone AL, Torchin ME, Jurgens LJ, Bonfim M, López DP, Repetto MF, Schlöder C, Sewall BJ, Ruiz GM (2021) Stronger predation intensity and impact on prey communities in the tropics. Ecology 102(8): e03428. https://doi.org/10.1002/ecy.3428

Fridley JD, Sax DF (2014) The imbalance of nature: Revisiting a Darwinian framework for invasion biology. Global Ecology and Biogeography 23(11): 1157–1166. https://doi.org/10.1111/geb.12221

Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. Nature 446(7139): 1079–1081. https://doi.org/10.1038/nature05719

Gebauer R, Veselý L, Kouba A, Buric M, Drozd B (2018) Forecasting impact of existing and emerging invasive gobiids under temperature change using comparative functional responses. Aquatic Invasions 13(2): 289–297. https://doi.org/10.3391/ai.2018.13.2.09

Gherardi F (2007) Biological invaders in inland waters: Profiles, distribution, and threats. Gherardi F (Ed.). Springer, Dordrecht, 733 pp.

Giacomini HC (2022) Metabolic responses of predators to prey density. Frontiers in Ecology and Evolution 10: 980812. https://doi.org/10.3389/fevo.2022.980812

Gioria M, Osborne BA (2014) Resource competition in plant invasions: Emerging patterns and research needs. Frontiers in Plant Science 5: 501. https://doi.org/10.3389/fpls.2014.00501

Goss-Custard JD, West AD, Yates MG, Caldow RWG, Stillman RA, Bardsley L, Castilla J, Castro M, Dierschke V, Durell SEALV, Eichhorn G, Ens BJ, Exo K-M, Udayangani-Fernando PU, Ferns PN, Hockey PAR, Gill JA, Johnstone I, Kalejta-Summers B, Masero JA, Moreira F, Nagarajan RV, Owens IPF, Pacheco C, Perez-Hurtado A, Rogers D, Scheiffarth G, Sitters H, Sutherland WJ, Triplet P, Worrall DH, Zharikov Y, Zwarts L, Pettifor RA (2006) Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. Biological Reviews of the Cambridge Philosophical Society 81(4): 501–529. https://doi.org/10.1017/S1464793106007093

Griffen BD (2006) Detecting emergent effects of multiple predator species. Oecologia 148(4): 702–709. https://doi.org/10.1007/s00442-006-0414-3

Griffen BD (2021) Considerations when applying the consumer functional response measured under artificial conditions. Frontiers in Ecology and Evolution 9: 713147. https://doi.org/10.3389/fevo.2021.713147

Grimm J, Dick JTA, Verreycken H, Jeschke JM, Linzmaier SM, Ricciardi A (2020) Context-dependent differences in the functional responses of conspecific native and non-native crayfishes. NeoBiota 54: 71–88. https://doi.org/10.3897/neobiota.54.38668

Haddaway NR, Wilcox RH, Heptonstall REA, Griffiths HM, Mortimer RJG, Christmas M, Dunn AM (2012) Predatory functional response and prey choice identify predation differences between native/invasive and parasitised/unparasitised crayfish. PLoS One 7(2): e32229. https://doi.org/10.1371/journal.pone.0032229

Hassell MP, Waage JK (1984) Host-parasitoid population interactions. Annual Review of Entomology 29(1): 89–114. https://doi.org/10.1146/annurev.en.29.010184.000513

Heikinheimo O (2001) Effect of predation on the low-density dynamics of vendace: Significance of the functional response. Canadian Journal of Fisheries and Aquatic Sciences 58(10): 1909–1923. https://doi.org/10.1139/f01-132

Hodges KE (2008) Defining the problem: Terminology and progress in ecology. Frontiers in Ecology and the Environment 6(1): 35–42. https://doi.org/10.1890/060108

Holling CS (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomologist 91(5): 234–261. https://doi.org/10.4039/Ent91293-5

Howard BR, Barrios-O’Neill D, Alexander ME, Dick JTA, Therriault TW, Robinson TB, Côté IM (2018) Functional responses of a cosmopolitan invader demonstrate intraspecific variability in consumer-resource dynamics. PeerJ 6: e5634. https://doi.org/10.7717/peerj.5634

Iacarella JC, Ricciardi A (2015) Dissolved ions mediate body mass gain and predatory response of an invasive fish. Biological Invasions 17(11): 3237–3246. https://doi.org/10.1007/s10530-015-0949-5

Iacarella JC, Dick JTA, Ricciardi A (2015a) A spatio-temporal contrast of the predatory impact of an invasive freshwater crustacean. Diversity & Distributions 21(7): 803–812. https://doi.org/10.1111/ddi.12318

Iacarella JC, Dick JTA, Alexander ME, Ricciardi A (2015b) Ecological impacts of invasive alien species along temperature gradients: Testing the role of environmental matching. Ecological Applications 25(3): 706–716. https://doi.org/10.1890/14-0545.1

Iacarella JC, Hudgins EJ, Dick JTA, Ricciardi A (2018) Predatory behaviour of an invasive amphipod in response to varying conspecific densities under higher-order predation risk. Canadian Journal of Fisheries and Aquatic Sciences 75(1): 131–140. https://doi.org/10.1139/cjfas-2016-0417

IPCC (2021) Summary for Policymakers. In: Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, et al. (Eds) Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York, 3–32. https://doi.org/10.1017/9781009157896.001

Jeschke JM, Heger T (2018) Invasion Biology: Hypotheses and Evidence. CABI, Boston, MA.

Jeschke JM, Kopp M, Tollrian R (2002) Predator functional responses: Discriminating between handling and digesting prey. Ecological Monographs 72(1): 95–112. https://doi.org/10.1890/0012-9615(2002)072[0095:PFRDBH]2.0.CO;2

Jeschke J, Kopp M, Tollrian R (2004) Consumer-food systems: Why type I functional responses are exclusive to filter feeders. Biological Reviews of the Cambridge Philosophical Society 79(2): 337–349. https://doi.org/10.1017/S1464793103006286

Jeschke JM, Lokatis S, Bartram I, Tockner K (2019) Knowledge in the dark: Scientific challenges and ways forward. Facets 4(1): 423–441. https://doi.org/10.1139/facets-2019-0007

Johnson BM, Carpenter SR (1994) Functional and numerical responses - a framework for fish-angler interactions. Ecological Applications 4(4): 808–821. https://doi.org/10.2307/1942010

Johnson BM, Martinez PJ, Hawkins JA, Bestgen KR (2008) Ranking predatory threats by nonnative fishes in the Yampa River, Colorado, via bioenergetics modeling. North American Journal of Fisheries Management 28(6): 1941–1953. https://doi.org/10.1577/M07-199.1

Joyce PWS, Dick JTA, Kregting LT (2020) Lack of biotic resistance to an invasive bivalve irrespective of season or hydrodynamic disturbance. Journal of Experimental Marine Biology and Ecology 528: 151382. https://doi.org/10.1016/j.jembe.2020.151382

Kalinkat G, Rall BC, Uiterwaal SF, Uszko W (2023) Empirical evidence of type III functional responses and why it remains rare. Frontiers in Ecology and Evolution 11: 1033818. https://doi.org/10.3389/fevo.2023.1033818

Kemp JS, Aldridge DC (2018) Comparative functional responses to explain the impact of sympatric invasive bivalves (*Dreissena* spp.) under different thermal regimes. The Journal of Molluscan Studies 84(2): 175–181. https://doi.org/10.1093/mollus/eyy006

Kestrup ÅM, Ricciardi A (2009) Environmental heterogeneity limits the local dominance of an invasive freshwater crustacean. Biological Invasions 11(9): 2095–2105. https://doi.org/10.1007/s10530-009-9490-8

King WMCG, Wilson JB (2006) Differentiation between native and exotic plant species from a dry grassland: fundamental responses to resource availability, and growth rates. Austral Ecology 31(8): 996–1004. https://doi.org/10.1111/j.1442-9993.2006.01693.x

Kumschick S, Gaertner M, Vilà M, Essl F, Jeschke J, Pyšek P, Ricciardi A, Bacher S, Blackburn TM, Dick JTA, Evans T, Hulme PE, Kühn I, Mrugala A, Pergl J, Rabitsch W, Richardson DM, Sendek A, Winter M (2015) Ecological impacts of alien species: Quantification, scope, caveats, and recommendations. Bioscience 65(1): 55–63. https://doi.org/10.1093/biosci/biu193

Kushner RB, Hovel KA (2006) Effects of native predators and eelgrass habitat structure on the introduced Asian mussel *Musculista senhousia* (Benson in Cantor) in southern California. Journal of Experimental Marine Biology and Ecology 332(2): 166–177. https://doi.org/10.1016/j.jembe.2005.11.011

Landi P, McCoy MW, Vonesh JR (2022) Predicting invasive consumer impact via the comparative functional response approach: Linking application to ecological theory. Biological Invasions 24(11): 3565–3579. https://doi.org/10.1007/s10530-022-02862-y

Latombe G, Catford JA, Essl F, Lenzner B, Richardson DM, Wilson JRU, McGeoch MA (2022) GIRAE: A generalised approach for linking the total impact of invasion to species' range, abundance and per-unit effects. Biological Invasions 24(10): 3147–3167. https://doi.org/10.1007/s10530-022-02836-0

Laverty C, Brenner D, McIlwaine C, Lennon JJ, Dick JTA, Lucy FE, Christian KA (2017) Temperature rise and parasitic infection interact to increase the impact of an invasive species. International Journal for Parasitology 47(5): 291–296. https://doi.org/10.1016/j.ijpara.2016.12.004

Luger AM, South J, Alexander ME, Ellender BR, Weyl OLF, Nagelkerke LAJ (2020) Ecomorphology of largemouth bass relative to a native trophic analogue explains its high invasive impact. Biological Invasions 22(7): 2223–2233. https://doi.org/10.1007/s10530-020-02252-2

MacNeil C, Dick JTA, Alexander ME, Dodd J, Ricciardi A (2013) Predators vs. alien: Differential biotic resistance to an invasive species by two resident predators. NeoBiota 19: 1–19. https://doi.org/10.3897/neobiota.19.4839

Madadi H, Mohajeri Parizi E, Allahyari H, Enkegaard A (2011) Assessment of the biological control capability of *Hippodamia variegata* (Col.: Coccinellidae) using functional response experiments. Journal of Pest Science 84(4): 447–455. https://doi.org/10.1007/s10340-011-0387-9

Marescaux J, Falisse E, Lorquet J, Van Doninck K, Beisel J-N, Descy J-P (2016) Assessing filtration rates of exotic bivalves: Dependence on algae concentration and seasonal factors. Hydrobiologia 777(1): 67–78. https://doi.org/10.1007/s10750-016-2764-0

Matadha D, Hamilton GC, Lashomb JH, Zhang J (2005) Ovipositional preferences and functional response of parasitoids of euonymus scale, *Unaspis euonymi* (Comstock) and San Jose scale, *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae). Biological Control 32(3): 337–347. https://doi.org/10.1016/j.biocontrol.2004.12.005

McGlade CLO, Dickey JWE, Kennedy R, Donnelly S, Nelson CA, Dick JTA, Arnott G (2022) Behavioural traits of rainbow trout and brown trout may help explain their differing invasion success and impacts. Scientific Reports 12(1): 1757. https://doi.org/10.1038/s41598-022-05484-5

Médoc V, Spataro T (2015) Predicting the impact of invasive species: A look forward on the comparative functional response approach. Revue d'Écologie 70(1): 114–126. https://doi.org/10.3406/revec.2015.1821 [Terre et Vie]

Médoc V, Albert H, Spataro T (2015) Functional response comparisons among freshwater amphipods: Ratio-dependence and higher predation for *Gammarus pulex* compared to the non-natives *Dikerogammarus villosus* and *Echinogammarus berilloni*. Biological Invasions 17(12): 3625–3637. https://doi.org/10.1007/s10530-015-0984-2

Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H (2007) Invasion in a heterogeneous world: Resistance, coexistence or hostile takeover? Ecology Letters 10(1): 77–94. https://doi.org/10.1111/j.1461-0248.2006.00987.x

Mistri M (2004) Predatory behavior and preference of a successful invader, the mud crab *Dyspanopeus sayi* (Panopeidae), on its bivalve prey. Journal of Experimental Marine Biology and Ecology 312(2): 385–398. https://doi.org/10.1016/j.jembe.2004.07.012

Mofu L, South J, Wasserman RJ, Dalu T, Woodford DJ, Dick JTA, Weyl OLF (2019) Inter-specific differences in invader and native fish functional responses illustrate neutral effects on prey but superior invader competitive ability. Freshwater Biology 64(9): 1655–1663. https://doi.org/10.1111/fwb.13361

Mook LJ, Davies DM (1966) The European praying mantis (*Mantis religiosa* L.) as a predator of the red-legged grasshopper (*Melanoplus femurrubrum* (De Geer)). Canadian Entomologist 98(9): 913–918. https://doi.org/10.4039/Ent98913-9

Morrison WE, Hay ME (2011) Feeding and growth of native, invasive and non-invasive alien apple snails (Ampullariidae) in the United States: Invasives eat more and grow more. Biological Invasions 13(4): 945–955. https://doi.org/10.1007/s10530-010-9881-x

Murdoch WW (1969) Switching in general predators: Experiments on predator specificity and stability of prey populations. Ecological Monographs 39(4): 335–354. https://doi.org/10.2307/1942352

Murdoch WW, Oaten A (1975) Predation and population stability. Advances in Ecological Research 9: 1–131. https://doi.org/10.1016/S0065-2504(08)60288-3

Murray GPD, Stillman RA, Britton JR (2016) Habitat complexity and food item size modify the foraging behaviour of a freshwater fish. Hydrobiologia 766(1): 321–332. https://doi.org/10.1007/s10750-015-2465-0

Naranjo SE, Hagler JR (2001) Toward the quantification of predation with predator gut immunoassays: A new approach integrating functional response behavior. Biological Control 20(2): 175–189. https://doi.org/10.1006/bcon.2000.0892

Norbury G, van Overmeire W (2019) Low structural complexity of nonnative grassland habitat exposes prey to higher predation. Ecological Applications 29(2): e01830. https://doi.org/10.1002/eap.1830

Novak M, Stouffer DB (2021) Systematic bias in studies of consumer functional responses. Ecology Letters 24(3): 580–593. https://doi.org/10.1111/ele.13660

Oaten A, Murdoch WW (1975) Functional response and stability in predator-prey systems. American Naturalist 109(967): 289–298. https://doi.org/10.1086/282998

Otturi G, Reggi PE, Battini MÁ, Barriga JP (2020) The effects of trophic interaction between the Patagonian native *Percichthys trucha* and the invasive *Oncorhynchus mykiss* during the juvenile period. Biological Invasions 22(11): 3293–3305. https://doi.org/10.1007/s10530-020-02324-3

Paolucci EM, MacIsaac HJ, Ricciardi A (2013) Origin matters: Alien consumers inflict greater damage on prey populations than do native consumers. Diversity & Distributions 19(8): 988–995. https://doi.org/10.1111/ddi.12073

Papanikolaou NE, Kypraios T, Moffat H, Fantinou A, Perdikis DP, Drovandi C (2021) Predators' Functional Response: Statistical inference, experimental design, and biological interpretation of the handling time. Frontiers in Ecology and Evolution 9: 740848. https://doi.org/10.3389/fevo.2021.740848

Parker IM, Simberloff D, Lonsdale W, Goodell K, Wonham M, Kareiva P, Williamson M, Von Holle B, Moyle P, Byers J, Goldwasser L (1999) Impact: Toward a framework for understanding the ecological effects of invaders. Biological Invasions 1(1): 3–19. https://doi.org/10.1023/A:1010034312781

Paterson RA, Dick JTA, Pritchard DW, Ennis M, Hatcher MJ, Dunn AM (2015) Predicting invasive species impacts: A community module functional response approach reveals context dependencies. Journal of Animal Ecology 84(2): 453–463. https://doi.org/10.1111/1365-2656.12292

Pellan L, Médoc V, Renault D, Spataro T, Piscart C (2016) Feeding choice and predation pressure of two invasive gammarids, *Gammarus tigrinus* and *Dikerogammarus villosus*, under increasing temperature. Hydrobiologia 781(1): 43–54. https://doi.org/10.1007/s10750-015-2312-3

Penk M, Saul WC, Dick JTA, Donohue I, Alexander ME, Linzmaier S, Jeschke JM (2017) A trophic interaction framework for identifying the invasive capacity of novel organisms. Methods in Ecology and Evolution 8(12): 1786–1794. https://doi.org/10.1111/2041-210X.12817

Poley K, Bahlai C, Grieshop M (2018) Functional response of generalist predators to *Halyomorpha halys* (Hemiptera: Pentatomidae) eggs. Environmental Entomology 47(5): 1117–1127. https://doi.org/10.1093/ee/nvy110

Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. Trends in Ecology & Evolution 23(5): 237–244. https://doi.org/10.1016/j.tree.2008.02.002

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. Biological Reviews of the Cambridge Philosophical Society 95(6): 1511–1534. https://doi.org/10.1111/brv.12627

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Radford IJ (2013) Fluctuating resources, disturbance and plant strategies: Diverse mechanisms underlying plant invasions. Journal of Arid Land 5(3): 284–297. https://doi.org/10.1007/s40333-013-0164-0

Radford IJ, Dickinson KJM, Lord JM (2007) Functional and performance comparisons of invasive *Hieracium lepidulum* and co-occurring species in New Zealand. Austral Ecology 32(3): 338–354. https://doi.org/10.1111/j.1442-9993.2007.01700.x

Ricciardi A, Atkinson SK (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecology Letters 7(9): 781–784. https://doi.org/10.1111/j.1461-0248.2004.00642.x

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs 83(3): 263–282. https://doi.org/10.1890/13-0183.1

Ricciardi A, Iacarella JC, Aldridge DC, Blackburn TM, Carlton JT, Catford JA, Dick JTA, Hulme PE, Jeschke JM, Liebhold AM, Lockwood JL, MacIsaac HJ, Meyerson LA, Pyšek P, Richardson DM, Ruiz GM, Simberloff D, Vilà M, Wardle DA (2021) Four priority areas to advance invasion science in the face of rapid environmental change. Environmental Reviews 29(2): 119–141. https://doi.org/10.1139/er-2020-0088

Richardson DM, Ricciardi A (2013) Misleading criticisms of invasion science: A field guide. Diversity & Distributions 19(12): 1461–1467. https://doi.org/10.1111/ddi.12150

Robertson PA, Mill A, Novoa A, Jeschke JM, Essl F, Gallardo B, Geist J, Jarić I, Lambin X, Musseau C, Pergl J, Pyšek P, Rabitsch W, von Schmalensee M, Shirley M, Strayer DL, Stefansson RA, Smith K, Booy O (2020) A proposed unified framework to describe the management of biological invasions. Biological Invasions 22(9): 2633–2645. https://doi.org/10.1007/s10530-020-02298-2

Rosenbaum B, Rall BC (2018) Fitting functional responses: Direct parameter estimation by simulating differential equations. Methods in Ecology and Evolution 9(10): 2076–2090. https://doi.org/10.1111/2041-210X.13039

Rossiter-Rachor NA, Setterfield SA, Douglas MM, Hutley LB, Cook GD, Schmidt S (2009) Invasive *Andropogon gayanus* (gamba grass) is an ecosystem transformer of nitrogen relations in Australian savanna. Ecological Applications 19(6): 1546–1560. https://doi.org/10.1890/08-0265.1

Salo P, Korpimäki E, Banks PB, Nordström M, Dickman CR (2007) Alien predators are more dangerous than native predators to prey populations. Proceedings. Biological Sciences 274(1615): 1237–1243. https://doi.org/10.1098/rspb.2006.0444

Saul WC, Jeschke J (2015) Eco-evolutionary experience in novel species interactions. Ecology Letters 18(3): 236–245. https://doi.org/10.1111/ele.12408

Savino V, Coviella CE, Luna MG (2012) Reproductive biology and functional response of *Dineulophus phtorimaeae*, a natural enemy of the tomato moth, *Tuta absoluta*. Journal of Insect Science 12(153): 153. https://doi.org/10.1673/031.012.15301

Seebens H, Bacher S, Blackburn TM, Capinha C, Dawson W, Dullinger S, Genovesi P, Hulme PE, van Kleunen M, Kühn I, Jeschke JM, Lenzner B, Liebhold AM, Pattison Z, Pergl J, Pyšek P, Winter M, Essl F (2021) Projecting the continental accumulation of alien species through to 2050. Global Change Biology 27(5): 970–982. https://doi.org/10.1111/gcb.15333

Simberloff D (2006a) Invasional meltdown 6 years later: Important phenomenon, unfortunate metaphor, or both? Ecology Letters 9(8): 912–919. https://doi.org/10.1111/j.1461-0248.2006.00939.x

Simberloff D (2006b) Risk assessments, blacklists, and white lists for introduced species: Are predictions good enough to be useful? Agricultural and Resource Economics Review 35(1): 1–10. https://doi.org/10.1017/S1068280500010005

Simberloff D, Vitule JRS (2014) A call for an end to calls for the end of invasion biology. Oikos 123(4): 408–413. https://doi.org/10.1111/j.1600-0706.2013.01228.x

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: Invasional meltdown? Biological Invasions 1(1): 21–32. https://doi.org/10.1023/A:1010086329619

Simberloff D, Souza L, Nũnez MA, Barrios-Garcia MN, Bunn W (2012) The natives are restless, but not often and mostly when disturbed. Ecology 93(3): 598–607. https://doi.org/10.1890/11-1232.1

Sinclair ARE, Olsen PD, Redhead TD (1990) Can predators regulate small mammal populations? Evidence from house mouse outbreaks in Australia. Oikos 59(3): 382–392. https://doi.org/10.2307/3545150

Sinclair ARE, Pech RP, Dickman CR, Hik D, Mahon P, Newsome AE (1998) Predicting effects of predation on conservation of endangered prey. Conservation Biology 12(3): 564–575. https://doi.org/10.1046/j.1523-1739.1998.97030.x

Smout S, Asseburg C, Matthiopoulos J, Fernández C, Redpath S, Thirgood S, Harwood J (2010) The functional response of a generalist predator. PLoS One 5(5): e10761. https://doi.org/10.1371/journal.pone.0010761

Smout S, Rindorf A, Wanless S, Daunt F, Harris MP, Matthiopoulos J (2013) Seabirds maintain offspring provisioning rate despite fluctuations in prey abundance: A multi-species functional response for guillemots in the North Sea. Journal of Applied Ecology 50(4): 1071–1079. https://doi.org/10.1111/1365-2664.12095

Solomon ME (1949) The natural control of animal populations. Journal of Animal Ecology 18(1): 1–35. https://doi.org/10.2307/1578

Sorte CJB, Ibáñez I, Blumenthal DM, Molinari NA, Miller LP, Grosholz ED, Diez JM, D'Antonio CM, Olden JD, Jones SJ, Dukes JS (2013) Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecology Letters 16(2): 261–270. https://doi.org/10.1111/ele.12017

South J, Dick JTA, McCard M, Barrios-O'Neill D, Anton A (2017) Predicting predatory impact of juvenile invasive lionfish (Pterois volitans) on a crustacean prey using functional response analysis: Effects of temperature, habitat complexity and light regimes. Environmental Biology of Fishes 100(10): 1155–1165. https://doi.org/10.1007/s10641-017-0633-y

South J, McCard M, Khosa D, Mofu L, Madzivanzira TC, Dick JTA, Weyl OLF (2019) The effect of prey identity and substrate type on the functional response of a globally invasive crayfish. NeoBiota 52: 9–24. https://doi.org/10.3897/neobiota.52.39245

Strayer DL (2010) Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55: 152–174. https://doi.org/10.1111/j.1365-2427.2009.02380.x

Swanepoel LH, Somers MJ, Dalerum F (2015) Functional responses of retaliatory killing versus recreational sport hunting of leopards in South Africa. PLoS One 10(4): 1–11. https://doi.org/10.1371/journal.pone.0125539

Taylor NG, Dunn AM (2018) Predatory impacts of alien decapod Crustacea are predicted by functional responses and explained by differences in metabolic rate. Biological Invasions 20(10): 2821–2837. https://doi.org/10.1007/s10530-018-1735-y

Tilman D (1977) Resource competition between plankton algae: An experimental and theoretical approach. Ecology 58(2): 338–348. https://doi.org/10.2307/1935608

Tilves U, Purcell JE, Marambio M, Canepa A, Olariaga A, Fuentes V (2013) Predation by the scyphozoan *Pelagia noctiluca* on *Mnemiopsis leidyi* ctenophores in the NW Mediterranean Sea. Journal of Plankton Research 35(1): 218–224. https://doi.org/10.1093/plankt/fbs082

Toscano BJ, Griffen BD (2013) Predator size interacts with habitat structure to determine the allometric scaling of the functional response. Oikos 122(3): 454–462. https://doi.org/10.1111/j.1600-0706.2012.20690.x

Toscano BJ, Newsome B, Griffen BD (2014) Parasite modification of predator functional response. Oecologia 175(1): 345–352. https://doi.org/10.1007/s00442-014-2905-y

Twardochleb LA, Novak M, Moore JW (2012) Using the functional response of a consumer to predict biotic resistance to invasive prey. Ecological Applications 22(4): 1162–1171. https://doi.org/10.1890/11-0871.1

Uiterwaal SF, DeLong JP (2020) Functional responses are maximized at intermediate temperatures. Ecology 101(4): 1–10. https://doi.org/10.1002/ecy.2975

Uiterwaal SF, Dell AI, Delong JP (2019) Arena size modulates functional responses via behavioral mechanisms. Behavioral Ecology 30(2): 483–489. https://doi.org/10.1093/beheco/ary188

Uiterwaal SF, Lagerstrom IT, Lyon SR, DeLong JP (2022) FoRAGE database: A compilation of functional responses for consumers and parasitoids. Ecology 103(7): e3706. https://doi.org/10.1002/ecy.3706

Uszko W, Diehl S, Wickman J (2020) Fitting functional response surfaces to data: A best practice guide. Ecosphere 11(4): e03051. https://doi.org/10.1002/ecs2.3051

Valéry L, Fritz H, Lefeuvre JCC, Simberloff D (2008) In search of a real definition of the biological invasion phenomenon itself. Biological Invasions 10(8): 1345–1351. https://doi.org/10.1007/s10530-007-9209-7

van Driesche RG, Bellows TS (1996) Biological Control. Springer US, Boston, MA, 539 pp. https://doi.org/10.1007/978-1-4613-1157-7

Vonesh J, McCoy M, Altwegg R, Landi P, Measey J (2017) Functional responses can’t unify invasion ecology. Biological Invasions 19(5): 1673–1676. https://doi.org/10.1007/s10530-016-1356-2

Vucic-Pestic O, Rall BC, Kalinkat G, Brose U (2010) Allometric functional response model: Body masses constrain interaction strengths. Journal of Animal Ecology 79(1): 249–256. https://doi.org/10.1111/j.1365-2656.2009.01622.x

Wang X, Biondi A, Daane KM (2020) Functional responses of three candidate asian larval parasitoids evaluated for classical biological control of *Drosophila suzukii* (Diptera: Drosophilidae). Journal of Economic Entomology 113(1): 73–80. https://doi.org/10.1093/jee/toz265

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15(1): 393–425. https://doi.org/10.1146/annurev.es.15.110184.002141

Xu M, Mu X, Dick JTA, Fang M, Gu D, Luo D, Zhang J, Luo J, Hu Y (2016) Comparative functional responses predict the invasiveness and ecological impacts of alien herbivorous snails. PLoS One 11(1): e0147017. https://doi.org/10.1371/journal.pone.0147017

Yodzis P (1994) Predator-prey theory and management of multispecies fisheries. Ecological Applications 4(1): 51–58. https://doi.org/10.2307/1942114

2 NON-NATIVE CONSUMERS HAVE HIGHER FEEDING RATES THAN TROPHICALLY ANALOGOUS NATIVE SPECIES

This manuscript is a collaboration with the same team of researchers from the previous chapter. The initial idea was conceived by me and Professor Jean Vitule, with later inputs from all the other authors. I performed the collection and analysis of data and wrote the initial draft. All authors revised the first draft. The manuscript is under preparation to be submitted and is presented following the guidelines of the journal Ecology Letters.

Larissa Faria[1]; Ross N. Cuthbert[2]; James W. E. Dickey[3,4,5,6]; Jonathan M. Jeschke[3,4,5]; Anthony Ricciardi[7]; Jaimie T. A. Dick[2]; Jean R. S. Vitule[1]

[1] Laboratório de Ecologia e Conservação, Departamento de Engenharia Ambiental, Universidade Federal do Paraná, Curitiba, Paraná, Brazil

[2] Institute for Global Food Security, School of Biological Sciences, Queen's University Belfast, Belfast, Northern Ireland

[3] Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany

[4] Freie Universität Berlin, Institute of Biology, Berlin, Germany

[5] Berlin-Brandenburg Institute of Advanced Biodiversity Research, Berlin, Germany

[6] GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Kiel, Germany

[7] Department of Biology, McGill University, Montreal, Quebec, Canada

Correspondence: Larissa Faria, Universidade Federal do Paraná, Av. Cel. Francisco H. dos Santos, 100, Curitiba - PR, 81530-000, Brazil. Email: larissafaria@fulbrightmail.org

Running title: Higher feeding rates of non-native species

Abstract

Non-native species contribute greatly to global biodiversity loss. Impactful non-native species have in the past been linked to greater resource use efficiency relative to analogous native species (Resource Consumption hypothesis), but evidence remains equivocal. Here, we tested this prediction quantitatively in a global meta-analysis of comparative functional response studies. Data were extracted from studies published until 2023. We calculated the log response ratio of paired non-native and native consumers' functional responses, using attack rate and maximum feeding rate parameters as response variables. Explanatory variables were consumer taxonomic group and primary diet, non-native consumer invasiveness, habitat, native assemblage latitude, and non-native consumer taxonomic distinctiveness. Overall, non-native consumers had higher maximum feeding rates than their native counterparts; attack rates tended to be higher but were not significantly so. The magnitude of effect sizes varied primarily with consumer taxonomic group and primary diet. Differential non-native species impacts were greatest in freshwater habitats, suggesting insularity can exacerbate effects. In general, non-native consumers have higher feeding rates than trophically analogous native species, thus our results support the hypothesis that non-native species are more efficient in consuming resources, which can partly explain their negative impacts on biodiversity and food webs.

Keywords: ecological impact, effect size, feeding response, impact prediction, invasion hypothesis, invasion science, invasive alien species, meta-analysis, predation rate, risk assessment

2.1 INTRODUCTION

In our globalized world, the rates of introduction of non-native species into new environments can reach rates of hundreds of new species *per* year and there is no indication that this number will decelerate soon (IPBES, 2023; Seebens et al., 2021). This is worrisome once invasive non-native species are among the main drivers of biodiversity loss worldwide (Bellard et al., 2016; Blackburn et al., 2019; Jaureguiberry et al., 2022). Some of the main mechanisms through which non-native species cause negative impacts are competition for resources or direct consumption via predation and herbivory (Lockwood et al., 2007). Several examples of non-native species' potential to extirpate natives are known, such as the Nile perch introduced in Lake Victoria that led dozens of native cichlids to extinction and caused the decline of other carnivore species (Goudswaard et al., 2002; Kruuk & Goudswaard) as well as the case of the peacock bass (*Cichla* sp.) in South America, where significant negative effects on native prey due to predation and on native piscivores due to competition were observed after its introduction (Franco et al., 2021; Pelicice et al., 2015; Pelicice & Agostinho, 2009).

It has been shown that many impactful non-native species are highly efficient in consuming available resources (Funk & Vitousek, 2007; Morrison & Hay, 2011). Potential underlying reasons include a release of the non-native species from parasites and predators (Enemy Release) (Keane & Crawley, 2002) or a lack of evolutionary history of the native prey with the novel consumer (Prey Naïveté) (Buckley & Catford, 2016; Ricciardi et al., 2013). Whatever the reason, the likely result is that many non-native species that successfully establish and invade new environments can consume resources in greater rates. This leads to the selection of efficient consumers, a tangible trait that might be related to observed negative impacts of non-native species in the field (Dick et al., 2013).

Per capita rates of consumption, such as those expressed by functional responses (see Box 1), have been claimed to be useful when quantifying and predicting non-native species impacts (Dick et al., 2014; Faria et al., 2023). If efficient resource consumption is a general trait among invaders, it is expected that their functional responses would be higher when compared to those of native analogues (Dick et al., 2017). Functional responses quantify *per capita* effects across a gradient of resource densities. The functional response can therefore infer density-dependence of invader effects. At low resource densities, if non-native species are more efficient in consuming resources when they are scarce then they are more likely to extirpate populations. If resources are abundant and the non-native species displays higher consumption rates, this could in the long-term drive increased population abundance, fitness, and spread. Thus, the comparative functional response (CFR) approach has been increasingly used in invasion science to predict and quantify non-native species negative impact (Faria et al., 2023). *Per capita* effects quantified through laboratory experiments can be a proxy of field impacts, and could support rapid assessment and prioritisation of high impact species for management (Faria et al., 2023; Ricciardi et al., 2021).

Despite the rapid accumulation of evidence across study systems using CFR (Faria et al., 2023), the hypothesis that non-native consumers generally have higher functional responses than trophically analogous native species has not yet been quantitatively tested. A previous study, analysing data from fish, found that non-native status did not strongly influence FR parameters (Buba et al., 2022); however, data used in this study was not from comparative studies such as the approach proposed in Dick et al. (2014). Here, we perform the first meta-analysis of previously published CFR studies to test the Resource Consumption hypothesis (Dick et al., 2014; Faria et al., 2023; Ricciardi et al., 2013). Additionally, we test the following specific predictions: (i) differences in feeding rates are greater in freshwater than marine and terrestrial habitats, reflecting prey naïveté stemming from differences in insularity of their respective biota; (ii) differences in feeding rates will be lower in more diverse assemblages (i.e. from tropical and sub-tropical latitudes) than in less diverse assemblages (temperate latitudes) because greater predation pressure reduces the evolutionary mismatch created by a novel consumer; and (iii) non-native consumers that represent novel (unshared) genera in the region containing the native analogues to which they are compared will have higher impact than non-native consumers that belong to genera shared with the native biota (Taxonomic Distinctiveness hypothesis) (Ricciardi & Atkinson, 2004).

Box 1: Functional response in ecology.

The consumption rate of a consumer (e.g. a predator) as a function of the availability of a resource (e.g. prey) is known as the functional response (Holling, 1959b; Solomon, 1949). Generally, it describes how much an individual consumer can eat during a specified amount of time. This relationship can be broadly described by at least three different functional response types (Figure 1). If there is a linear increase in the consumption rate as the availability of resources increases up to an abrupt limit, this relationship is characterised by a Type I functional response (Holling, 1959b). However, many consumers will be limited by the time they spend pursuing one resource item, decelerating the rate of consumption as resources becomes more abundant. This results in a hyperbolic relationship between resource availability and consumer feeding rate that characterises a Type II functional response (Holling, 1959b). The third possibility is that, at low densities, resources are less likely to be found by the consumer or that the consumer will prefer a more abundant prey. In these cases, a Type III functional response can manifest, characterised by a sigmoidal curve (Holling, 1959b). Less common forms include a dome-shaped Type IV curve, with a reduction in consumption rate at very high densities of resource (DeLong, 2021). This happens when there are swarming effects at play, such as consumer confusion or accumulation of toxic substances produced by dangerous prey (Jeschke et al., 2004).

Usually, functional responses are derived through laboratory experiments, consisting of offering a gradient of resources to a consumer for a prespecified experimental duration, and then checking how much has been consumed in the available time (DeLong, 2021). Consumption data are modelled using the relevant equation according to the functional response type (i.e. Type I, II, or III, alongside flexible models across types). The most important parameters in functional response models are (cf. Jeschke et al., 2002): the attack rate and the handling time (Holling, 1959a). Attack rate (*a*; also called the attack constant, capture rate, maximum clearance rate, instantaneous rate of discovery and related terms) describes the space or volume containing resources that is effectively cleared by the consumer *per* unit of time

(DeLong, 2021; Holling, 1959a). This parameter describes the slope of the functional response curve, being directly related to consumption of resources when they are in low abundance (DeLong, 2021). The greater the attack rate, the greater will be the impact of a consumer on resources in low densities. Handling time (*h*) is the time needed for capturing, consuming, and digesting one resource item, and limits the amount of resource consumed when resources are highly abundant (DeLong, 2021; Holling, 1959a). The shorter the handling time, the greater the number of resource items consumed (note that the handling time is negligible in Type I functional responses and typically dissolves to zero). Because of that, the inverse of handling time (1/*h*) determines the maximum consumption of a consumer when resources are not limiting, a parameter called maximum feeding rate (MFR; sometimes maximum consumption rate, maximum predation rate, maximum attack rate, and related terms) that corresponds to the asymptote of the Type II and Type III functional response curves (DeLong, 2021). Furthermore, the attack rate and handling time have been assimilated into the ‘Functional Response Ratio’, through *a/h* (Cuthbert et al., 2019).

Determining the type and magnitude of functional responses is relevant, as it directly influences population dynamics (DeLong, 2021; Kalinkat et al., 2023). A Type II functional response may be destabilising as resources are consumed at high rates even when they are at low abundances, possibly leading to extinction (Hassell, 1978). On the other hand, a Type III functional response is more stabilising, as consumption rates are low when resources are scarce, giving the resource population a refugia to increase its abundance in the long term (Holling, 1959b; Murdoch & Oaten, 1975). It is important to note, however, that the functional response is not a fixed trait of a species or population; it can change from Type II to Type III when habitat complexity increases, for example (DeLong, 2021; Kalinkat et al., 2023). Yet, functional response parameters may change with several biotic and abiotic variables such as temperature, body size ratio, and parasite infection (DeLong, 2021).

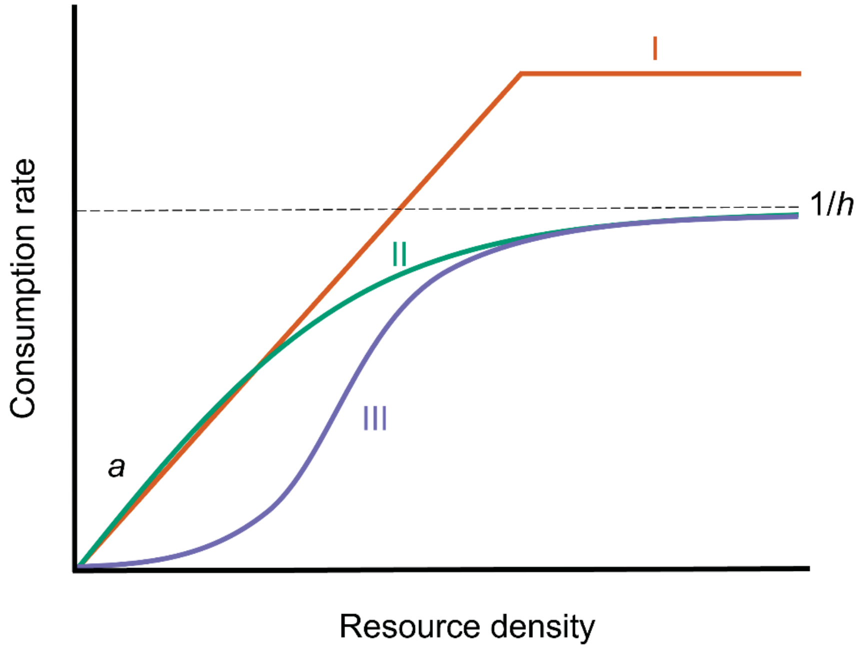


Figure 1. General functional response types (linear **I** – orange, hyperbolic **II** – green, and sigmoidal **III** – violet). The attack rate parameter (*a*) determines the slope of the curve in Type **II** functional responses, whereas the inverse of handling time (1/*h*, dashed line) coincides with the asymptote in Type **II** and Type **III** functional responses.

2.2 METHODS

2.2.1 Selection of studies and observations

We looked for a subset of CFR studies that compared the functional responses of native and non-native consumers feeding on the same resource. This subset was taken from a previously published systematic review about functional response in invasion science (Faria et al., 2023). Additionally, we updated the literature search in May 2023 following the same methodology employed by Faria et al. (2023) to increase the dataset. We assessed if non-native species have higher *per capita* effects on resources than their native counterparts, using proxies of feeding efficiency and voracity from functional response models. Therefore, we sought studies that provided the functional response parameters attack rate (*a*), handling time (*h*), and/or maximum feeding rate (MFR) comparably between native and non-native consumers (i.e. modelled using the same equation). Studies that failed to provide a detailed description of experiments (e.g. number of replicates for each resource density) were excluded. We only included studies where the response was consumption via feeding; thus, studies using parasitoids (response recorded as attacks or oviposition) were not included in our analyses.

We considered each pair of native and non-native consumer species preying on the same resource within studies as a separate observation. As previously reviewed by Faria et al. (2023), many studies perform more than one functional response experiment for the same pair of consumers under different biotic and abiotic treatments. In these cases, we chose to keep data from the most realistic treatment (when it was explicit from the text) or from the treatment that was comparable between studies. For example, Dickey et al. (2021) tested two salinities (10 and 16 ppt) and analysed data from consumption and consumption plus wounded prey. In this case, we decided to keep only observations from the ambient salinity (16 ppt) and excluded those that correspond to a future scenario of sea freshening (10 ppt, less representative currently). Likewise, we kept data from observations of consumption-only analysis, as these are comparable among studies. If the treatments within studies were deemed equally realistic (e.g. different temperatures that correspond to current natural seasonal ranges), we averaged all parameter estimates of each consumer into a single composite sample (when provided, standard errors were propagated from individual estimates), to avoid pseudoreplication. Nonetheless, our final dataset still has more than one observation *per* study (e.g. the same pair of consumers feeding on a different resource, or different non-native consumers compared to the same native analogue). This non-independence within studies is accounted for statistically (see later). The screening of observations was performed by one author (LF) and subsequently checked by two other authors (RNC and JWED) to ensure agreement.

2.2.2 Data extraction

When available, we extracted data of *a*, *h*, and MFR parameters estimated from functional response models and their corresponding standard errors (SEs) for each consumer from text or tables within research articles. For parameter data presented as figures, we used WebPlot Digitizer (https://automeris.io/WebPlotDigitizer) to extract mean values and standard errors. Input data used to model functional response parameters (i.e. the sum of replicates of all initial densities used in the experiment) were recorded as the sample size, except when SE from estimates were obtained through bootstrapping (in these cases, we considered the number of bootstraps as the sample size). Sample size and SE (when available) were used to calculate standard deviations (SDs) for each consumer.

We used the *h* parameter estimate to calculate the MFR for each consumer species as 1/*h*, to standardize it as ‘units of resource consumed per consumer, *per* experiment’. Corresponding MFR SE was propagated from the SE of *h*. When *h* was not provided, we extracted the MFR as calculated by the study. All data were extracted by the same author (LF).

Information on consumers' taxonomic group, consumers' primary diet, non-native consumer invasiveness, habitat, native consumer sampling site, resource origin and source were also recorded as provided by authors or searched in the relevant literature (see Table 1 for definitions). From the native consumer sampling site, we obtained coordinates to categorise the latitude of native assemblages as tropical/sub-tropical (0º to 35º N & S) or temperate (> 35º N & S). We also used the native consumer sampling site to check if the native community shared any species from the same genus as the non-native consumer considering the finer spatial scale possible, thereby inferring taxonomic distinctiveness. Taxonomic distinctiveness between non-native species and the native recipient community was only tested for those observations where the resource was a native species sourced in the wild.

Table 1. Variables extracted from studies for each observation included in the meta-analysis.

Variable	**Definition**
Consumers' taxonomic group	Taxonomic group of the consumer defined as *per* Pyšek et al. (2008).
Consumers' primary diet	Primary diet of the consumer defined as carnivore, herbivore or omnivore, according to the study or relevant literature.
Non-native consumer invasiveness	Classification of the non-native consumer as invasive or not, according to the study or relevant literature. Invasiveness is considered here as the capacity of a non-native species to spread in the study area or elsewhere (Blackburn et al., 2011), and does not denote impact directly.

Variable	Definition
Habitat	Type of habitat where consumer and resource interact, being freshwater, marine (including brackish) or terrestrial, according to the study.
Native consumer sampling site	Where native consumer specimens were collected to be used in the experiments, according to the study methods.
Resource origin	Origin of the resource species (native or non-native) according to the study or relevant literature. In some cases, resources were not specified as species and therefore origin was not identified.
Resource source	From where resource specimens used in the experiments were sourced (wild or cultivated). In some studies, it was not specified.

2.2.3 Meta-analysis

Considering that functional response parameters are usually estimated from the same model (and thus likely correlated), we performed a meta-analysis for each response variable, *a* and MFR, separately. As many studies did not provide SEs to allow us to calculate SDs (72% of missingness in the *a* dataset, and 61% of missingness in the MFR dataset), we employed the “Missing Cases” method, as proposed by Nakagawa, Noble, et al. (2023), where sampling variances of observations with missing SDs are estimated by imputing the pooled coefficient of variation (CV) from the subset of studies that report SDs. We decided to handle missing data as such because alternatively we would need to rely on an unweighted meta-analysis, given that the low number of complete case observations would significantly decrease the sample size (*k*) of our analysis.

For complete observations (i.e. with SD data), we calculated the effect size and sampling variance based on the log response ratio (lnRR), as originally proposed by Hedges et al. (1999), with the bias correction recommended by Lajeunesse (2015):

$$\ln \mathrm{RR} = \ln\left(\frac{m_{\mathrm{NN}}}{m_{\mathrm{N}}}\right) + \frac{1}{2}\left(\frac{\mathrm{CV}_{\mathrm{NN}}^2}{n_{\mathrm{NN}}} - \frac{\mathrm{CV}_{\mathrm{N}}^2}{n_{\mathrm{N}}}\right)$$

$$v(\ln \mathrm{RR}) = \frac{\mathrm{CV}_{\mathrm{NN}}^2}{n_{\mathrm{NN}}} + \frac{\mathrm{CV}_{\mathrm{N}}^2}{n_{\mathrm{N}}}$$

where m_{NN} is the mean functional response parameter (*a* or MFR) of the non-native consumer, m_{N} is the corresponding mean parameter estimated for the native comparator, CV (SD/*m*) is the coefficient of variation for each consumer and *n* is the sample size. For observations with missing SDs, we calculated the effect size (lnRR) and the sampling variance using the equations proposed by Nakagawa, Noble, et al. (2023):

$$\ln \mathrm{RR} = \ln\left(\frac{m_{\mathrm{NN}}}{m_{\mathrm{N}}}\right) + \frac{1}{2}\left(\frac{\left[\sum_{i=1}^{K}(n_{\mathrm{NN}i}\mathrm{CV}_{\mathrm{NN}i})/\sum_{i=1}^{K} n_{\mathrm{NN}i}\right]^2}{n_{\mathrm{NN}}} - \frac{\left[\sum_{i=1}^{K}(n_{\mathrm{N}i}\mathrm{CV}_{\mathrm{N}i})/\sum_{i=1}^{K} n_{\mathrm{N}i}\right]^2}{n_{\mathrm{N}}}\right)$$

$$\tilde{v}(\ln \mathrm{RR}) = \frac{\left[\sum_{i=1}^{K}(n_{\mathrm{NN}i}\mathrm{CV}_{\mathrm{NN}i})/\sum_{i=1}^{K} n_{\mathrm{NN}i}\right]^2}{n_{\mathrm{NN}}} + \frac{\left[\sum_{i=1}^{K}(n_{\mathrm{N}i}\mathrm{CV}_{\mathrm{N}i})/\sum_{i=1}^{K} n_{\mathrm{N}i}\right]^2}{n_{\mathrm{N}}} + \frac{\left[\sum_{i=1}^{K}(n_{\mathrm{NN}i}\mathrm{CV}_{\mathrm{NN}i})/\sum_{i=1}^{K} n_{\mathrm{NN}i}\right]^4}{2n_{\mathrm{NN}}^2} + \frac{\left[\sum_{i=1}^{K}(n_{\mathrm{N}i}\mathrm{CV}_{\mathrm{N}i})/\sum_{i=1}^{K} n_{\mathrm{N}i}\right]^4}{2n_{\mathrm{N}}^2}$$

where $\mathrm{CV}_{\mathrm{NN}i}$ and $\mathrm{CV}_{\mathrm{N}i}$ are the CVs from the *i*th study (study; $i = 1, 2, \ldots, K$; assuming the number of effect sizes = the number of studies = *K*). If functional response parameters of non-native consumers are greater than those of native consumers, the lnRR will be positive. Overall, a mean ratio that is significantly greater than zero (i.e. confidence intervals do not cross zero) would corroborate the hypothesis that non-native consumers have higher feeding rates than trophically analogous native species.

Given the dependence of our dataset (more than one observation *per* study and multiple non-native consumers compared to the same native analogue – "shared control"), we applied a multilevel meta-analysis model with study as a random effect (Mengersen et al., 2013; Nakagawa, Yang, et al., 2023; Noble et al., 2017). To account for shared-sampling variance between effect sizes due to a common native comparator species, we used Robust Variance Estimators (RVE) (Nakagawa, Yang, et al., 2023; Pustejovsky & Tipton, 2022). First, a null multilevel model was fitted using restricted maximum likelihood for each dataset without explanatory variables (moderators) to assess if the overall effect size differed significantly from zero. We then quantified the amount of heterogeneity (I^2 total) of the null model using the function *i2_ml* implemented in the 'orchaRd' package (Nakagawa, Lagisz, et al., 2023). Given the resulting high levels of I^2 total (>98% for both datasets) (Higgins & Thompson, 2002), we employed meta-regression models to explain heterogeneity and test our predictions.

We fitted univariate meta-regression models with consumer taxonomic group, consumer primary diet, and non-native consumer invasiveness (Table 1) as explanatory variables in exploratory analyses to assess their influence on the variability of calculated effect sizes, and with habitat, latitude, and taxonomic distinctiveness to test our predictions. We ran separate models including a single moderator each time due to insufficient sample sizes to assess interaction terms. We fitted our model to account for heterogeneous variances between groups, assuming heteroscedasticity to reduce Type 1 error rates (Rubio-Aparicio et al., 2020).

All meta-analytic and meta-regression models were fitted using the *rma.mv* function in the 'metafor' package v.4.4-0 (Viechtbauer, 2010)**,** setting *test* = *"t"* to obtain statistics and CIs based on a *t*-distribution. Moreover, meta-regressions were fitted setting *struct* = *"HCS"* to assume a heteroscedastic compound symmetry (heterogeneous variances). Visualisation of results was made through forest-like plots using the *orchard_plot* function in the 'orchaRd' package (Nakagawa, Lagisz, et al., 2023). All analyses and plots were performed in the R environment v. 4.3.1 (R Core Team, 2023).

2.2.4 Sensitivity analysis and publication bias

We checked the assumption of normality of our lnRR estimates using Geary's test improved by Lajeunesse (2015) and performed a sensitivity analysis excluding effect sizes that failed the test (i.e. ≥ 3) as suggested by the author (Lajeunesse, 2015). We decided to employ the "Missing Cases" method given the large amount of missing data in our dataset (more than the 55% previously assessed by Nakagawa, Noble, et al. (2023)). However, it has been suggested that the "All Cases" method may perform better under several situations (Nakagawa, Noble, et al., 2023). We therefore repeated our analysis using the "All Cases" method as a sensitivity analysis to compare the mean estimate and its confidence limits. Finally, because we chose an arbitrary value of $\rho = 0.6$ to calculate our adjusted sampling variance matrix in the RVE analysis, we re-ran our model with $\rho = 0.1$ and 0.9 to check the robustness of our results, as suggested by Tanner-Smith & Tipton (2014).

To check for publication bias, we used the approach proposed by Nakagawa et al. (2022), consisting of an extension of regression-based methods (i.e. Egger's regression test) that is suitable for lnRR effect sizes and non-independent data. For that, we ran a multilevel meta-regression model using the square root of the inverse of the effective sample size as the moderator. If the intercept of the model was not statistically different from 0, we considered it as a potential adjusted estimate to check the robustness of our results (Nakagawa et al., 2022; Noble et al., 2017).

2.3 RESULTS

A total of 62 studies were retrieved from our search and screened for eligibility. From these, 52 studies were included in the meta-analysis resulting in a total of 125 observations as pairs of non-native versus native consumers (Figure 2) that had either data on *a*, MFR or both response variables. A list of the data sources is found in the Appendix. Each study yielded an average of 2.4 ± 2.3 (mean ± SD) effect sizes, with a range of 1–12. Many observations involved non-unique comparisons from studies that compared more than one non-native consumer to the same native species (56% of effect sizes).

Most observations come from omnivorous consumers (74%) — mainly crustaceans and fishes (89%) — from freshwater habitats (86%) in temperate locations (72%). Invasive non-native consumers represented 80% of total observations. Only 44 observations were suitable to test the Taxonomic Distinctiveness hypothesis, and in most cases (82%) the native community did not share a species of the same genus as the non-native consumer.

Overall, we found higher maximum feeding rates for non-native consumers compared to native trophic analogues (lnRR_{MFR} = 0.285, 95% CI = 0.1 – 0.47; Figure 3b). Attack rates also tended to be higher for non-native consumers, but this difference was not significant (lnRR_{a} = 0.209, 95% CI = -0.02 – 0.44, Figure 3a). From total heterogeneity (I^2), the study random effect explained 41% of heterogeneity in the *a* dataset, and 30% in the MFR dataset.

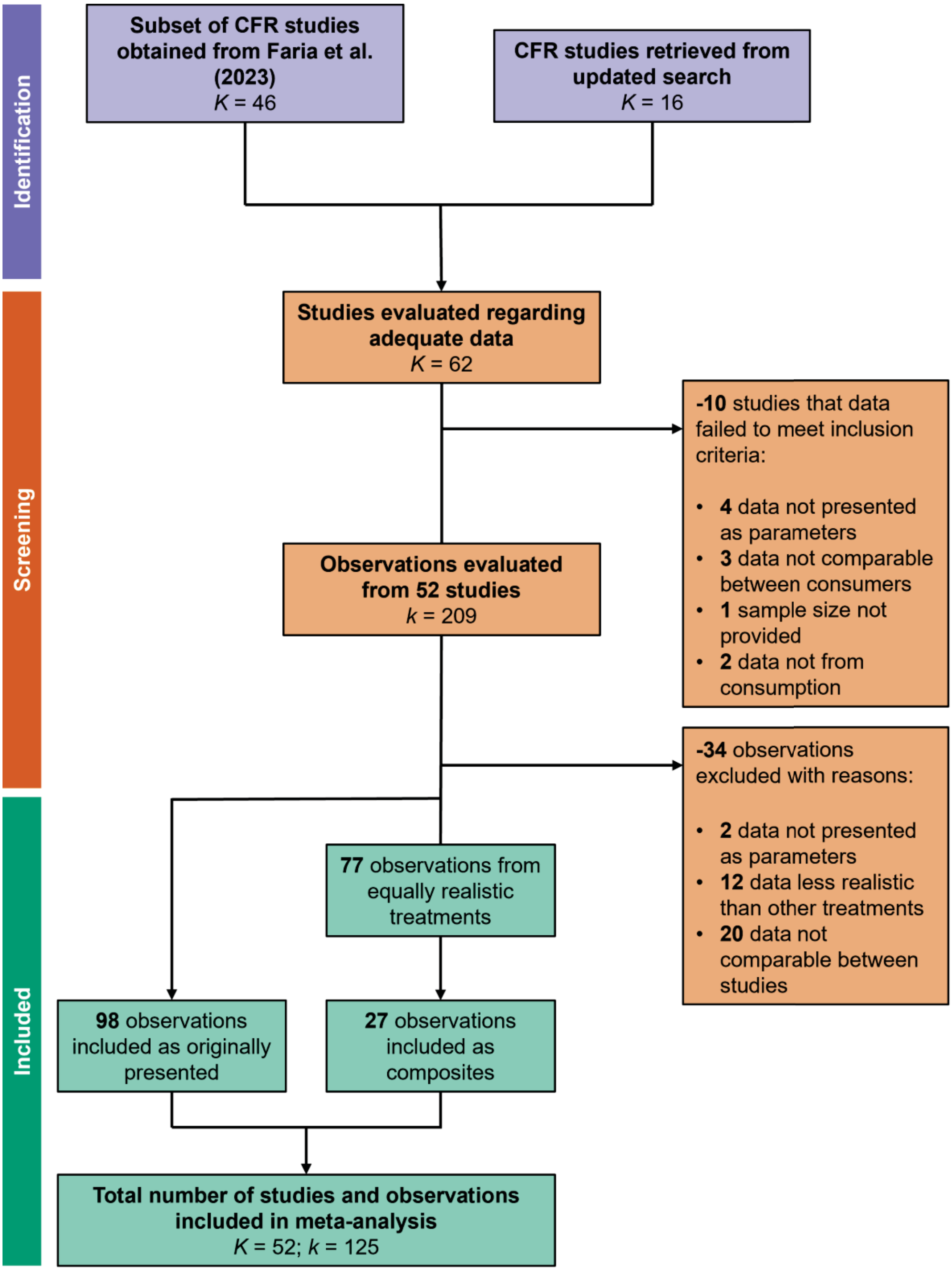


Figure 2. PRISMA flowchart showing the number of studies (*K*) that used the comparative functional response (CFR) approach and observations (*k*) as pairs of non-native and native consumers feeding on the same resource that were retrieved, screened and included in our final dataset.

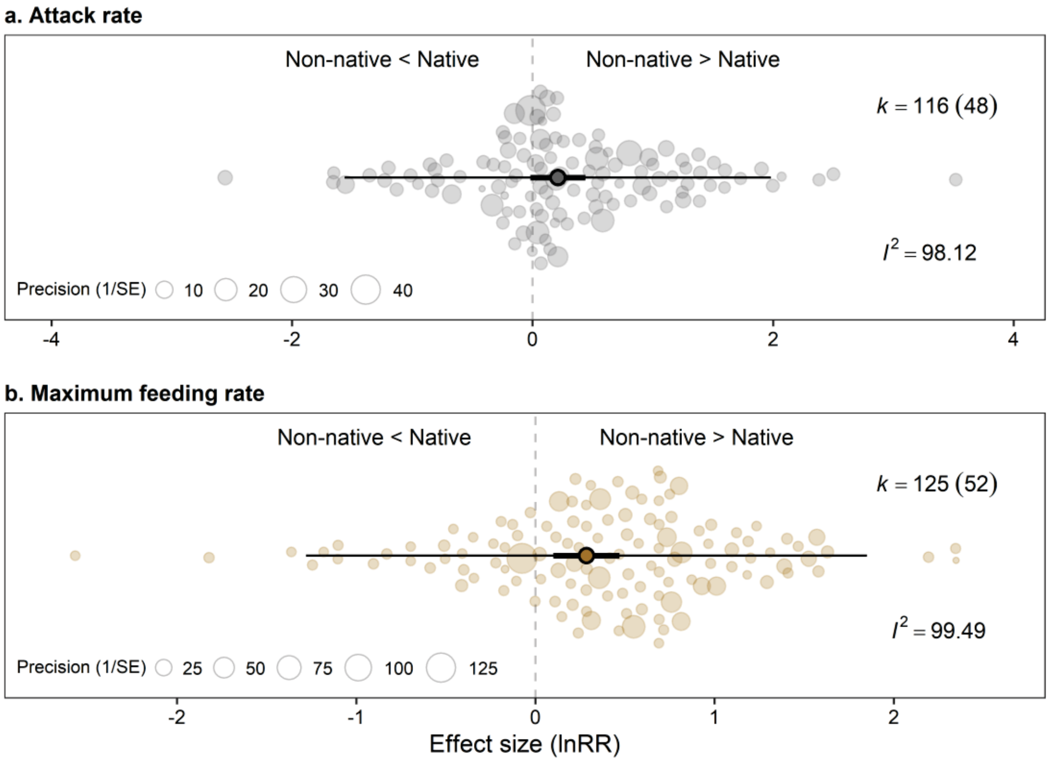


Figure 3. Orchard plots of the overall effect size (lnRR) obtained by our null multilevel meta-analysis model for both response variables: (a) attack rate and (b) maximum feeding rate. Positive effect sizes indicate that non-native consumers have higher functional response parameters than native consumers. The mean estimated effect size (solid filled circle) is considered statistically significant when the thick horizontal error bars (95% confidence intervals) do not cross the dashed line of zero. Thin horizontal whiskers indicate prediction intervals. *k* is the number of effect sizes followed by the number of studies in parentheses. I^2 depicts the total heterogeneity of the model.

Effect sizes of attack rate were not significantly positive regarding consumer taxonomic groups (Figure 4a). Regarding consumer primary diet, non-native carnivores presented a higher attack rate compared to native analogues (Table 2, Figure 4b); however, effect sizes did not differ significantly between different diet types (test of moderators: $F_{(2,45)} = 1.79$, $p = 0.17$). Non-native consumer invasiveness did not influence the effect size, as both invasive and non-invasive were not significantly different from zero (Figure 4c). Effect sizes of attack rate in freshwater habitats were significantly positive (Table 2, Figure 4d), and despite a negative tendency in terrestrial and marine habitats, effect sizes did not significantly differ between habitats ($F_{(2,45)} = 1.03$, $p = 0.36$). Effect sizes were not significantly different from zero regarding latitude of the native assemblage (Table 2, Figures 4e).

Molluscs, insects and crustaceans had significantly positive effect sizes of MFR (Table 2, Figure 5a); however, taxonomic groups did not differ significantly ($F_{(4,\ 47)} = 1.74$, $p =$

0.16). Carnivores did not have a significantly higher MFR compared to natives, but omnivores and herbivores did (Table 2, Figure 5b). Nevertheless, we found no significant differences among different diets' effect sizes ($F_{(2, 49)}$ = 2.35, *p* = 0.11). Invasive non-native consumers also presented higher effect sizes for MFR than their native comparators (Table 2, Figure 5c), while effect sizes did not differ significantly regarding invasiveness ($F_{(1, 123)}$ = 0.02, *p* = 0.9). As observed for attack rates, MFR was significantly positive only in freshwater habitats (Table 2, Figure 5d), while no significant differences in effect sizes were observed among habitats ($F_{(2, 49)}$ = 1.35, *p* = 0.27). Observations from tropical native assemblages were significantly positive (Table 2, Figure 5e) and also significantly different from observations of temperate regions ($F_{(1, 50)}$ = 5.08, *p* = 0.03).

Table 2. Mean estimated effect sizes for both response variables ($lnRR_a$: attack rate and $lnRR_{MFR}$: maximum feeding rate) and their corresponding 95% confidence intervals (CI), obtained for each group from univariate meta-regression models considering potential influential moderators.

	$lnRR_a$	**95% CI**	**$lnRR_{MFR}$**	**95% CI**
Consumer taxonomic group				
Arthropod	0.171	[-1.074 – 1.416]	0.216	[-0.592 – 1.024]
Crustacean	0.105	[-0.143 – 0.354]	0.302	[0.089 – 0.515]
Fish	0.351	[-0.027 – 0.729]	0.194	[-0.097 – 0.485]
Insect	0.452	[-0.250 – 1.154]	0.414	[0.068 – 0.760]
Mollusc	0.587	[-0.735 – 1.909]	1.042	[0.441 – 1.643]
Consumer primary diet				
Carnivore	0.517	[0.115 – 0.919]	0.177	[-0.238 – 0.591]
Herbivore	0.590	[-0.728 – 1.908]	1.004	[0.328 – 1.680]
Omnivore	0.106	[-0.131 – 0.344]	0.289	[0.099 – 0.479]
Non-native consumer invasiveness				
Invasive	0.214	[-0.016 – 0.444]	0.281	[0.083 – 0.479]
Non-invasive	0.256	[-0.254 – 0.766]	0.303	[-0.040 – 0.647]
Habitat				
Freshwater	0.287	[0.032 – 0.541]	0.341	[0.148 – 0.533]
Marine	-0.074	[-0.589 – 0.442]	-0.120	[-0.657 – 0.417]
Terrestrial	-0.116	[-1.147 – 0.915]	0.333	[-0.045 – 0.711]
Latitude of the native assemblage				
Temperate	0.176	[-0.081 – 0.433]	0.191	[-0.025 – 0.406]
Tropical	0.299	[-0.235 – 0.832]	0.607	[0.305 – 0.909]

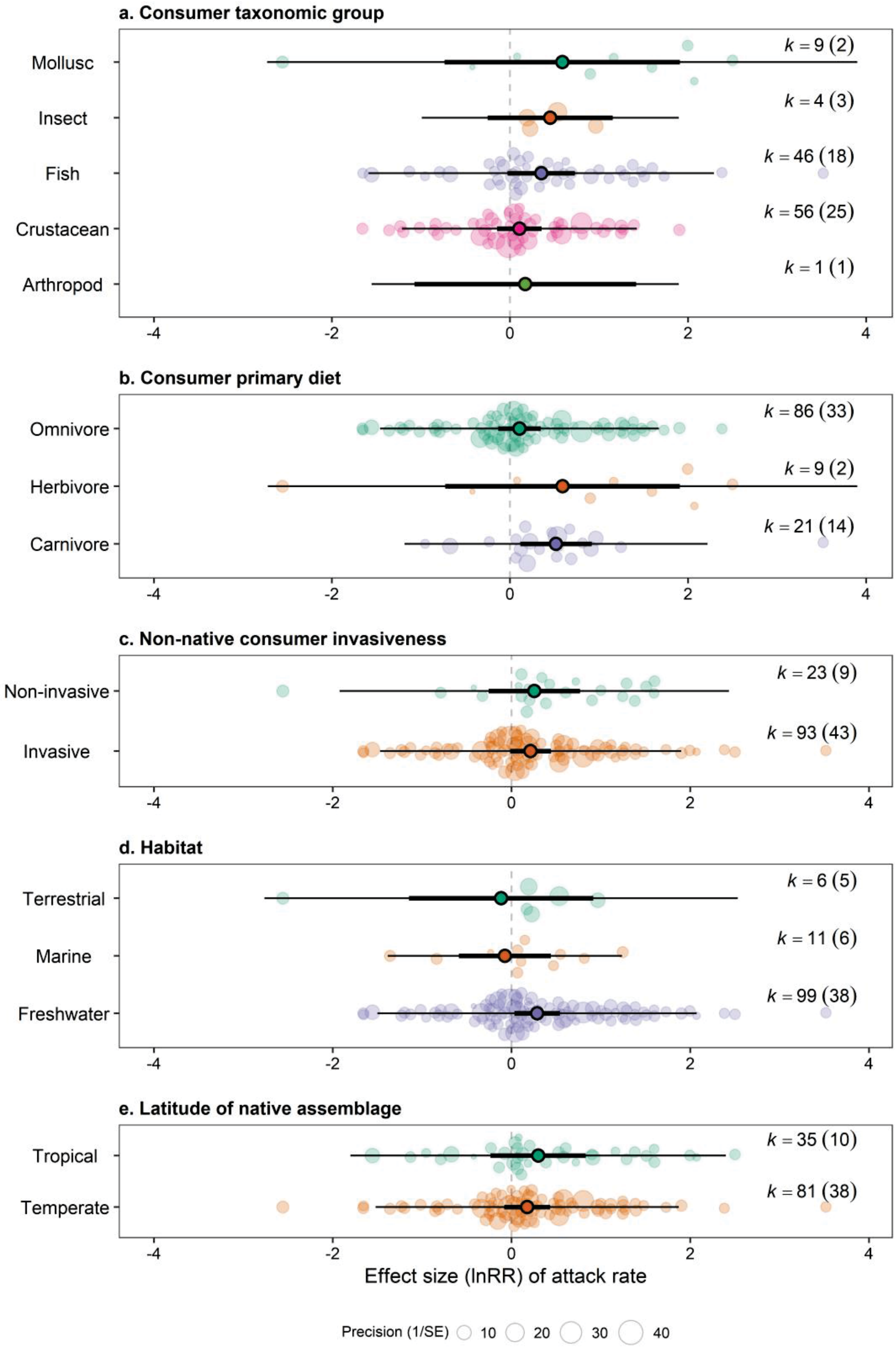


Figure 4. Orchard plots showing effect size (lnRR) estimates of attack rate from univariate meta-regressions with potentially influential moderators: (a) consumer taxonomic group, (b) consumer primary diet, (c) non-native consumer invasiveness, (d) habitat and (e) latitude of the native assemblage. Positive effect sizes indicate that non-native consumers have higher functional response parameters than native consumers in that group. Mean effects for each group (solid filled circles) are statistically significant when thick horizontal error bars (95% confidence intervals) do not cross the dashed line of zero. Thin horizontal whiskers indicate prediction intervals. *k* is the number of effect sizes followed by the number of studies in parentheses. Each shadowed circle represents individual effect sizes, scaled accordingly with their precision.

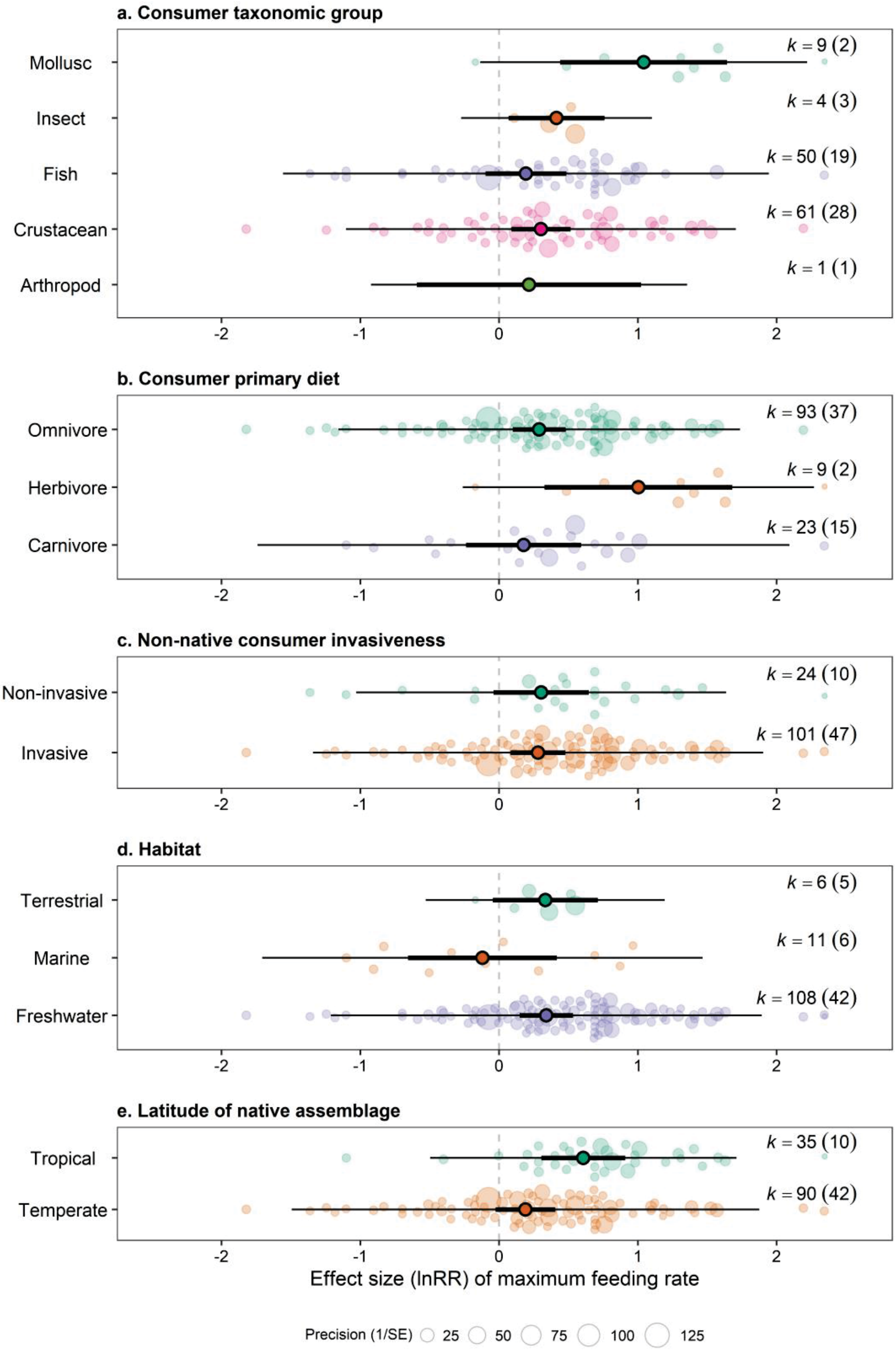


Figure 5. Orchard plots showing effect size (lnRR) estimates of maximum feeding rate from univariate meta-regressions with potentially influential moderators: (a) consumer taxonomic group, (b) consumer primary diet, (c) non-native consumer invasiveness, (d) habitat and (e) latitude of the native assemblage. Positive effect sizes indicate that non-native consumers have higher functional response parameters than native consumers in that group. Mean effects for each group (solid filled circles) are statistically significant when thick horizontal error bars (95% confidence intervals) do not cross the dashed line of zero. Thin horizontal whiskers indicate prediction intervals. *k* is the number of effect sizes followed by the number of studies in parentheses. Each shadowed circle represents individual effect sizes, scaled accordingly with their precision.

We did not find evidence that non-native consumers from a distinct genus of those in the native community have higher functional response parameters (Table 3, Figure 6). Actually, non-native consumers that share their genus with the native community had significantly positive effect sizes for MFR (Table 3, Figure 6b), with results differing in strength from consumers that do not share the same genus ($F_{(1,\,42)} = 4.99$, $p = 0.03$).

Table 3. Mean estimated effect sizes for both response variables ($\ln RR_a$: attack rate and $\ln RR_{MFR}$: maximum feeding rate) and their corresponding 95% confidence intervals (CI), considering taxonomic distinctiveness of the non-native consumer as a potential influential moderator.

	$\ln RR_a$	95% CI	$\ln RR_{MFR}$	95% CI
Non-native consumer of a distinct genus	0.278	[-0.143 – 0.698]	0.104	[-0.523 – 0.731]
Non-native consumer of a shared genus	0.006	[-0.514 – 0.526]	0.951	[0.082 – 1.82]

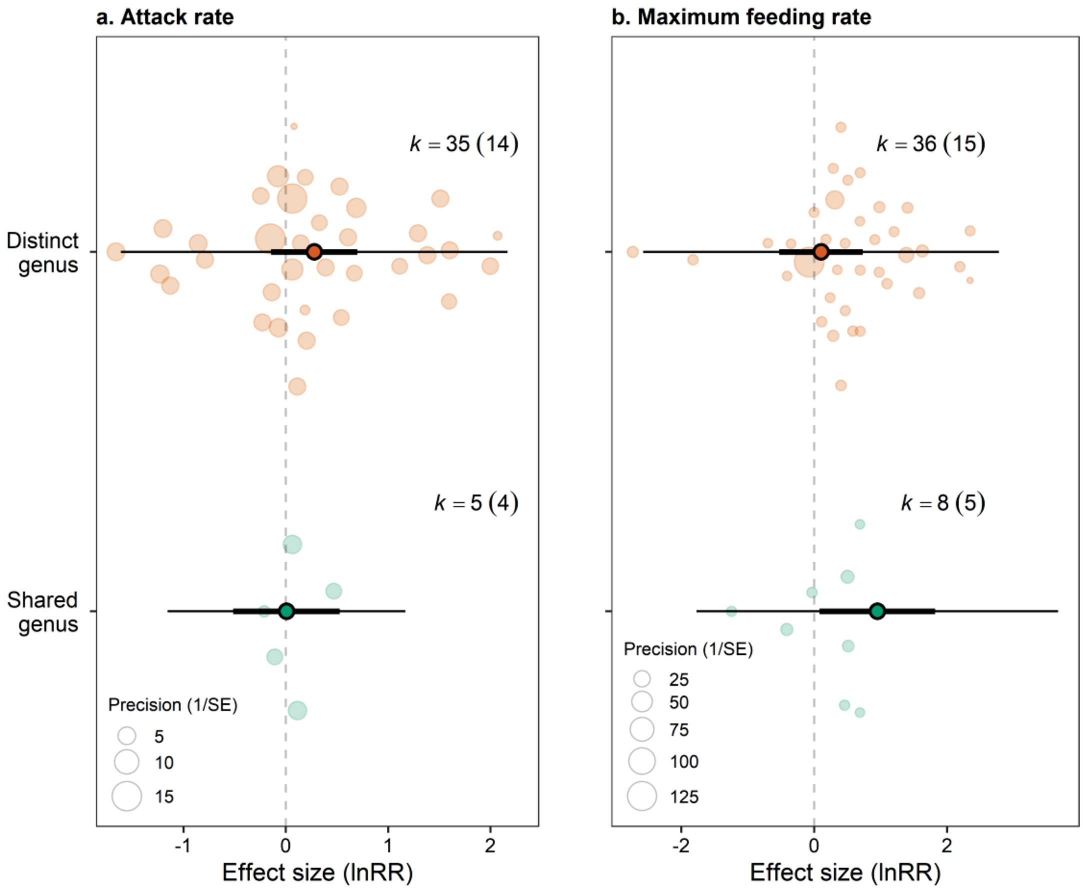


Figure 6. Orchard plots showing effect size (lnRR) estimates from univariate meta-regression considering taxonomic distinctiveness of the non-native consumer as an influential moderator, for both response variables: (a) attack rate and (b) maximum feeding rate. Positive effect sizes indicate that non-native consumers have higher functional response parameters than native consumers in that group. Mean effects for each group (solid filled circles) are statistically significant when thick horizontal error

bars (95% confidence intervals) do not cross the dashed line of zero. Thin horizontal whiskers indicate prediction intervals. *k* is the number of effect sizes followed by the number of studies in parentheses. Each shadowed circle represents individual effect sizes, scaled accordingly with their precision.

Only two effect sizes (*a* and MFR from the same observation pair) failed to meet the normality assumption calculated by Geary's test. The sensitivity analysis performed without these two effect sizes did not differ significantly from our original null model (Table S1; Supporting Information). Applying the "All Cases" method did not significantly change the results obtained using the "Missing Cases" method (i.e. similar estimates and 95% CI; Table S1). Finally, we obtained the same results using $\rho = 0.1$ and 0.9 as those originally obtained considering $\rho = 0.6$ (Table S1).

The intercept of our meta-regression testing for publication bias was not significant for both response variables (*a*: mean intercept = -0.591, $p = 0.22$; MFR: mean intercept = 0.128, $p = 0.75$), thus we did not find evidence of a publication bias using this method. Additionally, we can consider the mean estimate of this meta-regression as an adjusted estimate of our overall effect size (Table S1). Regarding *a*, the mean estimate changed to a higher value of 0.273 with 95% CI not crossing the zero line, and for MFR there was a subtle change from 0.285 to 0.295 (Table S1).

2.4 DISCUSSION

Many hypotheses in invasion science aim to explain the subset of successful non-native species that cause significant negative impacts in invaded ecosystems (Catford et al., 2009; Ricciardi et al., 2013), and it has been noted that non-native consumers are often more damaging than native species to resource populations (McKnight et al., 2016; Paolucci et al., 2013; Salo et al., 2007). Related to that, the Resource Consumption hypothesis posits that successful non-native species are able to use resources more efficiently than trophically analogous native species (Dick et al., 2014; Faria et al., 2023; Ricciardi et al., 2013). Here, we provide the largest quantitative test of this hypothesis to date using data from CFR studies. We found that, in general, non-native consumers have higher maximum feeding rates and a tendency of higher attack rates compared to native consumers, corroborating the hypothesis. Nevertheless, the consumptive impact of non-native species varies depending on other factors, such as their taxonomic group, primary diet and invasiveness, as well as with the ecosystem or habitat where the interaction takes place.

2.4.1 Feeding rates of non-native consumers are generally higher than trophically analogous native species

Attack rates were significantly higher only for non-native carnivores and in freshwater habitats, although tendencies were mostly positive in favour of non-native species. We found no differences between taxonomic groups and non-native invasiveness. These results reveal that, in general, non-native consumers do not differ in efficiency of consuming resources when these are at low densities. This aligns with two related hypotheses linked to resource availability: the Increased Resource Availability hypothesis, which states that the invasion success of non-native species increases with the availability of resources (Sher & Hyatt, 1999) and the Resource-Enemy Release hypothesis, which predicts that non-native species released from their natural enemies can spend more energy in reproduction, and likewise successfully invade when resources are highly available (Blumenthal, 2006). Both hypotheses are rooted in the idea of fluctuation of resources favouring non-native species over natives (Davis et al., 2000). At low availability of resources, native species could perform equally or better than more specialist non-native species, as they are well adapted to the conditions; however, when resource availability increases, for example in response to a disturbance, non-native species will likely outperform native species (Daehler, 2003). Although most of the studies demonstrating these hypotheses were performed with plants (Knauf et al., 2021; Liu & van Kleunen, 2017), these postulated mechanisms may also apply to animal consumers.

Conversely, maximum feeding rates were significantly higher overall, specifically for invertebrates (except arthropods), omnivores and herbivores, invasive non-native consumers, freshwater habitats and non-native consumers that shared the genus with the native community. Non-native invertebrates (except arthropods) presented higher MFR than native consumers, while this pattern was not observed for vertebrates, in line with the results obtained by Paolucci at al. (2013). Among invertebrates, molluscs presented the highest differential MFR, but results are mainly representative of two species of non-native herbivorous gastropods, the highly invasive *Pomacea canaliculata* (golden apple snail) and the non-invasive *Planorbarius corneus* (great ramshorn snail) preying on a diversity of macrophyte resources compared to the native snail *Bellamya aeruginosa* (Xu et al., 2016). Likewise, non-native omnivores and herbivores presented higher MFR compared to their native counterparts. This result, however, should be interpreted in line with the usual experimental setting applied in functional response studies. In general, experiments are performed offering the consumer a single type of prey in the absence of alternative resources, which may not be realistic for omnivores that feed on a wide range of items (Maselou et al., 2014; Médoc et al., 2018). Nevertheless, their capacity for consuming significantly more than native omnivores when resources are abundant reveal their opportunistic habits, an important trait in successful invasive species (Romanuk et al., 2009; Vatland & Budy, 2007). Herbivores represented by molluscs presented the highest MFR contributing to the body of evidence that non-native snails are highly efficient consumers when resources are abundant (Liu et al., 2021; Morrison & Hay, 2011).

We found that invasive non-native species have significantly higher MFR than other non-native species, while no differences were observed for attack rates. Although previous reviews have not found a strong relationship between a non-native species' invasiveness and its impact on the native biota (Ricciardi & Cohen, 2007), these results agree with the indication that invasiveness and availability of resources in the invaded site are strongly connected (Hui et al., 2016). When resources are abundant, invasive non-native species tend to perform better than non-invasive or native species given the greater opportunity niche created by more resources, consistent with the fluctuating resource hypothesis (Davis et al., 2000; Hui et al., 2016). For instance, this pattern was clear for herbivorous snails in a study demonstrating that non-invasive non-native consumers consistently had intermediate functional and numerical responses when compared to invasive and native species of snails, suggesting that CFR studies could also be applied to predict the invasiveness of non-native species (Xu et al., 2016).

2.4.2 Differences in consumption rates are greater in freshwater habitats, in the tropics and in absence of taxonomic distinctiveness

We found that the effect size of non-native consumer attack and feeding rates are significantly greater than zero only in freshwater habitats and not in marine and terrestrial habitats, in accordance with our related prediction. The greater degree of isolation in lakes and river systems creates an evolutionary isolation and thus greater naïveté of their populations compared with continental terrestrial and marine habitats (Cox & Lima, 2006). An interesting subsequent question surrounds whether this effect lessens with time since invasion as communities adapt and novelty lessens. Our results also align with the greater proportion of high-impact invasive species found in freshwater compared to marine habitats (Ricciardi & Kipp, 2008). Unfortunately, there are no studies from terrestrial islands to check the effect of insularity in this type of habitat too. Regarding the latitude of the native assemblage, our results were contrary to expectations, with significant differences in the MFR of non-native consumers that are introduced to tropical and sub-tropical latitudes. The stronger predation pressure in the tropics due to great diversity does not seem to provide a protection against novel consumers as anticipated (Freestone et al., 2021). In fact, as there are more specialised interactions in the tropics, prey might have evolved specific defences against their native predators, which are likely not effective against novel predators since they have a low level of eco-evolutionary experience in interacting with them (Saul & Jeschke, 2015). Nevertheless, the majority of the observations used in our meta-analysis come from temperate regions (72%), which creates a bias for this region, a pattern commonly observed in invasion ecology studies (Chong et al., 2021; Pyšek et al., 2008) and one that impedes a balanced interpretation of these results.

We expected that non-native consumers from a distinct genus would be more impactful to resources due to the lack of shared evolutionary history that make prey more vulnerable to them (Anton et al., 2020; Ricciardi & Atkinson, 2004). However, we found that MFRs of consumers that share a genus with the native community were significantly higher compared to native analogues. This could be explained by the alternative ‘pre-adaptation’ hypothesis: consumers more closely related to trophically analogous natives are more likely to perform well owing to pre-adaptation to an environment and available food resources (Ricciardi & Mottiar, 2006). Indeed, Ma et al. (2016) found that non-native species with greater impacts on native communities tend to be more closely related to natives at the local scale, consistent with the aforementioned hypothesis. Taxonomic distinctiveness, driven by prey naïveté and lack of resident enemies, might be most pronounced when the invader is a top predator (therefore lacking a native trophic analogue) or some other uncontrolled consumer (e.g. zebra mussels) (Ricciardi et al., 2013). From a methodological stance, the presence of common genera among native assemblages could improve native comparator selection and representativeness, thus potentially accentuating differences from analogous non-natives. Given our limited sample size with a higher proportion of consumers from a distinct genus than those from the native community (82%), these results cannot firmly refute any hypothesis.

2.4.3 Future directions and concluding remarks

The CFR approach was originally designed as a tool to predict the consumptive impact of newly introduced species with no history of invasion elsewhere (Dick et al., 2014, 2017). Here, we used studies that compared native versus non-native species with no explicit consideration of non-native negative impacts in the field. Therefore, a subset of invaders with demonstrable impact would likely show stronger effect sizes. We recognize that the selection of most established non-native consumers assessed in the studies was likely motivated by impact prior, but our results might still be conservative. Particularly because in some study systems, extreme ecological novelty results in a total paucity of available wild analogous comparators. We also note that impact can change over time (e.g. because novelty diminishes over time) (Saul & Jeschke, 2015), but few studies state the time period since the non-native study species was introduced, or assess changes in FR parameters over a long timescale, and our results might therefore vary according to this aspect (Crystal-Ornelas & Lockwood, 2020; Strayer et al., 2006). Indeed, it was observed for invasive plants that their negative effects on the native community decline after longer periods of time (Iacarella, Mankiewicz, et al., 2015). A study assessing the *per capita* effects of a known invasive predator *Hemimysis anomala* (bloody red mysid shrimp) from two different sites and times-since-introduction found that feeding rates were higher at the invasion front (i.e. a recently invaded site) (Iacarella, Dick, et al., 2015). This highlights the need for future studies to consider time since introduction and spatial factors in their analysis, clearly stating if they are evaluating a novel or established non-native population, since results may vary related to that.

Our findings that non-native consumers are more efficient than native counterparts, particularly in high resource availability scenarios has important implications for management and conservation. Greater exploitation of resources by non-natives can lead to an increase in their numerical response (i.e. abundance) in the long term, increasing competition and predation pressure on native biota, which may yet result in boom-bust dynamics that complicate our ability to control non-native populations (Strayer et al., 2016). Still this increased availability of resources can be the result of a non-native species itself, as in cases where an abundant non-native prey sustains a non-native predator population (Pope et al., 2008; Simberloff & Von Holle, 1999). What remains to be tested is if increased availability of resources coupled with multiple NNS will always result in more impact, or if other mechanisms, such as indirect effects, can prevent it. In other words, are highly resource abundant communities more susceptible to impacts than previously anticipated? Or does higher resource availability actually negate the impact, just because all species will have enough to consume (even tough non-natives will consume at higher rates)? In this case, we encourage more research by applying FR to reveal such feedback processes, informing best management practices.

So far, invasion science has relied on invasion history and assessment protocols to identify non-native species that should be managed (Faria et al., 2023); nonetheless, as the number of introductions worldwide continues to raise, lack of data will impede us to apply these tools to all non-native species (Seebens et al., 2021). To avoid higher rates of biodiversity loss that will result in a homogenised world with a few winner species (McKinney & Lockwood, 1999), our focus should be on prevention rather than remediation (Leung et al., 2002). As many invaders negative impacts are due to competition for or consumption of resources, quantifying such impacts in terms of resource use is a practical way of predicting and therefore proactively targeting the most likely to cause harm (Dick et al., 2017). Our meta-analysis corroborates this, showing that non-native consumers indeed present higher feeding rates, and in some cases greater attack rates, supporting the use of the CFR approach as a rapid risk assessment tool for existing and emerging non-native species negative impacts worldwide.

Acknowledgements

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

References

Anton, A., Geraldi, N. R., Ricciardi, A., & Dick, J. T. A. (2020). Global determinants of prey naiveté to exotic predators. *Proceedings of the Royal Society B*, *287*. https://doi.org/10.1098/rspb.2019.2978

Bellard, C., Cassey, P., & Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology Letters*, *12*, 1–4. https://doi.org/10.1098/rsbl.2015.0623

Blackburn, T. M., Bellard, C., & Ricciardi, A. (2019). Alien versus native species as drivers of recent extinctions. *Frontiers in Ecology and the Environment*, *17*(4), 203–207. https://doi.org/10.1002/fee.2020

Blumenthal, D. M. (2006). Interactions between resource availability and enemy release in plant invasion. *Ecology Letters*, *9*(7), 887–895. https://doi.org/10.1111/j.1461-0248.2006.00934.x

Buckley, Y. M., & Catford, J. A. (2016). Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *Journal of Ecology*, *104*(1), 4–17. https://doi.org/10.1111/1365-2745.12501

Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, *15*(1), 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Chong, K. Y., Corlett, R. T., Nuñez, M. A., Chiu, J. H., Courchamp, F., Dawson, W., Kuebbing, S., Liebhold, A. M., Padmanaba, M., Souza, L., Andersen, K. M., Fei, S., Lee, B. P. Y.-H., Lum, S., Luskin, M. S., Ngo, K. M., & Wardle, D. A. (2021). Are Terrestrial Biological Invasions Different in the Tropics? *Annual Review of Ecology, Evolution, and Systematics*, *52*(1), 291–314. https://doi.org/10.1146/annurev-ecolsys-012021-095454

Cox, J. G., & Lima, S. L. (2006). Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology and Evolution*, *21*(12), 674–680. https://doi.org/10.1016/j.tree.2006.07.011

Crystal-Ornelas, R., & Lockwood, J. L. (2020). The ‘known unknowns’ of invasive species impact measurement. *Biological Invasions*, *22*(4), 1513–1525. https://doi.org/10.1007/s10530-020-02200-0

Cuthbert, R. N., Dickey, J. W. E., Coughlan, N. E., Joyce, P. W. S., & Dick, J. T. A. (2019). The Functional Response Ratio (FRR): Advancing comparative metrics for predicting the ecological impacts of invasive alien species. *Biological Invasions*, *21*(8), 2543–2547. https://doi.org/10.1007/s10530-019-02002-z

Daehler, C. C. (2003). Performance Comparisons of Co-Occurring Native and Alien Invasive Plants: Implications for Conservation and Restoration. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 183–211.

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

DeLong, J. P. (2021). *Predator ecology: Evolutionary ecology of the functional response*. Oxford University Press.

Dick, J. T. A., Alexander, M. E., Jeschke, J., Ricciardi, A., MacIsaac, H. J., Robinson, T. B., Kumschick, S., Weyl, O. L. F., Dunn, A. M., Hatcher, M. J., Paterson, R. A., Farnsworth, K. D., & Richardson, D. M. (2014). Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions*, *16*(4), 735–753. https://doi.org/10.1007/s10530-013-0550-8

Dick, J. T. A., Alexander, M. E., Ricciardi, A., Laverty, C., Downey, P. O., Xu, M., Jeschke, J., Saul, W.C., Hill, M. P., Wasserman, R., Barrios-O'Neill, D., Weyl, O. L. F., & Shaw, R. H. (2017). Functional responses can unify invasion ecology. *Biological Invasions*, *19*(5), 1667–1672. https://doi.org/10.1007/s10530-016-1355-3

Dick, J. T. A., Gallagher, K., Avlijas, S., Clarke, H. C., Lewis, S. E., Leung, S., Minchin, D., Caffrey, J., Alexander, M. E., Maguire, C., Harrod, C., Reid, N., Haddaway, N. R., Farnsworth, K. D., Penk, M., & Ricciardi, A. (2013). Ecological impacts of an invasive predator explained and predicted by comparative functional responses. *Biological Invasions*, *15*(4), 837–846. https://doi.org/10.1007/s10530-012-0332-8

Dickey, J. W. E., Cuthbert, R. N., Steffen, G. T., Dick, J. T. A., & Briski, E. (2021). Sea freshening may drive the ecological impacts of emerging and existing invasive non-native species. *Diversity and Distributions*, *27*(1), 144–156. https://doi.org/10.1111/ddi.13178

Faria, L., Cuthbert, R. N., Dickey, J. W. E., Jeschke, J. M., Ricciardi, A., Dick, J. T. A., & Vitule, J. R. S. (2023). The rise of the Functional Response in invasion science: A systematic review. *NeoBiota*, *85*, 43–79. https://doi.org/10.3897/neobiota.85.98902

Franco, A. C. S., García-Berthou, E., & Santos, L. N. (2021). Ecological impacts of an invasive top predator fish across South America. *Science of The Total Environment*, 761, 143296. https://doi.org/10.1016/j.scitotenv.2020.143296

Freestone, A. L., Torchin, M. E., Jurgens, L. J., Bonfim, M., López, D. P., Repetto, M. F., Schlöder, C., Sewall, B. J., & Ruiz, G. M. (2021). Stronger predation intensity and impact on prey communities in the tropics. *Ecology*, *102*(8), e03428. https://doi.org/10.1002/ecy.3428

Funk, J. L., & Vitousek, P. M. (2007). Resource-use efficiency and plant invasion in low-resource systems. *Nature*, *446*(7139), 1079–1081. https://doi.org/10.1038/nature05719

Goudswaard, P. C., Witte, F., & Katunzi, E. F. B. (2002). The tilapiine fish stock of Lake Victoria before and after the Nile perch upsurge. *Journal of Fish Biology*, *60*(4), 838–856. https://doi.org/10.1111/j.1095-8649.2002.tb02413.x

Hassell, M. P. (1978). *The Dynamics of Arthopod Predator-Prey Systems* (Vol. 13). Princeton University Press.

Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The Meta-Analysis of Response Ratios in Experimental Ecology. *Ecology*, *80*(4), 1150–1156. https://doi.org/10.2307/177062

Higgins, J. P. T., & Thompson, S. G. (2002). Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine*, *21*(11), 1539–1558. https://doi.org/10.1002/sim.1186

Holling, C. S. (1959a). Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, *91*(7), 385–398. https://doi.org/10.4039/Ent91385-7

Holling, C. S. (1959b). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist*, *91*(5), 234–261. https://doi.org/10.4039/Ent91293-5

Hui, C., Richardson, D. M., Landi, P., Minoarivelo, H. O., Garnas, J., & Roy, H. E. (2016). Defining invasiveness and invasibility in ecological networks. *Biological Invasions*, *18*(4), 971–983. https://doi.org/10.1007/s10530-016-1076-7

Iacarella, J. C., Dick, J. T. A., & Ricciardi, A. (2015). A spatio-temporal contrast of the predatory impact of an invasive freshwater crustacean. *Diversity and Distributions*, *21*(7), 803–812. https://doi.org/10.1111/ddi.12318

Iacarella, J. C., Mankiewicz, P. S., & Ricciardi, A. (2015). Negative competitive effects of invasive plants change with time since invasion. *Ecosphere*, *6*(7), art123. https://doi.org/10.1890/ES15-00147.1

IPBES. (2023). *Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Roy, H. E., Pauchard, A., Stoett, P., Renard Truong, T., Bacher, S., Galil, B. S., Hulme, P. E., Ikeda, T., Sankaran, K. V., McGeoch, M. A., Meyerson, L. A., Nuñez, M. A., Ordonez, A., Rahlao, S. J., Schwindt, E., Seebens, H., Sheppard, A. W., and Vandvik, V. https://doi.org/10.5281/zenodo.7430692

Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D. E., Coscieme, L., Golden, A. S., Guerra, C. A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., & Purvis, A. (2022). The direct drivers of recent global anthropogenic biodiversity loss. *Science Advances*, *8*(45), eabm9982. https://doi.org/10.1126/sciadv.abm9982

Jeschke, J. M., Kopp, M., & Tollrian, R. (2002). Predator functional responses: Discriminating between handling and digesting prey. *Ecological Monographs*, *72*(1), 95–112. https://doi.org/10.2307/3100087

Jeschke, J. M., Kopp, M., & Tollrian, R. (2004). Consumer-food systems: Why type I functional responses are exclusive to filter feeders. *Biological Reviews*, *79*, 337–349. https://doi.org/10.1017/S1464793103006286

Kalinkat, G., Rall, B. C., Uiterwaal, S. F., & Uszko, W. (2023). Empirical evidence of type III functional responses and why it remains rare. *Frontiers in Ecology and Evolution*, *11*. https://doi.org/10.3389/fevo.2023.1033818

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, *17*(4), 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0

Knauf, A., Litton, C., Cole, R., Sparks, J., Giardina, C., Gerow, K., & Quiñones-Santiago, M. (2021). Nutrient use strategy and not competition determines native and invasive species response to changes in soil nutrient availability. *Restoration Ecology*, *29*. https://doi.org/10.1111/rec.13374

Kruuk, H., & Goudswaard, P. C. (1990). Effects of changes in fish populations in Lake Victoria on the food of otters (*Lutra maculicollis* Schinz and *Aonyx capensis* Lichtenstein). *African Journal of Ecology*, 28(4), 322–329. https://doi.org/10.1111/j.1365-2028.1990.tb01167.x

Lajeunesse, M. J. (2015). Bias and correction for the log response ratio in ecological meta-analysis. *Ecology*, *96*(8), 2056–2063. https://doi.org/10.1890/14-2402.1

Leung, B., Lodge, D. M., Finnof, D., Shogren, J. F., Lewis, M. E., & Lamberti, G. (2002). An ounce of prevention or a pound of cure: Bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society B*, *269*, 2407–2413. https://doi.org/10.1098/rspb.2002.2179

Liu, Y., He, L., Hilt, S., Wang, R., Zhang, H., & Ge, G. (2021). Shallow lakes at risk: Nutrient enrichment enhances top-down control of macrophytes by invasive herbivorous snails. *Freshwater Biology*, *66*(3), 436–446. https://doi.org/10.1111/fwb.13649

Liu, Y., & van Kleunen, M. (2017). Responses of common and rare aliens and natives to nutrient availability and fluctuations. *Journal of Ecology*, *105*(4), 1111–1122. https://doi.org/10.1111/1365-2745.12733

Lockwood, J. L., Hoopes, M., & Marchetti, M. (2007). *Invasion Ecology* (1st ed.). Blackwell Publishing.

Ma, C., Li, S. peng, Pu, Z., Tan, J., Liu, M., Zhou, J., Li, H., & Jiang, L. (2016). Different effects of invader-native phylogenetic relatedness on invasion success and impact: A meta-analysis of Darwin's naturalization hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1838). https://doi.org/10.1098/rspb.2016.0663

Maselou, D. A., Perdikis, D. Ch., Sabelis, M. W., & Fantinou, A. A. (2014). Use of plant resources by an omnivorous predator and the consequences for effective predation. *Biological Control*, *79*, 92–100. https://doi.org/10.1016/j.biocontrol.2014.09.002

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, *14*(11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

McKnight, E., García-Berthou, E., Srean, P., & Rius, M. (2016). Global meta-analysis of native and nonindigenous trophic traits in aquatic ecosystems. *Global Change Biology*, *23*(5), 1861–1870. https://doi.org/10.1111/gcb.13524

Médoc, V., Thuillier, L., & Spataro, T. (2018). Opportunistic omnivory impairs our ability to predict invasive species impacts from functional response comparisons. *Biological Invasions*, *20*, 1307–1319. https://doi.org/10.1007/s10530-017-1628-5

Mengersen, K., Jennions, M. D., & Schmid, C. H. (2013). Statistical Models for the Meta-analysis of Nonindependent Data. In *Handbook of Meta-analysis in Ecology and Evolution* (pp. 255–283). Princeton University Press.

Morrison, W. E., & Hay, M. E. (2011). Feeding and growth of native, invasive and non-invasive alien apple snails (Ampullariidae) in the United States: Invasives eat more and grow more. *Biological Invasions*, *13*(4), 945–955. https://doi.org/10.1007/S10530-010-9881-X/FIGURES/6

Murdoch, W. W., & Oaten, A. (1975). Predation and population stability. *Advances in Ecological Research*, *9*, 1–131. https://doi.org/10.1016/S0065-2504(08)60288-3

Nakagawa, S., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W. A., Parker, T. H., Sánchez-Tójar, A., Yang, Y., & O'Dea, R. E. (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution*, *13*(1), 4–21. https://doi.org/10.1111/2041-210X.13724

Nakagawa, S., Lagisz, M., O'Dea, R. E., Pottier, P., Rutkowska, J., Senior, A. M., Yang, Y., & Noble, D. W. A. (2023). orchaRd 2.0: An R package for visualising meta-analyses with orchard plots. *Methods in Ecology and Evolution*, *14*(8), 2003–2010. https://doi.org/10.1111/2041-210X.14152

Nakagawa, S., Noble, D. W. A., Lagisz, M., Spake, R., Viechtbauer, W., & Senior, A. M. (2023). A robust and readily implementable method for the meta-analysis of response ratios with and without missing standard deviations. *Ecology Letters*, *26*(2), 232–244. https://doi.org/10.1111/ele.14144

Nakagawa, S., Yang, Y., Macartney, E. L., Spake, R., & Lagisz, M. (2023). Quantitative evidence synthesis: A practical guide on meta-analysis, meta-regression, and publication bias tests for environmental sciences. *Environmental Evidence*, *12*(1), 8. https://doi.org/10.1186/s13750-023-00301-6

Noble, D. W. A., Lagisz, M., O'dea, R. E., & Nakagawa, S. (2017). Nonindependence and sensitivity analyses in ecological and evolutionary meta-analyses. *Molecular Ecology*, *26*(9), 2410–2425. https://doi.org/10.1111/mec.14031

Paolucci, E. M., MacIsaac, H. J., & Ricciardi, A. (2013). Origin matters: Alien consumers inflict greater damage on prey populations than do native consumers. *Diversity and Distributions*, *19*, 988–995. https://doi.org/10.1111/ddi.12073

Pelicice, F. M., & Agostinho, A. A. (2009). Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. *Biological Invasions*, 11, 1789–1801. https://doi.org/10.1007/s10530-008-9358-3

Pelicice, F. M., Latini, J. D., & Agostinho, A. A. (2015). Fish fauna disassembly after the introduction of a voracious predator: Main drivers and the role of the invader's demography. *Hydrobiologia*, 746(1), 271–283. https://doi.org/10.1007/s10750-014-1911-8

Pustejovsky, J. E., & Tipton, E. (2022). Meta-analysis with Robust Variance Estimation: Expanding the Range of Working Models. *Prevention Science*, *23*(3), 425–438. https://doi.org/10.1007/s11121-021-01246-3

Pyšek, P., Richardson, D. M., Pergl, J., Jarošík, V., Sixtová, Z., & Weber, E. (2008). Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution*, *23*(5), 237–244. https://doi.org/10.1016/j.tree.2008.02.002

R Core Team. (2023). *R: A language and environment for statistical computing* [Computer software]. R Foundation for Statistical Computing. https://www.r-project.org/

Ricciardi, A., & Atkinson, S. K. (2004). Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecology Letters*, *7*, 781–784. https://doi.org/10.1111/j.1461-0248.2004.00642.x

Ricciardi, A., & Cohen, J. (2007). The invasiveness of an introduced species does not predict its impact. *Biological Invasions*, *9*(3), 309–315. https://doi.org/10.1007/s10530-006-9034-4

Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs*, *83*(3), 263–282. https://doi.org/10.1890/13-0183.1

Ricciardi, A., Iacarella, J. C., Aldridge, D. C., Blackburn, T. M., Carlton, J. T., Catford, J. A., Dick, J. T. A., Hulme, P. E., Jeschke, J. M., Liebhold, A. M., Lockwood, J. L., MacIsaac, H. J., Meyerson, L. A., Pyšek, P., Richardson, D. M., Ruiz, G. M., Simberloff, D., Vilà, M., & Wardle, D. A. (2021). Four priority areas to advance invasion science in the face of rapid environmental change. *Environmental Reviews*, *29*(2), 119–141. https://doi.org/10.1139/er-2020-0088

Ricciardi, A., & Kipp, R. (2008). Predicting the number of ecologically harmful exotic species in an aquatic system. *Diversity and Distributions*, *14*(2), 374–380. https://doi.org/10.1111/j.1472-4642.2007.00451.x

Ricciardi, A., & Mottiar, M. (2006). Does Darwin's naturalization hypothesis explain fish invasions? *Biological Invasions*, *8*(6), 1403–1407. https://doi.org/10.1007/s10530-006-0005-6

Romanuk, T. N., Zhou, Y., Brose, U., Berlow, E. L., Williams, R. J., & Martinez, N. D. (2009). Predicting invasion success in complex ecological networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1524), 1743–1754. https://doi.org/10.1098/rstb.2008.0286

Rubio-Aparicio, M., López-López, J. A., Viechtbauer, W., Marín-Martínez, F., Botella, J., & Sánchez-Meca, J. (2020). Testing Categorical Moderators in Mixed-Effects Meta-analysis in the Presence of Heteroscedasticity. *The Journal of Experimental Education*, *88*(2), 288–310. https://doi.org/10.1080/00220973.2018.1561404

Salo, P., Korpimäki, E., Banks, P. B., Nordström, M., & Dickman, C. R. (2007). Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B*, *274*, 1237–1243. https://doi.org/10.1098/rspb.2006.0444

Saul, W. C., & Jeschke, J. (2015). Eco-evolutionary experience in novel species interactions. *Ecology Letters*, *18*(3), 236–245. https://doi.org/10.1111/ele.12408

Seebens, H., Bacher, S., Blackburn, T. M., Capinha, C., Dawson, W., Dullinger, S., Genovesi, P., Hulme, P. E., van Kleunen, M., Kühn, I., Jeschke, J. M., Lenzner, B., Liebhold, A. M., Pattison, Z., Pergl, J., Pyšek, P., Winter, M., & Essl, F. (2021). Projecting the continental accumulation of alien species through to 2050. *Global Change Biology*, *27*(5), 970–982. https://doi.org/10.1111/GCB.15333

Sher, A. A., & Hyatt, L. A. (1999). The Disturbed Resource-Flux Invasion Matrix: A New Framework for Patterns of Plant Invasion. *Biological Invasions*, *1*(2), 107–114. https://doi.org/10.1023/A:1010050420466

Solomon, M. E. (1949). The natural control of animal populations. *Journal of Animal Ecology*, *18*(1), 1–35. https://doi.org/10.2307/1578

Strayer, D. L., Eviner, V. T., Jeschke, J. M., & Pace, M. L. (2006). Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution*, *21*(11), 645–651. https://doi.org/10.1016/j.tree.2006.07.007

Tanner-Smith, E. E., & Tipton, E. (2014). Robust variance estimation with dependent effect sizes: Practical considerations including a software tutorial in Stata and SPSS: Robust variance estimation. *Research Synthesis Methods*, *5*(1), 13–30. https://doi.org/10.1002/jrsm.1091

Vatland, S., & Budy, P. (2007). Predicting the invasion success of an introduced omnivore in a large, heterogeneous reservoir. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(10), 1329–1345. https://doi.org/10.1139/f07-100

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*(3), 1–48.

Xu, M., Mu, X., Dick, J. T. A., Fang, M., Gu, D., Luo, D., Zhang, J., Luo, J., & Hu, Y. (2016). Comparative functional responses predict the invasiveness and ecological impacts of alien herbivorous snails. *PLoS ONE*, *11*(1), e0147017. https://doi.org/10.1371/journal.pone.0147017

Appendix – Data sources

Alexander, M. E., Dick, J. T. A., Weyl, O. L. F., Robinson, T. B., & Richardson, D. M. (2014). Existing and emerging high impact invasive species are characterized by higher functional responses than natives. *Biology Letters*, *10*, 20130946. https://doi.org/10.1098/rsbl.2013.0946

Barrios-O'Neill, D., Dick, J. T. A., Emmerson, M. C., Ricciardi, A., & MacIsaac, H. J. (2015). Predator-free space, functional responses and biological invasions. *Functional Ecology*, *29*(3), 377–384. https://doi.org/10.1111/1365-2435.12347

Barrios-O'Neill, D., Dick, J. T. A., Emmerson, M. C., Ricciardi, A., MacIsaac, H. J., Alexander, M. E., & Bovy, H. C. (2014). Fortune favours the bold: A higher predator reduces the impact of a native but not an invasive intermediate predator. *Journal of Animal Ecology*, *83*(3), 693–701. https://doi.org/10.1111/1365-2656.12155

Barrios-O’Neill, D., Dick, J. T. A., Ricciardi, A., MacIsaac, H. J., & Emmerson, M. C. (2014). Deep impact: *In situ* functional responses reveal context-dependent interactions between vertically migrating invasive and native mesopredators and shared prey. *Freshwater Biology*, *59*(10), 2194–2203. https://doi.org/10.1111/fwb.12423

Boets, P., Laverty, C., Fukuda, S., Verreycken, H., Green, K., Britton, R. J., … Dick, J. T. A. (2019). Intra- and intercontinental variation in the functional responses of a high impact alien invasive fish. *Biological Invasions*, *21*, 1751–1762. https://doi.org/10.1007/s10530-019-01932-y

Bollache, L., Dick, J. T. A., Farnsworth, K. D., & Montgomery, W. I. (2008). Comparison of the functional responses of invasive and native amphipods. *Biology Letters*, *4*(2), 166–169. https://doi.org/10.1098/rsbl.2007.0554

Bovy, H. C., Barrios-O’Neill, D., Emmerson, M. C., Aldridge, D. C., & Dick, J. T. A. (2015). Predicting the predatory impacts of the “demon shrimp” *Dikerogammarus haemobaphes*, on native and previously introduced species. *Biological Invasions*, *17*(2), 597–607. https://doi.org/10.1007/s10530-014-0751-9

Britton, J. R., Roberts, C. G., Trigo, F. A., Nolan, E. T., & De Santis, V. (2019). Predicting the ecological impacts of an alien invader: Experimental approaches reveal the trophic consequences of competition. *Journal of Animal Ecology*, *88*, 1066–1078. https://doi.org/10.1111/1365-2656.12996

Bunke, M., Dick, J. T. A., Hatcher, M. J., & Dunn, A. M. (2019). Parasites influence cannibalistic and predatory interactions within and between native and invasive amphipods. *Diseases of Aquatic Organisms*, *136*(1), 79–86. https://doi.org/10.3354/dao03415

Carvalho, T. L., Ferreira, E. A., Pelicice, F. M., & Fernandes, R. (2021). Comparative functional responses predict the predatory impact of the highly invasive fish *Cichla kelberi*. *Hydrobiologia*, *848*, 2203–2211. https://doi.org/10.1007/s10750-020-04440-6

Chucholl, F., & Chucholl, C. (2021). Differences in the functional responses of four invasive and one native crayfish species suggest invader-specific ecological impacts. *Freshwater Biology*, *66*(11), 2051–2063. https://doi.org/10.1111/fwb.13813

Coughlan, N. E., Dickey, J. W. E., Dick, J. T. A., Médoc, V., McCard, M., Lacroix, G., … Cuthbert, R. N. (2022). When worlds collide: Invader-driven benthic habitat complexity alters predatory impacts of invasive and native predatory fishes. *Science of The Total Environment*, *843*, 156876. https://doi.org/10.1016/j.scitotenv.2022.156876

Crookes, S., DeRoy, E. M., Dick, J. T. A., & MacIsaac, H. J. (2019). Comparative functional responses of introduced and native ladybird beetles track ecological impact through predation and competition. *Biological Invasions*, *21*(2), 519–529. https://doi.org/10.1007/s10530-018-1843-8

Cuthbert, R. N., & Briski, E. (2023). Divergent desalination effects on alien and native gammarid functional responses. *Marine Biology*, *170*(3), 32. https://doi.org/10.1007/s00227-023-04180-w

Cuthbert, R. N., Kotronaki, S. G., Hütt, J. C., Renk, E., Warlo, N., & Briski, E. (2022). Do alternative resources dampen functional responses of native but not alien gammarids? *Ecology and Evolution*, *12*(9). https://doi.org/10.1002/ece3.9262

DeRoy, E. M., Crookes, S., Matheson, K., Scott, R., McKenzie, C. H., Alexander, M. E., … MacIsaac, H. J. (2022). Predatory ability and abundance forecast the ecological impacts of two aquatic invasive species. *NeoBiota*, *71*, 91–112. https://doi.org/10.3897/neobiota.71.75711

DeRoy, E. M., Scott, R., Hussey, N., & MacIsaac, H. (2020). High predatory efficiency and abundance drive expected ecological impacts of a marine invasive fish. *Marine Ecology Progress Series*, *637*, 195–208. https://doi.org/10.3354/meps13251

Dick, J. T. A., Gallagher, K., Avlijas, S., Clarke, H. C., Lewis, S. E., Leung, S., … Ricciardi, A. (2013). Ecological impacts of an invasive predator explained and predicted by comparative functional responses. *Biological Invasions*, *15*(4), 837–846. https://doi.org/10.1007/s10530-012-0332-8

Dickey, J. W. E., Arnott, G., McGlade, C. L. O., Moore, A., Riddell, G. E., & Dick, J. T. A. (2022). Threats at home? Assessing the potential ecological impacts and risks of commonly traded pet fishes. *NeoBiota*, *73*, 109–136. https://doi.org/10.3897/neobiota.73.80542

Dickey, J. W. E., Coughlan, N. E., Dick, J. T. A., Médoc, V., McCard, M., Leavitt, P. R., … Cuthbert, R. N. (2021). Breathing space: Deoxygenation of aquatic environments can drive differential ecological impacts across biological invasion stages. *Biological Invasions*, *23*(9), 2831–2847. https://doi.org/10.1007/s10530-021-02542-3

Dickey, J. W. E., Cuthbert, R. N., Steffen, G. T., Dick, J. T. A., & Briski, E. (2021). Sea freshening may drive the ecological impacts of emerging and existing invasive non-native species. *Diversity and Distributions*, *27*(1), 144–156. https://doi.org/10.1111/ddi.13178

Dominguez Almela, V., South, J., & Britton, J. R. (2021). Predicting the competitive interactions and trophic niche consequences of a globally invasive fish with threatened native species. *Journal of Animal Ecology*, *90*, 2651–2662. https://doi.org/10.1111/1365-2656.13571

Farazmand, A., Fathipour, Y., & Kamali, K. (2012). Functional response and mutual interference of *Neoseiulus californicus* and *Typhlodromus bagdasarjani* (Acari: Phytoseiidae) on *Tetranychus urticae* (Acari: Tetranychidae). *International Journal of Acarology*, *38*(5), 369–376. https://doi.org/10.1080/01647954.2012.655310

Faria, L., Alexander, M. E., & Vitule, J. R. S. (2019). Assessing the impacts of the introduced channel catfish *Ictalurus punctatus* using the comparative functional response approach. *Fisheries Management and Ecology*, *26*(6), 570–577. https://doi.org/10.1111/fme.12353

Fincham, W. N. W., Dunn, A. M., Brown, L. E., Hesketh, H., & Roy, H. E. (2019). Invasion success of a widespread invasive predator may be explained by a high predatory efficacy but may be influenced by pathogen infection. *Biological Invasions*, *21*(12), 3545–3560. https://doi.org/10.1007/s10530-019-02067-w

Griffith, R. M., Cuthbert, R. N., Johnson, J. V., Hardiman, G., & Dick, J. T. A. (2023). Resilient amphipods: Gammarid predatory behaviour is unaffected by microplastic exposure and deoxygenation. *Science of the Total Environment*, *883*, 163582. https://doi.org/10.1016/j.scitotenv.2023.163582

Grimm, J., Dick, J. T. A., Verreycken, H., Jeschke, J. M., Linzmaier, S. M., & Ricciardi, A. (2020). Context-dependent differences in the functional responses of conspecific native and non-native crayfishes. *NeoBiota*, *54*, 71–88. https://doi.org/10.3897/neobiota.54.38668

Guo, Z., Sheath, D., Amat Trigo, F., & Britton, J. R. (2017). Comparative functional responses of native and high-impacting invasive fishes: Impact predictions for native prey populations. *Ecology of Freshwater Fish*, *26*(4), 533–540. https://doi.org/10.1111/eff.12297

Haddaway, N. R., Wilcox, R. H., Heptonstall, R. E. A., Griffiths, H. M., Mortimer, R. J. G., Christmas, M., & Dunn, A. M. (2012). Predatory functional response and prey choice identify predation differences between native/invasive and parasitised/unparasitised crayfish. *PLoS ONE*, *7*(2), e32229. https://doi.org/10.1371/journal.pone.0032229

Hoki, E., Losey, J., & Ugine, T. A. (2014). Comparing the consumptive and non-consumptive effects of a native and introduced lady beetle on pea aphids (*Acyrthosiphon pisum*). *Biological Control*, *70*, 78–84. https://doi.org/10.1016/j.biocontrol.2013.12.007

Howard, B. R., Barrios-O’Neill, D., Alexander, M. E., Dick, J. T. A., Therriault, T. W., Robinson, T. B., & Côté, I. M. (2018). Functional responses of a cosmopolitan invader demonstrate intraspecific variability in consumer-resource dynamics. *PeerJ*, *6*. https://doi.org/10.7717/peerj.5634

Hoxha, T., Crookes, S., MacIsaac, I., Chang, X., Johansson, M., Dick, J. T. A., … MacIsaac, H. J. (2019). Comparative feeding behaviour of native and introduced terrestrial snails tracks their ecological impacts. *NeoBiota*, *47*, 81–94. https://doi.org/10.3897/neobiota.47.35000

Hsiung, A. R., Tan, C. L. Y., Zeng, Y., & Yeo, D. C. J. (2021). Anthropogenic water conditions amplify predatory impact of the non-native Oriental river prawn *Macrobrachium nipponense*. *Biological Invasions*, *23*(6), 1707–1718. https://doi.org/10.1007/s10530-021-02466-y

Iltis, C., Spataro, T., Wattier, R., & Médoc, V. (2018). Parasitism may alter functional response comparisons: A case study on the killer shrimp *Dikerogammarus villosus* and two non-invasive gammarids. *Biological Invasions*, *20*, 619–632. https://doi.org/10.1007/s10530-017-1563-5

Kestrup, Å. M., Dick, J. T. A., & Ricciardi, A. (2011). Interactions between invasive and native crustaceans: Differential functional responses of intraguild predators towards juvenile hetero-specifics. *Biological Invasions*, *13*(3), 731–737. https://doi.org/10.1007/s10530-010-9863-z

Laverty, C., Dick, J. T. A., Alexander, M. E., & Lucy, F. E. (2015). Differential ecological impacts of invader and native predatory freshwater amphipods under environmental change are revealed by comparative functional responses. *Biological Invasions*, *17*(6), 1761–1770. https://doi.org/10.1007/s10530-014-0832-9

Laverty, C., Green, K. D., Dick, J. T. A., Barrios-O’Neill, D., Mensink, P. J., Médoc, V., … Gallagher, C. (2017). Assessing the ecological impacts of invasive species based on their functional responses and abundances. *Biological Invasions*, *19*(5), 1653–1665. https://doi.org/10.1007/s10530-017-1378-4

Madzivanzira, T. C., South, J., & Weyl, O. L. F. (2021). Invasive crayfish outperform Potamonautid crabs at higher temperatures. *Freshwater Biology*, *66*(5), 978–991. https://doi.org/10.1111/fwb.13691

McGlade, C. L. O., Dickey, J. W. E., Kennedy, R., Donnelly, S., Nelson, C.-A., Dick, J. T. A., & Arnott, G. (2022). Behavioural traits of rainbow trout and brown trout may help explain their differing invasion success and impacts. *Scientific Reports*, *12*(1), 1757. https://doi.org/10.1038/s41598-022-05484-5

Médoc, V., Albert, H., & Spataro, T. (2015). Functional response comparisons among freshwater amphipods: Ratio-dependence and higher predation for *Gammarus pulex* compared to the non-natives *Dikerogammarus villosus* and *Echinogammarus berilloni*. *Biological Invasions*, *17*(12), 3625–3637. https://doi.org/10.1007/s10530-015-0984-2

Médoc, V., Thuillier, L., & Spataro, T. (2018). Opportunistic omnivory impairs our ability to predict invasive species impacts from functional response comparisons. *Biological Invasions*, *20*, 1307–1319. https://doi.org/10.1007/s10530-017-1628-5

Mofu, L., Cuthbert, R. N., Dalu, T., Woodford, D. J., Wasserman, R. J., Dick, J. T. A., & Weyl, O. L. F. (2019). Impacts of non-native fishes under a seasonal temperature gradient are forecasted using functional responses and abundances. *NeoBiota*, *49*, 57–75. https://doi.org/10.3897/neobiota.49.34986

Mofu, L., South, J., Wasserman, R. J., Dalu, T., Woodford, D. J., Dick, J. T. A., & Weyl, O. L. F. (2019). Inter-specific differences in invader and native fish functional responses illustrate neutral effects on prey but superior invader competitive ability. *Freshwater Biology*, *64*, 1655–1663. https://doi.org/10.1111/fwb.13361

Otturi, G., Reggi, P. E., Battini, M. Á., & Barriga, J. P. (2020). The effects of trophic interaction between the Patagonian native *Percichthys trucha* and the invasive *Oncorhynchus mykiss* during the juvenile period. *Biological Invasions*, *22*(11), 3293–3305. https://doi.org/10.1007/s10530-020-02324-3

Paterson, R. A., Dick, J. T. A., Pritchard, D. W., Ennis, M., Hatcher, M. J., & Dunn, A. M. (2015). Predicting invasive species impacts: A community module functional response approach reveals context dependencies. *Journal of Animal Ecology*, *84*, 453–463. https://doi.org/10.1111/1365-2656.12292

Paton, R. A., Gobin, J., Rooke, A. C., & Fox, M. G. (2019). Population density contributes to the higher functional response of an invasive fish. *Biological Invasions*, *21*(5), 1737–1749. https://doi.org/10.1007/s10530-019-01931-z

Rosewarne, P. J., Mortimer, R. J. G., Newton, R. J., Grocock, C., Wing, C. D., & Dunn, A. M. (2016). Feeding behaviour, predatory functional responses and trophic interactions of the invasive Chinese mitten crab (*Eriocheir sinensis*) and signal crayfish (*Pacifastacus leniusculus*). *Freshwater Biology*, *61*, 426–443. https://doi.org/10.1111/fwb.12717

Taylor, N. G., & Dunn, A. M. (2017). Size matters: Predation of fish eggs and larvae by native and invasive amphipods. *Biological Invasions*, *19*(1), 89–107. https://doi.org/10.1007/s10530-016-1265-4

Taylor, N. G., & Dunn, A. M. (2018). Predatory impacts of alien decapod Crustacea are predicted by functional responses and explained by differences in metabolic rate. *Biological Invasions*, *20*(10), 2821–2837. https://doi.org/10.1007/s10530-018-1735-y

Tsang, A. H. F., & Dudgeon, D. (2021). Can the functional response to prey predict invasiveness? A comparison of native fishes and alien poeciliids in Hong Kong. *Biological Invasions*, *23*(7), 2143–2154. https://doi.org/10.1007/s10530-021-02493-9

Warren, D. A., Bradbeer, S. J., & Dunn, A. M. (2021). Superior predatory ability and abundance predicts potential ecological impact towards early-stage anurans by invasive 'Killer Shrimp' (*Dikerogammarus villosus*). *Scientific Reports*, *11*(1), 4570. https://doi.org/10.1038/s41598-021-82630-5

Xu, M., Mu, X., Dick, J. T. A., Fang, M., Gu, D., Luo, D., … Hu, Y. (2016). Comparative functional responses predict the invasiveness and ecological impacts of alien herbivorous snails. *PLoS ONE*, *11*(1), e0147017. https://doi.org/10.1371/journal.pone.0147017

Supporting information

Table S1. Results from sensitivity analysis: mean effect size (lnRR) estimates and their corresponding 95% confidence interval (CI) for both response variables ($lnRR_a$: attack rate and $lnRR_{MFR}$: maximum feeding rate). The original model is the null multilevel meta-analysis model, calculated using the Missing Cases imputation method for missing data and rho = 0.6 to estimate the sampling variance matrix. See the 'Methods' section for details about how comparator models were fitted.

	$lnRR_a$	**95% CI**	**$lnRR_{MFR}$**	**95% CI**
Original model	0.209	[-0.019 - 0.438]	0.285	[0.1 - 0.469]
Geary's test	0.211	[-0.019 - 0.439]	0.285	[0.1 - 0.469]
All Cases	0.204	[-0.019 - 0.426]	0.284	[0.098 - 0.470]
rho = 0.1	0.209	[-0.019 - 0.437]	0.285	[0.1 - 0.469]
rho = 0.9	0.209	[-0.019 - 0.437]	0.285	[0.1 - 0.469]
Publication bias	0.273	[0.038 - 0.508]	0.295	[0.101 - 0.488]

3 PREDATION RISK BY LARGEMOUTH BASS MODULATES FEEDING FUNCTIONAL RESPONSES OF NATIVE AND NON-NATIVE CRAYFISH

This paper is a product of my stay as a visiting researcher at the University of Washington – Seattle, granted by the Doctoral Dissertation Research Award of the Fulbright Commission in Brazil, and is already published in NeoBiota. The idea of this manuscript was conceived jointly by me, Professor Jean Vitule, and Professor Julian Olden, who advised me during this time. I performed the collection and analysis of data and wrote the initial draft. All authors revised the manuscript. The supplementary material of this paper can be found in Appendix 2.

Published as[2]: Faria, L., Vitule, J. R. S., & Olden, J. D. (2023). Predation risk by largemouth bass modulates feeding functional responses of native and non-native crayfish. *NeoBiota*, *87*, 191–212. https://doi.org/10.3897/neobiota.87.108457

Abstract

Context-dependency is prevalent in nature, challenging our understanding and prediction of the potential ecological impacts of non-native species (NNS). The presence of a top predator, for example, can modify the foraging behaviour of an intermediate consumer, by means of non-consumptive effects. This raises the question of whether the fear of predation might modulate consumption rates of NNS, thus shaping the magnitude of ecological impacts. Here, we quantified the functional feeding responses of three non-native crayfish species – red swamp crayfish *Procambarus clarkii*, rusty crayfish *Faxonius rusticus* and virile crayfish *Faxonius virilis* – compared to the native analogue signal crayfish *Pacifastacus leniusculus*, considering the predation risk imposed by a top fish predator, the globally invasive largemouth bass *Micropterus salmoides*. We applied the comparative functional response (FR) approach using snails as prey and exposing crayfish to water containing predator and dietary chemical cues or not. All crayfish species presented a destabilising Type II FR, regardless of the presence of chemical cues. Predation risk resulted in significantly longer handling times or lower attack rates in non-native crayfish; however, no significant differences were observed in signal crayfish. We estimated *per capita* impacts for each species using the functional response ratio (FRR; attack rate divided by handling time). The FRR metric was lower for all crayfish species when exposed to predation risk. Rusty crayfish demonstrated the highest FRR in the absence of chemical cues, followed by signal crayfish, virile crayfish and red swamp crayfish. By contrast, the FRR of signal crayfish was nearly twice that of rusty crayfish and virile crayfish and ten times greater than red swamp crayfish when

---

chemical cues were present. The latter result agrees with the well-recognised ecological impacts of signal crayfish throughout its globally-introduced range. This study demonstrates the importance of considering the non-consumptive effects of predators when quantifying the ecological impacts of intermediate non-native consumers on prey. The direction and magnitude of the modulating effects of predators have clear implications for our understanding of NNS impacts and the prioritisation of management actions.

Keywords: ecology of fear, decapods, higher-order predator, kairomones, trait-mediated indirect effects

3.1 INTRODUCTION

Non-native species (NNS) are a primary driver of environmental change, with negative impacts on individuals to entire ecosystems and severely disrupting important services provided by nature (Ricciardi et al. 2013). Economic burdens are also concerning, with estimated costs to prevent and control NNS impacts exceeding a hundred million dollars *per* year globally (Pyšek et al. 2020; Diagne et al. 2021), possibly increasing in the future (Ahmed et al. 2022). Management and policy strategies rely on identifying the most impactful species to help target prevention efforts and allocate limited resources to control or eradicate burgeoning populations. Still, this task is challenging due to variations in NNS impacts, based on ecosystem, geographical location, time since establishment and individual values (Závorka et al. 2018; Santos et al. 2019). Considering the increasing rate of invasions, comparative studies of the context-dependency of NNS impacts will help prioritise which species should be managed in the future (Lockwood et al. 2007; Dick et al. 2017a; Seebens et al. 2017).

Quantifying *per capita* effects of NNS remains central to most frameworks evaluating their ecological impacts (Parker et al. 1999; Kumschick et al. 2015; Griffen et al. 2020). Given the challenges of estimating *per capita* effects, focus has shifted to the use of experiments to quantify resource consumption rates as a proxy (Dick et al. 2017b). Non-native consumers often consume resources more efficiently than their native counterparts (Funk and Vitousek 2007; Salo et al. 2007; Paolucci et al. 2013), making comparative rates of consumption between native and NNS a useful currency to anticipate negative impacts from species introductions (Dick et al. 2014).

The fundamental ecological concept of functional responses (FR) – resource use as a function of availability – provides a measurable estimate of the *per capita* effect of a consumer on a given resource (Solomon 1949; Holling 1959; Dick et al. 2014). Type I FR describes a linear relationship between consumption and resource availability, typical of filter-feeding species (Jeschke et al. 2004). Type II FRs are destabilising due to high consumption rates at low resource densities, while Type III FRs promote stabilising effects due to low consumption rates when resources are scarce (Oaten and Murdoch 1975). The utility of FRs lies in comparing the maximum consumption rate between NNS and native trophic analogues in the same environmental context (Dick et al. 2014, 2017a), making this approach increasingly applied to quantify and predict ecological impacts of NNS (Faria et al. 2023).

The comparative FR approach enables the evaluation of *per capita* effects in different contexts, allowing more realistic and practical impact assessments (Dick et al. 2017a; Dickey et al. 2020). Despite this, investigations involving trophic levels beyond the focal consumer-resource interaction remain limited (e.g. Barrios-O’Neill et al. (2014); Paterson et al. (2015)). Foraging behaviour and consumption rates of consumers are sensitive to the presence of higher-order predators, which invoke trade-offs in resource acquisition versus mortality risk by predation (Lima and Dill 1990; Brown and Kotler 2004). Fear of predation can shape entire ecosystems through trait-mediated indirect effects (TMIEs) on prey traits, such as behaviour and physiology (Werner and Peacor 2003; Peckarsky et al. 2008; Laundré et al. 2010). In some circumstances, the non-consumptive effects of predators are thought to be as strong as direct consumption for population dynamics, leading to greater system stability (Brown et al. 1999) or even causing trophic cascades (Schmitz et al. 2004; Preisser et al. 2005; Peckarsky et al. 2008).

Trait-mediated indirect effects are particularly prominent in freshwater ecosystems, likely due to the effective transmission of visual and chemical cues indicating predator presence (Preisser et al. 2005). For example, the presence of largemouth bass (*Micropterus salmoides*) altered the foraging behaviour and habitat use of bluegill sunfish (*Lepomis macrochirus*) prey leading to cascading changes in zooplankton communities (Turner and Mittelbach 1990). In another example, rusty crayfish (*Faxonius rusticus*) displayed greater consumption of macrophytes when exposed to chemical cues from largemouth bass, suggesting a robust effect of predation risk on crayfish foraging behaviour (Wood et al. 2018).

Despite the strong effects of non-consumptive effects in shaping communities, they are relatively underexplored compared to consumptive effects in the context of quantifying NNS impacts. Applying the comparative FR approach, we aim to test whether the non-consumptive effects of a top predator, the non-native largemouth bass, mediate the consumptive impacts of three non-native crayfish species (*Procambarus clarkii*, *Faxonius virilis* and *F. rusticus*) and a native analogue (*Pacifastacus leniusculus*) preying on snails. We hypothesise that non-consumptive effects of a top predator will reduce consumption rates of all crayfish species, but to a lesser extent for non-native crayfish with a shorter evolutionary history with the predator. The differential response to predation risk imposed by the largemouth bass may explain the expected higher *per capita* effects of non-native consumers compared to native analogue species.

3.2 METHODS

3.2.1 Study system

Our study system is a three-level food chain composed by a non-native top predator, the largemouth bass, an intermediate consumer represented by non-native or native crayfish (Table 1) and native freshwater snails (Gastropoda, Planorbidae) as the basal resource. Crayfish are known to be highly sensitive to different chemical cues such as predator odour, dietary and alarm cues (Beattie and Moore 2018; Wood et al. 2018; Wood and Moore 2020b, 2020a) and these cues show utility in assessing TMIEs (Paterson et al. 2013). Thus, we used a combination of predator and dietary chemical cues to provide the biological context of predation risk in our comparative FR approach.

The geographic context of the study is the Pacific Northwest region of the US, where all species were sourced (Table 1). The apex predator largemouth bass has a native distribution that extends from north-eastern US to northern Mexico (Brown et al. 2009), with a long history of intentional introduction for recreational fishing in many regions of the US and the world, including the study region dating back to the beginning of the 20th century (Stein 1970). The non-native crayfish used in this study have a varied history of introductions in the region (Table 1) and are amongst the most widespread and harmful invasive crayfish species in the world (Twardochleb et al. 2013). Signal crayfish is the most widely distributed native crayfish species in the region (Larson and Olden 2011) and also highly invasive outside its native range (Usio et al. 2007; Twardochleb et al. 2013; Vaeßen and Hollert 2015). All crayfish species used in this study are omnivorous and nocturnal, presenting maximum feeding or growth rates between 20 and 30ºC (Crandall and Buhay 2008; Westhoff and Rosenberger 2016; Rodríguez Valido et al. 2021; Ruokonen and Karjalainen 2022).

Table 1. Crayfish species examined in this study, including scientific and common names, history of introduction in the Pacific Northwest region, sampled populations (coordinates) and carapace length (CL) and mass, presented as the mean (SD), of the individuals used in the experiments.

Crayfish	**Scientific name**	**Common name**	**Estimated time of introduction**	**Sampled population**	**CL (mm)**	**Mass (g)**
	*Pacifastacus leniusculus*	Signal crayfish	Native	Skykomish River, WA (47.8482, -121.8403)	50.2 (4.3)	36.9 (10.3)
	*Procambarus clarkii*	Red swamp crayfish	1970s	Pine Lake, WA (47.5907, -122.0389)	53.6 (5.7)	39.7 (13.0)
	*Faxonius rusticus*	Rusty crayfish	2005	Magone Lake, OR (44.5486, -118.9119)	41.1 (3.1)	25.9 (5.3)
	*Faxonius virilis*	Virile crayfish	1980s	Rattlesnake Lake, WA (47.4308, -121.7715)	46.0 (3.5)	32.6 (7.6)

3.2.2 Animal collection and maintenance

Largemouth bass were collected using electrofishing from Lake Washington, WA (47.6469, -122.2991) in October 2022. A total of 33 fish were captured and transported to the lab facility at the University of Washington, where they were maintained in a circular tank of approximately 800 l without shelter (hereafter stimulus tank), aerated and continuously filled with water from Lake Washington, in an open circulation system (mean total length = 194 mm, SD = 53). Fish were acclimatised to the stimulus tank for two weeks before the beginning of the trials.

A total of 433 crayfish were sampled using baited traps deployed overnight from lakes in Washington and Oregon States in October 2022 (Table 1). Crayfish were kept in tanks of 256 l separated by species, with a maximum stock density of 30 individuals *per* tank. Stock tanks were continuously filled with water from Lake Washington, in an open circulation system and contained abundant structure for shelter. Crayfish were fed daily with commercial algae pellets until satiation and were acclimatised for at least two weeks before being used in the experiment. Snails used as prey were obtained from various commercial pet retailers (shell length mean = 10.3 mm, SD = 2.4). Snails were kept in a separate tank, in the same conditions as crayfish.

3.2.3 Functional response experiments

Native and NNS of crayfish were tested for differences in their predatory rate of snail prey supplied in seven different initial densities (2, 4, 8, 12, 16, 24 and 40 snails) under the presence or absence of waterborne predator and dietary chemical cues (hereafter, predator treatment and control, respectively). Experiments were conducted in a fully-randomised design with respect to crayfish species and initial prey densities assigned to predator treatment and control. Experimental arenas were round opaque tanks (44.5 cm diameter, 42.5 cm height) filled with 10 l of water and no substrate or shelter were provided (Fig. 1A). At the predator treatment, water was supplied from the stimulus tank containing water from Lake Washington and bass (Fig. 1B), whereas under the control, just water from Lake Washington was supplied (as in the stock tanks) (Fig. 1C). Lake Washington water is piped directly from 10 m depth where largemouth bass and other fish species are at low abundance. Water was supplied continuously by dripping through small hoses (5 mm diameter) to ensure that chemical cues were present throughout the experiment (Fig. 1D). Water temperature in experimental arenas and stock tanks were similar, all demonstrating natural diel ranges of 12.5 º - 18.5 ºC.

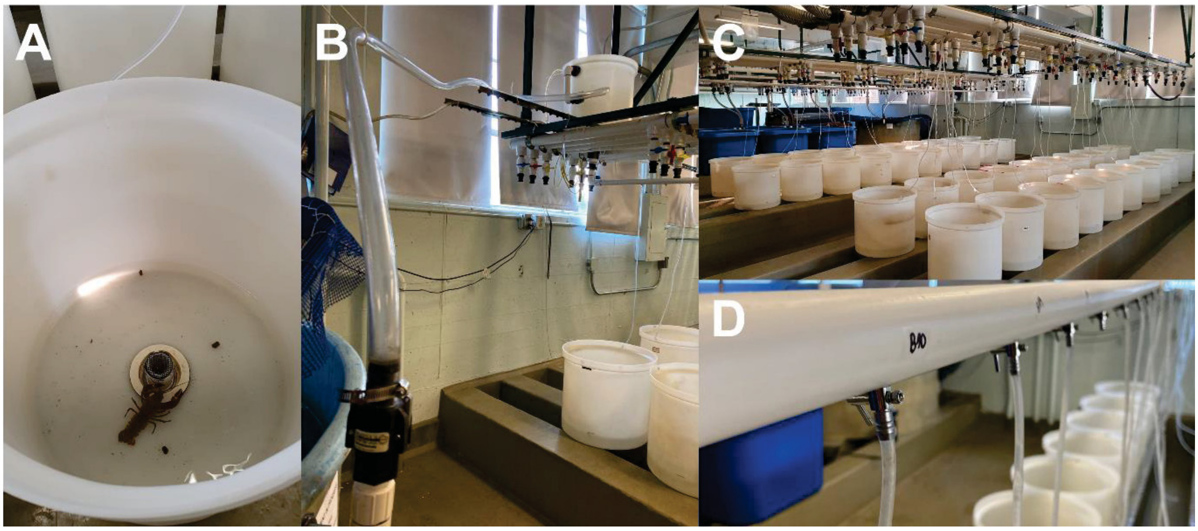


Figure 1. Experimental setup used in the functional response trials. **A** Experimental arena with a signal crayfish and snail prey during a trial. **B** Water from the tank containing largemouth bass (left) was pumped to a head tank (upper right) and **C** distributed to the experimental arenas in the predator treatment (upper-left row) or water was supplied directly from Lake Washington to the control arenas (lower-right row). Blue tanks in the background were stock and starvation tanks where crayfish were kept before being used in trials. **D** The water from both treatments was supplied to each experimental arena via individually controlled hoses.

Fish were starved for a week and then fed every other day a diet of crayfish before and during the experiments. Small individuals of all crayfish species were supplied simultaneously until satiation to enhance the response of crayfish to conspecific dietary cues released by the fish (Beattie and Moore 2018; Wood et al. 2018). Crayfish were starved in a separate tank for 48 h before use in experiments to standardise hunger levels. After the starvation period, an individual crayfish was allocated to each experimental arena containing one of the seven initial densities of prey and allowed to forage for 24 h. The number of remaining prey was recorded at the end of the trials, along with the number of attacked, but uneaten prey. Crayfish sex, carapace length (CL) and mass were recorded, as well as the water temperature at the end of the trial.

There were seven replicates for each combination of crayfish species, initial density of prey and treatment. At least five replicates of each combination were performed in the absence of crayfish to account for any background mortality of prey. Prey survivorship in these replicates was 99.9%, thus all prey deaths during experiments were attributed to crayfish predation. Crayfish were not reused in the experimental trials and replicates where crayfish moulted during the trial or one week after were repeated.

3.2.4 Data analysis

All statistical analyses were carried out in R version 4.1.2 (R Core Team 2021). Functional response analyses were conducted using the number of prey consumed as the response variable, under the frair package (Pritchard et al. 2017). For each crayfish species x treatment combination, FR type was determined by logistic regression of the proportion of prey consumed against initial prey density (Juliano 2001). If the proportion of prey consumed decreases with increasing prey density, it produces a significantly negative first-order term, indicating a Type II FR; if otherwise, a significantly positive first-order term is obtained then it indicates a Type III FR (Juliano 2001). When the results of the logistic regression were not conclusive, different FR models were fitted directly and compared using Akaike's Information Criterion (AIC) (Pritchard et al. 2017).

Based on these analyses, all FRs were then modelled as Type II. Maximum Likelihood model fitting was used to fit data to the Rogers' random predator equation (Rogers 1972) that accounts for the depletion of prey along the experimental duration:

$$N_e = N_0(1 - \exp(a(N_e h - T)))$$

where N_e is the number of prey consumed, N_0 is the initial density of prey, *a* is the attack rate, *h* is the handling time and T is the time available for predation in days (i.e. experimental duration). As N_e is obtained experimentally, the estimated FR parameters are attack rate and handling time, representing a measure of successful attacks and the time needed for a predator to handle and ingest a prey item, respectively. The Lambert W function is implemented to solve the fact that N_e appears on both sides of the equation (Bolker 2008).

To compare FR parameters *a* and *h* between predator treatment and control, we used the indicator variables method (Juliano 2001; Pritchard et al. 2017), as:

$$0 = N_0 - N_0 \exp\{[a + Da(j)]\{[h + Dh(j)](N_e) - T\}\} - N_e$$

where *j* is an indicator variable that takes value 0 for control and 1 for predator treatment. The parameters *Da* and *Dh* estimate the differences between treatments in the value of the parameters *a* and *h*, respectively. If *Da* and *Dh* are significantly different from zero, then the estimated FR parameters differ between treatment and control (Juliano 2001). The maximum feeding rate of each crayfish species x treatment combination was calculated as 1/(*h*T) indicating the maximum number of prey that one crayfish can consume in one day (T = 1 day). Additionally, the functional response ratio (FRR) was calculated, as a comparative metric of the ecological impact of NNS (Cuthbert et al. 2019), dividing the attack rate parameter by the handling time (*a/h*). High values of FRR are indicative of strong *per capita* impacts, while low values indicate less impactful predators (Cuthbert et al. 2019).

Potential differences in the trial's water temperature amongst species and initial densities of prey were evaluated through Kruskal-Wallis tests, as well as differences in crayfish weight and carapace length (CL) amongst species and initial densities of prey. Water temperature in trials did not vary amongst species (Kruskal–Wallis $X^2(3) = 7.366$, $p = 0.06$) nor in association with the initial densities of prey tested (Kruskal–Wallis $X^2(6) = 11.339$, $p = 0.08$). Crayfish mass and carapace length varied amongst species (Mass: Kruskal–Wallis $X^2(3) = 96.73$, $p < 0.001$; CL: Kruskal–Wallis $X^2(3) = 224.73$, $p < 0.001$). The effect of crayfish size and sex on the proportion of prey consumed was investigated with Spearman's correlation and Mann-Whitney tests, respectively. Crayfish size (Mass: r = 0.01, $p = 0.84$; CL: r = -0.08, $p = 0.12$) and sex (Mann-Whitney U = 14828, $p = 0.74$) had no relation to the proportion of prey consumed.

3.3 RESULTS

All crayfish species presented a destabilising Type II FR towards snail prey, regardless of the presence of chemical cues (Fig. 2). This was confirmed by the significantly negative first-order term of the logistic regression, except for red swamp crayfish under predator treatment and rusty crayfish under control, where the estimates were non-significant (Table 2). For these two specific cases, the FR type was determined by comparing the AIC of different model fittings. For red swamp crayfish, Type I had a lower AIC (ΔAIC = 0.8), while for rusty crayfish, Type II presented a better fit (ΔAIC = 1.1) compared to other models (generalised FR model, Type I and Type III).

Non-consumptive effects were observed for all non-native crayfish species, except for native signal crayfish (Fig. 2). Predation risk lowered the magnitude of the FR, which reflects reduced maximum consumption rates estimated in the predator treatment compared to the control (Table 2). These differences were driven by significantly longer handling time of snails for virile crayfish (*Dh* = -0.03 ± 0.008, $p < 0.001$) and rusty crayfish (*Dh* = -0.02 ± 0.008, $p = 0.01$) (Fig. 3A) and significantly lower attack rate displayed by red swamp crayfish (*Da* = 0.25 ± 0.09, $p = 0.006$) (Fig. 3B) in the presence of chemical cues. No significant differences in handling time or attack rates were evidenced for signal crayfish between treatment and control.

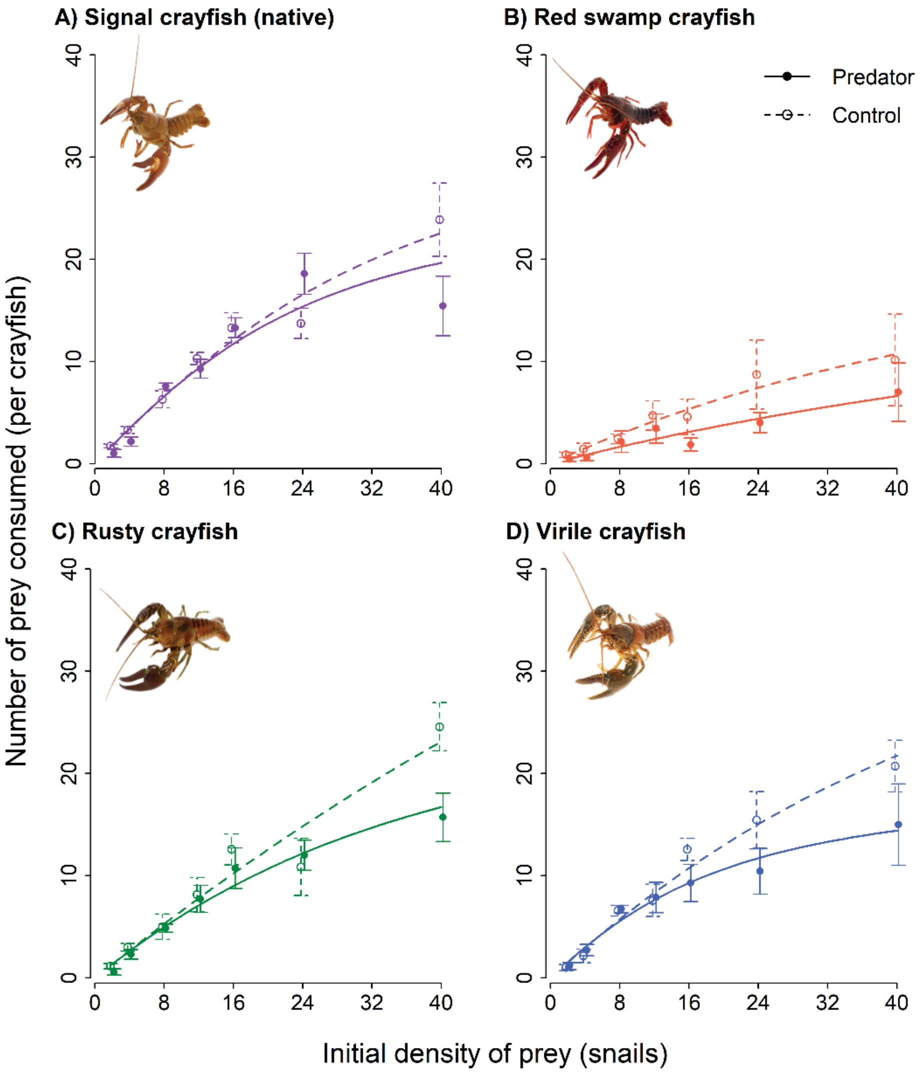


Figure 2. Functional responses of native and non-native crayfish feeding on snails under predator treatment and control. **A** Native signal crayfish; **B** non-native red swamp crayfish; **C** non-native rusty crayfish and **D** non-native virile crayfish. Lines represent model fit (solid line: predator treatment, dashed line: control). Points represent mean consumption and error bars represent ± SE *per* density (filled circles: predator treatment, open circles: control; n = 7 *per* initial density x treatment combination).

Table 2. Functional response estimates of native and non-native crayfish species under predator treatment and control. The 1st order term of the logistic regression (see Methods), the functional response (FR) type, estimated parameters attack rate (a) and handling time (h), the maximum feeding rate ($1/h$T) and the functional response ratio (FRR).

Treatment/ Species	**1st order term (p-value)**	**FR type**	**a ± SE (p-value)**	**h ± SE (p-value)**	**$1/h$T**	**FRR**
Predator						
Signal crayfish (native)	-0.0617 (> 0.001)*	II	2.26 ± 0.23 (>0.001)*	0.04 ± 0.004 (> 0.001)*	28.02	63.5
Red swamp crayfish	-0.0078 (0.29)	I[†]	0.25 ± 0.05 (> 0.001)*	0.04 ± 0.037 (0.271)	24.81	6.1
Rusty crayfish	-0.0283 (> 0.001)*	II	1.16 ± 0.14 (> 0.001)*	0.03 ± 0.006 (> 0.001)*	31.37	36.3
Virile crayfish	-0.0411 (> 0.001)*	II	1.64 ± 0.23 (> 0.001)*	0.05 ± 0.006 (> 0.001)*	19.81	32.5
Control						
Signal crayfish (native)	-0.0358 (> 0.001)*	II	2.08 ± 0.24 (> 0.001)*	0.03 ± 0.004 (> 0.001)*	37.53	78.2
Red swamp crayfish	-0.0142 (0.022)*	II	0.50 ± 0.08 (> 0.001)*	0.04 ± 0.015 (0.021)*	28.59	14.3
Rusty crayfish	-0.0101 (0.086)	II	1.14 ± 0.13 (> 0.001)*	0.01 ± 0.006 (0.061)	94.99	108.0
Virile crayfish	-0.0252 (> 0.001)*	II	1.43 ± 0.15 (> 0.001)*	0.02 ± 0.005 (> 0.001)*	47.95	68.8

* = significant results. [†]Despite being categorised as Type I using AIC, we fitted data to the Type II model to allow comparison of parameters between treatment and control.

Native signal crayfish demonstrated a greater consumption rate when exposed to predation risk compared to non-native crayfish (Fig. 2). *Per capita* effects of signal crayfish on snails, according to the FRR, was nearly twice that of rusty crayfish and virile crayfish and ten times greater than red swamp crayfish (Fig. 4, Table 2). By contrast, rusty crayfish demonstrated the highest FRR in the control, followed by signal crayfish, virile crayfish and red swamp crayfish (Fig. 4, Table 2).

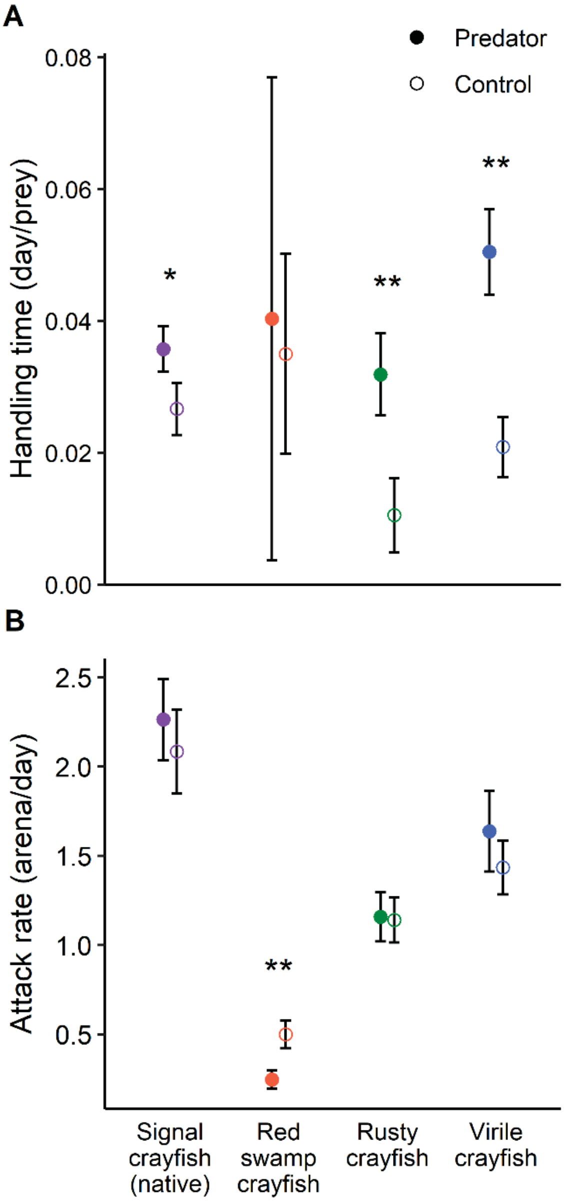


Figure 3. Estimated functional response parameters of native and non-native crayfish species under predator treatment and control. **A** Handling time parameter *h* and **B** attack rate parameter *a*. Points represent the mean estimate of the model (filled circles: predator treatment, open circles: control) and error bars represent ± SE. *$p < 0.1$ and **$p < 0.05$.

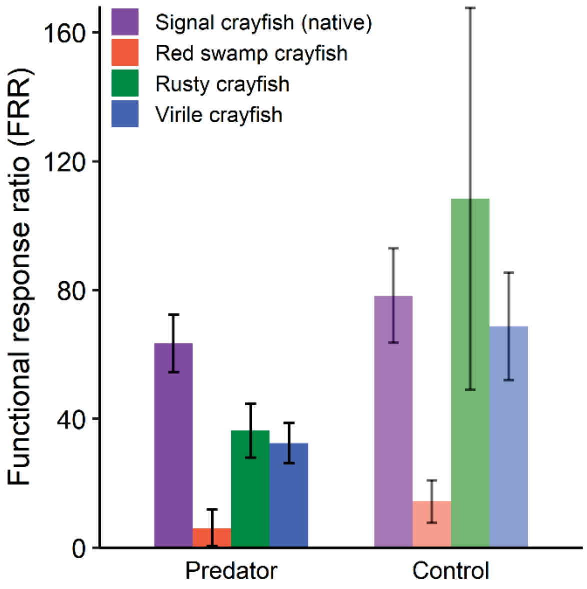


Figure 4. The functional response ratio (FRR) of native and non-native crayfish species under predator treatment and control. The calculated FRR (*a/h*) is represented as bars (solid bars: predator treatment, shadowed bars: control) and error bars represent propagated standard errors of original estimates of parameters attack rate *a* and handling time *h*.

3.4 DISCUSSION

Predators can exert non-consumptive effects on prey that are comparable in magnitude to consumptive effects (Werner and Peacor 2003; Preisser et al. 2005). Despite that, non-consumptive effects remain largely under-studied in evaluations of ecological impacts of NNS (Sih et al. 2010). Here, we quantified rates of snail predation by multiple non-native and a native crayfish species in the presence or absence of chemical and dietary cues from a higher-order predator. We found that predation risk reduced maximum consumption rates of snails due to longer handling times or lower attack rates, but did not alter the shape of the FR curve. Reduced foraging activity is a common antipredator behavioural response of crayfish when exposed to predation risk (Gherardi et al. 2011b; Beattie and Moore 2018; Kenison et al. 2018). For example, red swamp crayfish significantly reduces the time spent feeding by adopting a lowered posture after being exposed to largemouth bass cues (Gherardi et al. 2011b).

Native signal crayfish was the only study species demonstrating little evidence for the effect of predation risk on the FR magnitude. This outcome is supported by a body of literature suggesting that the response of signal crayfish to predation risk is highly variable and context-dependent (Stebbing et al. 2010; Gherardi et al. 2011b; Beattie and Moore 2018; Wood and Moore 2020b). For instance, Stebbing et al. (2010)

observed altered behaviour as raised posture in signal crayfish exposed to the chemical cues of European eels (*Anguilla anguilla*), but not to European perch (*Perca fluviatilis*), whereas Hirvonen et al. (2007) reported crayfish reduced shelter use when exposed to eel odour. These studies were performed in the invaded range of signal crayfish; thus, unexpected behavioural responses were attributed to naïve juvenile individuals with a lack of evolutionary history with these predators (Hirvonen et al. 2007; Stebbing et al. 2010). However, this may not be the case in our study where signal crayfish is native and has experience with largemouth bass in the region for over a hundred years. This suggests that signal crayfish may better assess the risk posed by a familiar predator using both chemical and visual cues (Blake and Hart 1993), whereas all three non-native crayfish species responded in a more conservative manner to the presence of chemical cues alone in a novel environment (Gherardi et al. 2002; Hazlett et al. 2003). Another possible mechanism is related to the larger body sizes of signal crayfish compared to other species (both in the wild and individuals used in this experiment: Table 1). There is evidence that crayfish can assess predator size through chemical cues (Wood and Moore 2020a; Wagner and Moore 2022); thus, the size of the largemouth bass in the experiment may have been too small relative to signal crayfish to elicit an antipredator behaviour resulting in reduced foraging rates.

All crayfish species presented a Type II FR, which is deemed to destabilise resource populations. This result aligns with the known impacts of these species on biomass and abundance of benthic invertebrates, particularly snails (Twardochleb et al. 2013). Moreover, when applying an FR-based metric to evaluate impacts, our native comparator species generally showed a higher FRR than non-natives, which contradicts the pattern of invaders being more impactful than their native counterparts (Cuthbert et al. 2019). Nevertheless, signal crayfish is itself highly invasive in Europe, Japan and the south-western United States, usually reaching higher abundances than those observed in its native range (Larson and Olden 2013) and causing significant impact through their omnivorous feeding habits (Usio et al. 2009; Twardochleb et al. 2013; Vaeßen and Hollert 2015). Our results also align with a previous study that experimentally compared the predation rate of signal crayfish and non-native crayfish towards Chinese mystery snail (*Bellamya chinensis*), where native signal crayfish consumed significantly more snails of all size classes than did non-native crayfish (Olden et al. 2009). Indeed, previous studies that used the comparative FR approach to assess the impacts of signal crayfish where it is non-native found that the species generally present higher FR magnitude when compared to European native analogues, such as white-clawed crayfish (*Austropotamobius pallipes*) and noble crayfish (*Astacus astacus*), although impact varied with prey type (Haddaway et al. 2012; Rosewarne et al. 2016; Taylor and Dunn 2018; Chucholl and Chucholl 2021). Differences in experimental systems, such as diverse prey types and arena sizes, preclude us from comparing the native signal crayfish findings here to those of invasive populations of the species. Future comparative studies of the FRs of native and non-native populations are recommended.

We found significant differences amongst NNS predatory impacts towards prey. Rusty crayfish and virile crayfish showed consumption rates similar to those of native signal crayfish, whereas red swamp crayfish demonstrated the lowest feeding rate, despite the latter species being considered one of the most impactful invasive crayfish in the world (Lodge et al. 2012; Twardochleb et al. 2013). Even though all crayfish are considered omnivorous or polytrophic, there are marked differences in their predominant trophic ecology (Reynolds et al. 2013). For instance, red swamp crayfish has a lower trophic position than signal crayfish, which is consistent with the perceived impact on macrophyte communities of the former species (Matsuzaki et al. 2009; Larson et al. 2017). Similarly, Madzivanzira et al. (2021) also reported a lower FR magnitude of red swamp crayfish preying on catfish fry compared to a native analogue crab. Despite this, it has been demonstrated that invasive populations of red swamp crayfish in Europe present ontogenetic niche shifts and have opportunistic feeding habits, adjusting its diet to different biotic and abiotic contexts, which further explains its success as an invader (Correia 2002, 2003; Carreira et al. 2017; Jackson et al. 2017). Additionally, red swamp crayfish has weaker chelae closing force compared to other decapods, which helps explain its preference for feeding on softer resources (South et al. 2020). Our findings support previously observed impacts of rusty crayfish and virile crayfish on snail communities where they are invasive (Dorn and Wojdak 2004; McCarthy et al. 2006; Kreps et al. 2012). The greater consumption rate of invasive crayfish is likely associated with selected traits, such as boldness and foraging voracity in NNS populations, which are known to differ from their native range (Pintor and Sih 2009; Reisinger et al. 2017; Glon et al. 2018).

Previous studies that investigated TMIEs using the FR approach reported mixed outcomes. Considering simple habitats, the presence of predator cues reduced consumption rates of the amphipod *Echinogammarus marinus*, an intermediate predator, towards isopod prey (Alexander et al. 2013). By contrast, fish cues did not influence the FR's magnitude of two amphipod species (the native *Gammarus duebeni* and the invasive *Gammarus pulex*) towards three different invertebrate preys (Paterson et al. 2015). Our study reinforces the need for considering the wider biological context of ecological interactions when quantifying the impacts of NNS. Moving forward, we suggest three primary ways that future studies could further explore context-dependencies.

First, the effect of abiotic contexts, such as habitat complexity and presence of shelter, continues to be a research need. The Type II FR curves reported here align with general expectations from the broader literature (Jeschke et al. 2004); however, the lack of habitat complexity in experimental arenas may prevent the observation of more stabilising Type III responses (Alexander et al. 2012; Griffen 2021). Likewise, gravel substrate has been reported to reduce crayfish consumption of pelagic, but not benthic prey (Vollmer and Gall 2014; South et al. 2019). Additionally, shelter use is a common behavioural response of crayfish to predator cues (Blake and Hart 1993; Garvey et al. 1994) and could have further magnified the observed differences between the predator treatment and control reported in our study.

Second, it would be valuable to evaluate additional biotic contexts, such as alternative resource availability, the presence of intra- and inter-specific competitors and effects of visual predator cues. For instance, prey preference for different resources, such as macrophyte or detritus, could have a significant effect on FRs for omnivorous crayfish (Cuthbert et al. 2018; Médoc et al. 2018), ultimately defining their ecological impacts when invasive (South et al. 2019; Chucholl and Chucholl 2021). Better incorporating the effects of competitive interactions in FR experiments are also fundamental to more realistic scaling of NNS *per capita* effects in the wild (Dickey et al. 2020; Latombe et al. 2022). As crayfish can respond to predation risk using a variety of different cues, the relative importance of visual and alarm cues can also be investigated using FRs (Blake and Hart 1993; Ramberg-Pihl and Yurewicz 2020). Third, future research investigations discussed above would benefit from the linking of mesocosms experiments with *in situ* field studies to ensure robust scaling of our understanding (Iacarella et al. 2018).

3.5 CONCLUSIONS

Ecological impacts of NNS are notoriously challenging to anticipate given a myriad of biotic and abiotic context-dependencies that can affect the organismal performance in nature. The comparative FR approach has been used to incorporate these context-dependencies to predict the impact of NNS, through relative comparisons of *per capita* effects (Dick et al. 2014; Cuthbert et al. 2019; Faria et al. 2023). Here we showed that the presence of a higher-order predator can alter important parameters of FR, with direct effects on maximum consumption rates and predicted impact of intermediate non-native consumers. These findings suggest that the broader biological context in which consumer activities take place should not be overlooked if we aim to understand the ecological impacts of NNS. Likewise, biogeographic origin alone is not the sole indicator of impact, as we found that native signal crayfish demonstrated the highest estimated impact on prey in the presence of predation risk by a fish predator.

The ecology of fear predicts that the cost of anti-predator behaviour is associated with reduced offspring, thus modulating consumer abundance (Zanette and Clinchy 2019). Given the immense challenges in eradicating and controlling invasive crayfish populations (Gherardi et al. 2011a; Manfrin et al. 2019), this raises the interesting question of whether chemical cues could be used as an additional management tool to reduce their short-term ecological impacts, while other control strategies are being implemented. We encourage more research on which and how chemical components of predator and dietary cues trigger behavioural responses in crayfish, as these are not entirely elucidated (Mitchell et al. 2017), but have potential management applications.

Acknowledgements

Assistance in the collection of fish provided by the Washington Department of Fish and Wildlife and the collection of crayfish by the Oregon Department of Fish and Wildlife, the Washington Crawfish Company and Dwayne Lamb. We thank Alexandre Bee Amaral, Jon Wittouck and lab-mates in the Freshwater Ecology & Conservation Lab for their help in assembling the mesocosms. We are grateful to Fulbright Brazil, the Fulbright Scholarship Board and the Bureau of the Educational and Cultural Affairs of the United States Department of State for the scholarship granted to LF as part of the Doctoral Dissertation Research Award programme. JRSV was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) – Process Numbers 02367/2018-7 and 303776/2015-3. JDO was supported by the Richard C. and Lois M. Worthington Endowed Professor in Fisheries Management from the School of Aquatic and Fishery Sciences, University of Washington. This study was also supported by Coordenação de Aperfeiçoamento de Pessoal do Nível Superior (CAPES) – Finance Code 001. All experiments were approved by the University of Washington Institutional Animal Care and Use Committee (permit 4172-12).

References

Ahmed DA, Hudgins EJ, Cuthbert RN, Haubrock PJ, Renault D, Bonnaud E, Diagne C, Courchamp F (2022) Modelling the damage costs of invasive alien species. Biological Invasions 24(7): 1949–1972. https://doi.org/10.1007/s10530-021-02586-5

Alexander ME, Dick JTA, O'Connor NE, Haddaway NR, Farnsworth KD (2012) Functional responses of the intertidal amphipod *Echinogammarus marinus*: Effects of prey supply, model selection and habitat complexity. Marine Ecology Progress Series 468: 191–202. https://doi.org/10.3354/meps09978

Alexander ME, Dick JTA, O'Connor NE (2013) Trait-mediated indirect interactions in a marine intertidal system as quantified by functional responses. Oikos 122(11): 1521–1531. https://doi.org/10.1111/j.1600-0706.2013.00472.x

Barrios-O'Neill D, Dick JTA, Emmerson MC, Ricciardi A, MacIsaac HJ, Alexander ME, Bovy HC (2014) Fortune favours the bold: A higher predator reduces the impact of a native but not an invasive intermediate predator. Journal of Animal Ecology 83(3): 693–701. https://doi.org/10.1111/1365-2656.12155

Beattie MC, Moore PA (2018) Predator recognition of chemical cues in crayfish: Diet and experience influence the ability to detect predation threats. Behaviour 155(6): 505–530. https://doi.org/10.1163/1568539X-00003501

Blake MA, Hart PJB (1993) The behavioural responses of juvenile signal crayfish *Pacifastacus leniusculus* to stimuli from perch and eels. Freshwater Biology 29(1): 89–97. https://doi.org/10.1111/j.1365-2427.1993.tb00747.x

Bolker B (2008) Ecological Models and Data in R. Princeton University Press (Princeton): 1- 408. https://doi.org/10.1086/644667

Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecology Letters 7(10): 999–1014. https://doi.org/10.1111/j.1461-0248.2004.00661.x

Brown JS, Laundré JW, Gurung M (1999) The ecology of fear: Optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80(2): 385–399. https://doi.org/10.2307/1383287

Brown TG, Runciman B, Pollard S, Grant ADA (2009) Biological synopsis of largemouth bass (*Micropterus salmoides*). Canadian Manuscript Report of Fisheries and Aquatic Sciences 2884: 27 p.

Buba Y, DeLong JP, Belmaker J (2022) Synthesizing drivers of fish functional responses across species. Fish and Fisheries 23(2): 376–391. https://doi.org/10.1111/faf.12622

Carreira BM, Segurado P, Laurila A, Rebelo R (2017) Can heat waves change the trophic role of the world's most invasive crayfish? Diet shifts in *Procambarus clarkii.* PLoS One 12(9): e0183108. https://doi.org/10.1371/journal.pone.0183108

Chucholl F, Chucholl C (2021) Differences in the functional responses of four invasive and one native crayfish species suggest invader-specific ecological impacts. Freshwater Biology 66(11): 2051–2063. https://doi.org/10.1111/fwb.13813

Correia AM (2002) Niche breadth and trophic diversity: Feeding behaviour of the red swamp crayfish (*Procambarus clarkii*) towards environmental availability of aquatic macroinvertebrates in a rice field (Portugal). Acta Oecologica 23(6): 421–429. https://doi.org/10.1016/S1146-609X(02)01166-9

Correia AM (2003) Food choice by the introduced crayfish *Procambarus clarkii*. Annales Zoologici Fennici 40: 517–528.

Crandall KA, Buhay JE (2008) Global diversity of crayfish (Astacidae, Cambaridae, and Parastacidae - Decapoda) in freshwater. Hydrobiologia 595(1): 295–301. https://doi.org/10.1007/s10750-007-9120-3

Cuthbert RN, Dickey JWE, McMorrow C, Laverty C, Dick JTA (2018) Resistance is futile: Lack of predator switching and a preference for native prey predict the success of an invasive prey species. Royal Society Open Science 5(8): 180339. https://doi.org/10.1098/rsos.180339

Cuthbert RN, Dickey JWE, Coughlan NE, Joyce PWS, Dick JTA (2019) The Functional Response Ratio (FRR): Advancing comparative metrics for predicting the ecological impacts of invasive alien species. Biological Invasions 21(8): 2543–2547. https://doi.org/10.1007/s10530-019-02002-z

Diagne C, Leroy B, Vaissière AC, Gozlan RE, Roiz D, Jarić I, Salles JM, Bradshaw CJA, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. Nature 592(7855): 571–576. https://doi.org/10.1038/s41586-021-03405-6

Dick JTA, Alexander ME, Jeschke J, Ricciardi A, MacIsaac HJ, Robinson TB, Kumschick S, Weyl OLF, Dunn AM, Hatcher MJ, Paterson RA, Farnsworth KD, Richardson DM (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biological Invasions 16(4): 735–753. https://doi.org/10.1007/s10530-013-0550-8

Dick JTA, Alexander ME, Ricciardi A, Laverty C, Downey PO, Xu M, Jeschke J, Saul WC, Hill MP, Wasserman R, Barrios-O'Neill D, Weyl OLF, Shaw RH (2017a)

Functional responses can unify invasion ecology. Biological Invasions 19(5): 1667–1672. https://doi.org/10.1007/s10530-016-1355-3

Dick JTA, Laverty C, Lennon JJ, Barrios-O'Neill D, Mensink PJ, Britton JR, Médoc V, Boets P, Alexander ME, Taylor NG, Dunn AM, Hatcher MJ, Rosewarne PJ, Crookes S, MacIsaac HJ, Xu M, Ricciardi A, Wasserman RJ, Ellender BR, Weyl OLF, Lucy FE, Banks PB, Dodd JA, MacNeil C, Penk M, Aldridge DC, Caffrey JM (2017b) Invader Relative Impact Potential: A new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. Journal of Applied Ecology 54(4): 1259–1267. https://doi.org/10.1111/1365-2664.12849

Dickey JWE, Cuthbert RN, South J, Britton JR, Caffrey J, Chang X, Crane K, Coughlan NE, Fadaei E, Farnsworth KD, Ismar-Rebitz SMH, Joyce PWS, Julius M, Laverty C, Lucy FE, MacIsaac HJ, McCard M, McGlade CLO, Reid N, Ricciardi A, Wasserman RJ, Weyl OLF, Dick JTA (2020) On the RIP: Using Relative Impact Potential to assess the ecological impacts of invasive alien species. NeoBiota 55: 27–60. https://doi.org/10.3897/neobiota.55.49547

Dorn NJ, Wojdak JM (2004) The role of omnivorous crayfish in littoral communities. Oecologia 140(1): 150–159. https://doi.org/10.1007/s00442-004-1548-9

Faria L, Cuthbert RN, Dickey JWE, Jeschke JM, Ricciardi A, Dick JTA, Vitule JRS (2023) The rise of the Functional Response in invasion science: A systematic review. NeoBiota 85: 43–79. https://doi.org/10.3897/neobiota.85.98902

Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. Nature 446(7139): 1079–1081. https://doi.org/10.1038/nature05719

Garvey JE, Stein RA, Thomas HM (1994) Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. Ecology 75(2): 532–547. https://doi.org/10.2307/1939556

Gherardi F, Acquistapace P, Hazlett BA, Whisson G (2002) Behavioural responses to alarm odours in indigenous and non-indigenous crayfish species: A case study from Western Australia. Marine and Freshwater Research 53(1): 93–98. https://doi.org/10.1071/MF00131

Gherardi F, Aquiloni L, Diéguez-Uribeondo J, Tricarico E (2011a) Managing invasive crayfish: Is there a hope? Aquatic Sciences 73(2): 185–200. https://doi.org/10.1007/s00027-011-0181-z

Gherardi F, Mavuti KM, Pacini IC, Tricarico E, Harper DM (2011b) The smell of danger: Chemical recognition of fish predators by the invasive crayfish *Procambarus clarkii*. Freshwater Biology 56(8): 1567–1578. https://doi.org/10.1111/j.1365-2427.2011.02595.x

Glon MG, Reisinger LS, Pintor LM (2018) Biogeographic differences between native and non-native populations of crayfish alter species coexistence and trophic interactions in mesocosms. Biological Invasions 20(12): 3475–3490. https://doi.org/10.1007/s10530-018-1788-y

Griffen BD (2021) Considerations when applying the consumer functional response measured under artificial conditions. Frontiers in Ecology and Evolution 9: 713147. https://doi.org/10.3389/fevo.2021.713147

Griffen BD, van den Akker D, DiNuzzo ER, Anderson L, Vernier A (2020) Comparing methods for predicting the impacts of invasive species. Biological Invasions 23(2): 491–505. https://doi.org/10.1007/s10530-020-02377-4

Haddaway NR, Wilcox RH, Heptonstall REA, Griffiths HM, Mortimer RJG, Christmas M, Dunn AM (2012) Predatory functional response and prey choice identify predation differences between native/invasive and parasitised/unparasitised crayfish. PLoS One 7(2): e32229. https://doi.org/10.1371/journal.pone.0032229

Hazlett BA, Burba A, Gherardi F, Acquistapace P (2003) Invasive species of crayfish use a broader range of predation-risk cues than native species. Biological Invasions 5(3): 223–228. https://doi.org/10.1023/A:1026114623612

Hirvonen H, Holopainen S, Lempiäinen N, Selin M, Tulonen J (2007) Sniffing the trade-off: Effects of eel odours on nocturnal foraging activity of native and introduced crayfish juveniles. Marine and Freshwater Behaviour and Physiology 40(3): 213–218. https://doi.org/10.1080/10236240701556919

Holling CS (1959) Some characteristics of simple types of predation and parasitism. Canadian Entomologist 91(7): 385–398. https://doi.org/10.4039/Ent91385-7

Iacarella JC, Hudgins EJ, Dick JTA, Ricciardi A (2018) Predatory behaviour of an invasive amphipod in response to varying conspecific densities under higher-order predation risk. Canadian Journal of Fisheries and Aquatic Sciences 75(1): 131–140. https://doi.org/10.1139/cjfas-2016-0417

Jackson MC, Evangelista C, Zhao T, Lecerf A, Britton JR, Cucherousset J (2017) Between-lake variation in the trophic ecology of an invasive crayfish. Freshwater Biology 62(9): 1501–1510. https://doi.org/10.1111/fwb.12957

Jeschke J, Kopp M, Tollrian R (2004) Consumer-food systems: Why type I functional responses are exclusive to filter feeders. Biological Reviews of the Cambridge Philosophical Society 79(2): 337–349. https://doi.org/10.1017/S1464793103006286

Juliano SA (2001) Nonlinear curve fitting: Predation and functional response curves. In: Scheiner SM, Gurevitch J (Eds), Design and Analysis of Ecological Experiments. Oxford University Press, New York, 178–196.

Kenison EK, Weldy PY, Williams RN (2018) There must be something in the water: Assessing the behavioral responses of rusty crayfish (*Orconectes rusticus*) to fish and amphibian predator kairomones. Journal of Ethology 36(1): 77–84. https://doi.org/10.1007/s10164-017-0529-5

Kreps TA, Baldridge AK, Lodge DM (2012) The impact of an invasive predator (*Orconectes rusticus*) on freshwater snail communities: Insights on habitat-specific effects from a multilake long-term study. Canadian Journal of Fisheries and Aquatic Sciences 69(7): 1164–1173. https://doi.org/10.1139/f2012-052

Kumschick S, Gaertner M, Vilà M, Essl F, Jeschke J, Pyšek P, Ricciardi A, Bacher S, Blackburn TM, Dick JTA, Evans T, Hulme PE, Kühn I, Mrugala A, Pergl J, Rabitsch W, Richardson DM, Sendek A, Winter M (2015) Ecological impacts of alien species: Quantification, scope, caveats, and recommendations. Bioscience 65(1): 55–63. https://doi.org/10.1093/biosci/biu193

Larson ER, Olden JD (2011) The state of crayfish in the Pacific Northwest. Fisheries (Bethesda, Md.) 36(2): 60–73. https://doi.org/10.1577/03632415.2011.10389069

Larson ER, Olden JD (2013) Crayfish occupancy and abundance in lakes of the Pacific Northwest, USA. Freshwater Science 32(1): 94–107. https://doi.org/10.1899/12-051.1

Larson ER, Twardochleb LA, Olden JD (2017) Comparison of trophic function between the globally invasive crayfishes *Pacifastacus leniusculus* and *Procambarus clarkii*. Limnology 18(3): 275–286. https://doi.org/10.1007/s10201-016-0505-8

Latombe G, Catford JA, Essl F, Lenzner B, Richardson DM, Wilson JRU, McGeoch MA (2022) GIRAE: A generalised approach for linking the total impact of invasion to species' range, abundance and per-unit effects. Biological Invasions 24(10): 3147–3167. https://doi.org/10.1007/s10530-022-02836-0

Laundré JW, Hernández L, Ripple WJ (2010) The landscape of fear: Ecological implications of being afraid. The Open Ecology Journal 3(3): 1–7. https://doi.org/10.2174/1874213001003030001

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology 68(4): 619–640. https://doi.org/10.1139/z90-092

Lockwood JL, Hoopes M, Marchetti M (2007) Invasion Ecology. 1st ed. Blackwell Publishing, Oxford, 312 pp.

Lodge DM, Deines A, Gherardi F, Yeo DCJ, Arcella T, Baldridge AK, Barnes MA, Chadderton WL, Feder JL, Gantz CA, Howard GW, Jerde CL, Peters BW, Peters JA, Sargent LW, Turner CR, Wittmann ME, Zeng Y (2012) Global introductions of crayfishes: Evaluating the impact of species invasions on ecosystem services. Annual Review of Ecology, Evolution, and Systematics 43(1): 449–472. https://doi.org/10.1146/annurev-ecolsys-111511-103919

Madzivanzira TC, South J, Weyl OLF (2021) Invasive crayfish outperform Potamonautid crabs at higher temperatures. Freshwater Biology 66(5): 978–991. https://doi.org/10.1111/fwb.13691

Manfrin C, Souty-Grosset C, Anastácio PM, Reynolds J, Giulianini PG (2019) Detection and control of invasive freshwater crayfish: From traditional to innovative methods. Diversity (Basel) 11(1): 5. https://doi.org/10.3390/d11010005

Matsuzaki SIS, Usio N, Takamura N, Washitani I (2009) Contrasting impacts of invasive engineers on freshwater ecosystems: An experiment and meta-analysis. Oecologia 158(4): 673–686. https://doi.org/10.1007/s00442-008-1180-1

McCarthy JM, Hein CL, Olden JD, Jake Vander Zanden M (2006) Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. Freshwater Biology 51(2): 224–235. https://doi.org/10.1111/j.1365-2427.2005.01485.x

Médoc V, Thuillier L, Spataro T (2018) Opportunistic omnivory impairs our ability to predict invasive species impacts from functional response comparisons. Biological Invasions 20(5): 1307–1319. https://doi.org/10.1007/s10530-017-1628-5

Mitchell MD, Bairos-Novak KR, Ferrari MCO (2017) Mechanisms underlying the control of responses to predator odours in aquatic prey. The Journal of Experimental Biology 220(11): 1937–1946. https://doi.org/10.1242/jeb.135137

Oaten A, Murdoch WW (1975) Functional response and stability in predator-prey systems. American Naturalist 109(967): 289–298. https://doi.org/10.1086/282998

Olden JD, Larson ER, Mims MC (2009) Home-field advantage: Native signal crayfish (*Pacifastacus leniusculus*) out consume newly introduced crayfishes for invasive Chinese mystery snail (*Bellamya chinensis*). Aquatic Ecology 43(4): 1073–1084. https://doi.org/10.1007/s10452-009-9244-9

Paolucci EM, MacIsaac HJ, Ricciardi A (2013) Origin matters: Alien consumers inflict greater damage on prey populations than do native consumers. Diversity & Distributions 19(8): 988–995. https://doi.org/10.1111/ddi.12073

Parker IM, Simberloff D, Lonsdale W, Goodell K, Wonham M, Kareiva P, Williamson M, Von Holle B, Moyle P, Byers J, Goldwasser L (1999) Impact: Toward a framework for understanding the ecological effects of invaders. Biological Invasions 1(1): 3–19. https://doi.org/10.1023/A:1010034312781

Paterson RA, Pritchard DW, Dick JTA, Alexander ME, Hatcher MJ, Dunn AM (2013) Predator cue studies reveal strong trait-mediated effects in communities despite variation in experimental designs. Animal Behaviour 86(6): 1301–1313. https://doi.org/10.1016/j.anbehav.2013.09.036

Paterson RA, Dick JTA, Pritchard DW, Ennis M, Hatcher MJ, Dunn AM (2015) Predicting invasive species impacts: A community module functional response approach reveals context dependencies. Journal of Animal Ecology 84(2): 453–463. https://doi.org/10.1111/1365-2656.12292

Peckarsky BL, Abrams PA, Bolnick DI, Dill LM, Grabowski JH, Luttbeg B, Orrock JL, Peacor SD, Preisser EL, Schmitz OJ, Trussell GC (2008) Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator–prey interactions. Ecology 89(9): 2416–2425. https://doi.org/10.1890/07-1131.1

Pintor LM, Sih A (2009) Differences in growth and foraging behavior of native and introduced populations of an invasive crayfish. Biological Invasions 11(8): 1895–1902. https://doi.org/10.1007/s10530-008-9367-2

Pope KL, Garwood JM, Welsh HH, Lawler SP (2008) Evidence of indirect impacts of introduced trout on native amphibians via facilitation of a shared predator. Biological Conservation 141(5): 1321–1331. https://doi.org/10.1016/j.biocon.2008.03.008Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86(2): 501–509. https://doi.org/10.1890/04-0719

Pritchard DW, Paterson RA, Bovy HC, Barrios-O'Neill D (2017) frair: An R package for fitting and comparing consumer functional responses. Methods in Ecology and Evolution 8(11): 1528–1534. https://doi.org/10.1111/2041-210X.12784

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. Biological Reviews of the Cambridge Philosophical Society 95(6): 1511–1534. https://doi.org/10.1111/brv.12627

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ramberg-Pihl NC, Yurewicz KL (2020) Behavioral responses of northern crayfish (*Faxonius virilis*) to conspecific alarm cues and predator cues from smallmouth bass (*Micropterus dolomieu*). Marine and Freshwater Behaviour and Physiology 53(1): 1–16. https://doi.org/10.1080/10236244.2020.1717338</jrn>

Reisinger LS, Elgin AK, Towle KM, Chan DJ, Lodge DM (2017) The influence of evolution and plasticity on the behavior of an invasive crayfish. Biological Invasions 19(3): 815–830. https://doi.org/10.1007/s10530-016-1346-4

Reynolds J, Souty-Grosset C, Richardson A (2013) Ecological roles of crayfish in freshwater and terrestrial habitats. Freshwater Crayfish 19: 197–218. https://doi.org/10.5869/fc.2013.v19-2.197

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs 83(3): 263–282. https://doi.org/10.1890/13-0183.1

Rodríguez Valido CA, Johnson MF, Dugdale SJ, Cutts V, Fell HG, Higgins EA, Tarr S, Templey CM, Algar AC (2021) Thermal sensitivity of feeding and burrowing activity of an invasive crayfish in UK waters. Ecohydrology 14(1): e2258. https://doi.org/10.1002/eco.2258

Rogers D (1972) Random search and insect population models. Journal of Animal Ecology 41(2): 369–383. https://doi.org/10.2307/3474

Rosewarne PJ, Mortimer RJG, Newton RJ, Grocock C, Wing CD, Dunn AM (2016) Feeding behaviour, predatory functional responses and trophic interactions of the invasive Chinese mitten crab (*Eriocheir sinensis*) and signal crayfish (*Pacifastacus leniusculus*). Freshwater Biology 61(4): 426–443. https://doi.org/10.1111/fwb.12717

Ruokonen TJ, Karjalainen J (2022) Divergent temperature-specific metabolic and feeding rates of native and invasive crayfish. Biological Invasions 24(3): 787–799. https://doi.org/10.1007/s10530-021-02687-1

Salo P, Korpimäki E, Banks PB, Nordström M, Dickman CR (2007) Alien predators are more dangerous than native predators to prey populations. Proceedings. Biological Sciences 274(1615): 1237–1243. https://doi.org/10.1098/rspb.2006.0444

Santos DA, Affonso IP, Message HJ, Okada EK, Gomes LC, Bornatowski H, Vitule JRS (2019) Societal perception, impacts and judgment values about invasive freshwater stingrays. Biological Invasions 21(12): 3593–3606. https://doi.org/10.1007/s10530-019-02071-0

Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: The primacy of trait-mediated indirect interactions. Ecology Letters 7(2): 153–163. https://doi.org/10.1111/j.1461-0248.2003.00560.x

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, Van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nature Communications 8(1): 14435. https://doi.org/10.1038/ncomms14435

Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage JS, Vonesh JR (2010) Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119(4): 610–621. https://doi.org/10.1111/j.1600-0706.2009.18039.x

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: Invasional meltdown? Biological Invasions 1: 21–32. https://doi.org/10.1023/A:1010086329619

Solomon ME (1949) The natural control of animal populations. Journal of Animal Ecology 18(1): 1–35. https://doi.org/10.2307/1578

South J, McCard M, Khosa D, Mofu L, Madzivanzira TC, Dick JTA, Weyl OLF (2019) The effect of prey identity and substrate type on the functional response of a globally invasive crayfish. NeoBiota 52: 9–24. https://doi.org/10.3897/neobiota.52.39245

South J, Madzivanzira TC, Tshali N, Measey J, Weyl OLF (2020) In a pinch: Mechanisms behind potential biotic resistance toward two invasive crayfish by native African freshwater crabs. Frontiers in Ecology and Evolution 8: 72. https://doi.org/10.3389/fevo.2020.00072

Stebbing PD, Watson GJ, Bentley MG (2010) The response to disturbance chemicals and predator odours of juvenile and adult signal crayfish *Pacifastacus leniusculus* (Dana). Marine and Freshwater Behaviour and Physiology 43(3): 183–195. https://doi.org/10.1080/10236244.2010.487301

Stein JN (1970) A study of the largemouth bass population in Lake Washington. University of Washington

Strayer DL, D'Antonio CM, Essl F, Fowler MS, Geist J, Hilt S, Jarić I, Jöhnk K, Jones CG, Lambin X, Latzka AW, Pergl J, Pyšek P, Robertson P, Von Schmalensee M, Stefansson RA, Wright J, Jeschke JM. (2017) Boom-bust dynamics in biological invasions: Towards an improved application of the concept. Ecology Letters 20(10): 1337–1350. https://doi.org/10.1111/ele.12822

Taylor NG, Dunn AM (2018) Predatory impacts of alien decapod Crustacea are predicted by functional responses and explained by differences in metabolic rate. Biological Invasions 20(10): 2821–2837. https://doi.org/10.1007/s10530-018-1735-y

Turner AM, Mittelbach GG (1990) Predator avoidance and community structure: Interactions among piscivores, planktivores, and plankton. Ecology 71(6): 2241–2254. https://doi.org/10.2307/1938636

Twardochleb LA, Olden JD, Larson ER (2013) A global meta-analysis of the ecological impacts of nonnative crayfish. Freshwater Science 32(4): 1367–1382. https://doi.org/10.1899/12-203.1

Usio N, Nakata K, Kawai T, Kitano S (2007) Distribution and control status of the invasive signal crayfish (*Pacifastacus leniusculus*) in Japan. Japanese Journal of Limnology 68(3): 471–482. https://doi.org/10.3739/rikusui.68.471

Usio N, Kamiyama R, Saji A, Takamura N (2009) Size-dependent impacts of invasive alien crayfish on a littoral marsh community. Biological Conservation 142(7): 1480–1490. https://doi.org/10.1016/j.biocon.2009.02.016

Vaeßen S, Hollert H (2015) Impacts of the North American signal crayfish (*Pacifastacus leniusculus*) on European ecosystems. Environmental Sciences Europe 27(1): 33. https://doi.org/10.1186/s12302-015-0065-2

Vollmer KL, Gall BG (2014) Complex predator–prey interactions between the rusty crayfish (*Orconectes rusticus*) and invertebrate and vertebrate prey within their native range. Journal of Freshwater Ecology 29(2): 267–277. https://doi.org/10.1080/02705060.2014.888688

Wagner MJ, Moore PA (2022) Are you scared yet? Variations to cue indices elicit differential prey behavioral responses even when gape-limited predators are relatively small. Canadian Journal of Zoology 100(9): 583–595. https://doi.org/10.1139/cjz-2022-0050

Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. Ecology 84(5): 1083–1100. https://doi.org/10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2

Westhoff JT, Rosenberger AE (2016) A global review of freshwater crayfish temperature tolerance, preference, and optimal growth. Reviews in Fish Biology and Fisheries 26(3): 329–349. https://doi.org/10.1007/s11160-016-9430-5

Wood TC, Moore PA (2020a) Big and bad: How relative predator size and dietary information influence rusty crayfish (*Faxonius rusticus*) behavior and resource-use decisions. Canadian Journal of Zoology 98(1): 62–72. https://doi.org/10.1139/cjz-2019-0089

Wood TC, Moore PA (2020b) Fine-tuned responses to chemical landscapes: Crayfish use predator odors to assess threats based on relative sizes. Ecosphere 11(9): e03188. https://doi.org/10.1002/ecs2.3188

Wood TC, Kelley RE, Moore PA (2018) Feeding in fear: Indirect effects of predatory fish on macrophyte communities mediated by altered crayfish foraging behaviour. Freshwater Biology 63(12): 1523–1533. https://doi.org/10.1111/fwb.13181

Zanette LY, Clinchy M (2019) Ecology of fear. Current Biology 29(9): R309–R313. https://doi.org/10.1016/j.cub.2019.02.042

Závorka L, Buoro M, Cucherousset J (2018) The negative ecological impacts of a globally introduced species decrease with time since introduction. Global Change Biology 24(9): 4428–4437. https://doi.org/10.1111/gcb.14323

FINAL REMARKS

This thesis aimed to investigate the contribution of the classical ecological concept of functional response (FR) to the invasion science field, particularly the comparative FR approach. This methodology was proposed in the early 2010s and has been claimed as capable of unifying invasion science since it can be used as a universal metric of invasion impacts. Since its proposal almost 10 years ago, an increasing number of studies started to apply this approach, accumulating important knowledge about its utility and limitations. With that, the need for compiling all this information to provide a critical view and propose novel or sub-explored pathways is urged. Here, three complementary chapters starting from a wide theoretical perspective and a meta-analytical approach, until an applied experiment, investigated that. A summary of the three chapters can be viewed in the Figure 1 below.

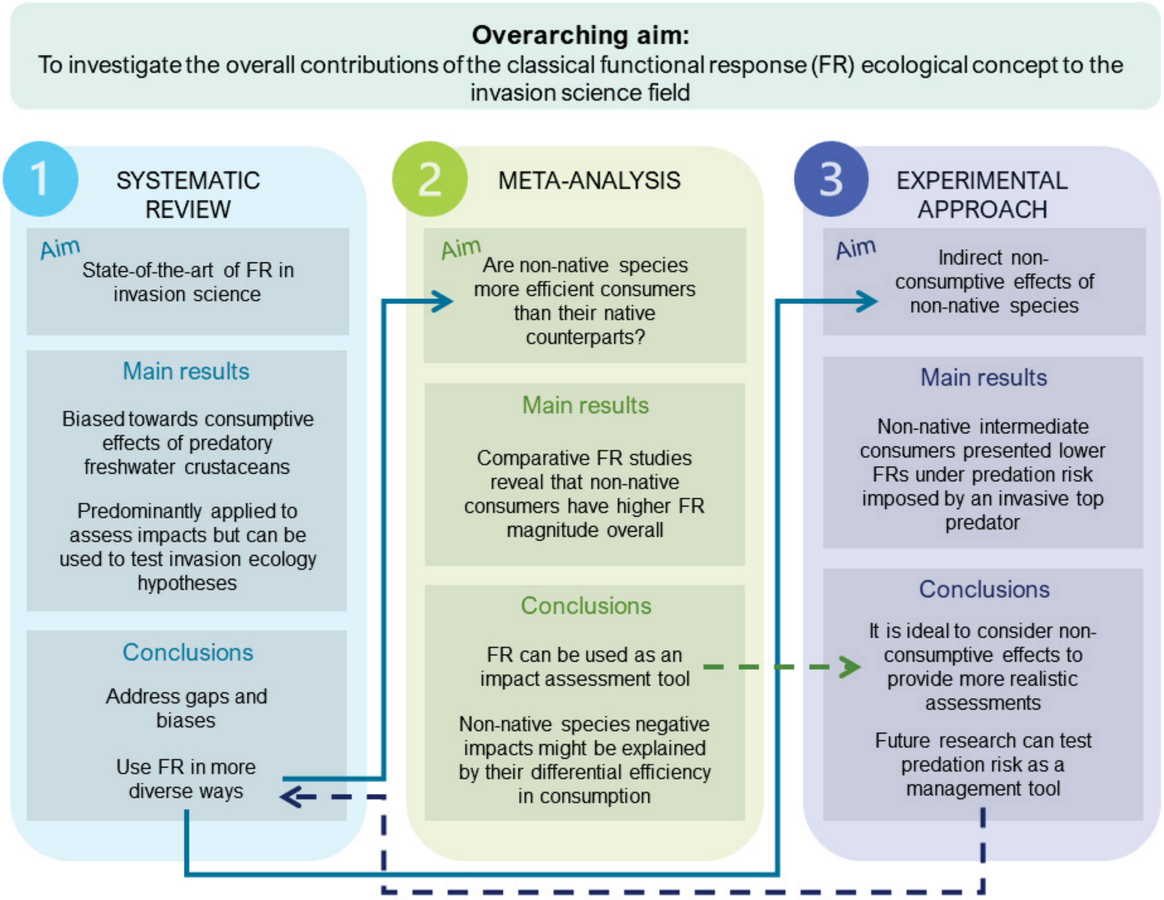


Figure 1. Summary figure showing the overarching aim of this thesis and how it was achieved in three complementary chapters. Numbers are depicting each chapter, characterised by their different methodological approaches. Each chapter's main aim, results and conclusions are summarised in the corresponding boxes. Solid arrows show the direct relationship between the conclusions and aims of each chapter, whereas dashed arrows demonstrate the feedback between chapters' conclusions.

The systematic review revealed conspicuous biases and gaps, as most studies investigate direct consumption effects and single resource-consumer pairs, ignoring other important facets of ecological interactions, such as non-consumptive effects of non-native species (NNS). When focussing on a subset of studies that used the comparative FR approach it was possible to test the underlying hypothesis that NNS are more efficient consumers than trophically analogous native species. The meta-analysis showed that non-native consumers indeed have higher maximum feeding rates than their native counterparts; thus, when it comes to resource exploitation, the species' origin seems to matter. Accordingly, the comparative FR approach is a useful tool to assess that as previously suggested. Finally, after theoretically investigating this approach, it was applied in a still sub-explored design that examines the non-consumptive effects of NNS. The results show the significance of considering a broader biological context of other interactions occurring in nature, to provide more realistic assessments.

Future studies applying this approach should start planning it from the main objective, as illustrated in Figure 2. If it aims to assess NNS impacts through differential consumption of resources, these are the initial steps before conducting the experiments:

- First, identify which is the target non-native consumer and the basic aspects of its ecology where it is native or elsewhere it has invaded.
- After having a good understanding of the target species, it is time to look at the native community, in order to find a suitable native comparator, i.e. a native species that is trophically or functionally similar to the target NNS.
- When consumers are defined, key resources should be identified. These could be food, but also refugia, depending on the context of the interaction between native and NNS. The resource choice can be based on previous impacts of the NNS observed in other communities. It is recommended to choose an ecologically relevant resource to obtain an applicable result.
- After having identified all species involved in the main interaction, it is important to carefully assess which biotic and abiotic contexts may be influencing this interaction such as temperature, habitat complexity, consumer or resource life stage, or the presence of a top predator, for

example. A starting list of applied contexts can be found in the supplementary material of the first chapter (Faria et al. 2023; Appendix 1). As long as possible, all contexts identified as highly influential should be assessed.

- Likewise, having an estimate of the field densities of all species involved in the interaction is a good starting point to define the gradient of resource availability, as well as the arena size.

On the other hand, if the main objective of the study is to test a hypothesis, these are the initial steps:

- First, it is needed to clearly define the question or hypothesis to be tested, such as those suggested in the first chapter (Faria et al. 2023).
- Having this, it is key to select suitable species to be used as consumers and resources, considering species abundances and traits, as well as other logistics, such as ethics restrictions. In this case, an ecologically relevant resource may not be essential to provide the answers sought.
- The next stage will involve delineating the experimental design needed to answer the question or test the hypothesis. Here, it is important to list all the variables that may influence the results obtained, such as biotic and abiotic contexts and species densities.

With all this information, pilot experiments could be performed to define experimental duration, for example, and then the FR experiment itself. At the data analysis step, it is key to be aware of all the available possibilities to fit experimental data to a model, such as flexible models or even the Bayesian approach. The parameters estimated in the laboratory can be used in simulations or mathematical models to predict the effects of the NNS and inform management. Finally, it is desirable to validate the results obtained in the lab setting at the field, conducting *in situ* or mesocosms experiments incorporating more realism. Depending on the habitat and species involved, this could be done using large cages, cameras, or bigger arenas. With the results of many experiments following these basic steps it would be possible to perform meta-analyses and syntheses to advance knowledge in the field.

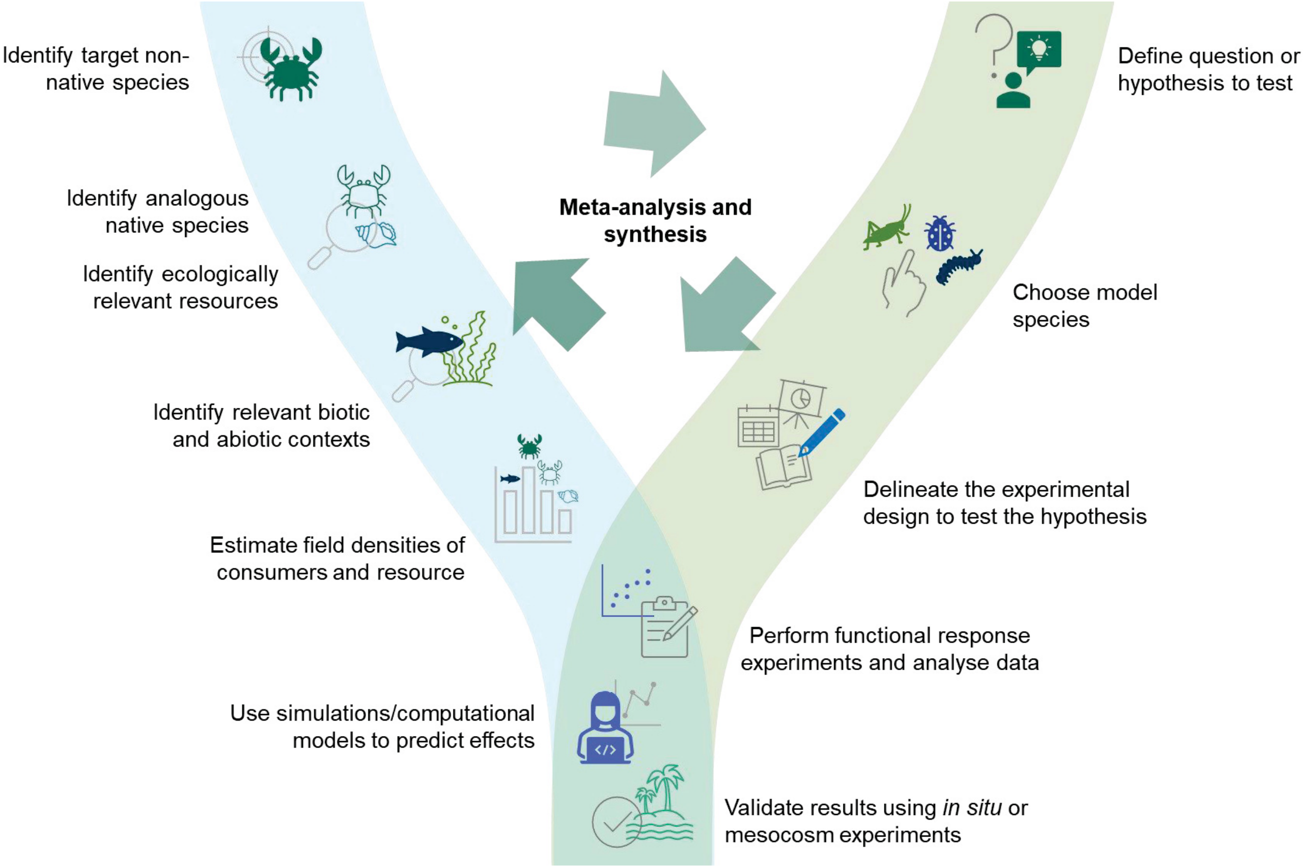


Figure 2. Illustrated roadmap of the main suggested steps to apply the functional response approach to invasion science studies.

To conclude, the contributions of the FR to the invasion science are manifold, and there are still many directions in which this approach can be leveraged. For instance, it can be used for quantifying the relative impacts of NNS, testing several hypotheses in invasion ecology, predicting which NNS will be more impactful in different biotic and abiotic contexts and providing insights for management. Future research should focus on exploring all this potential with creativity to apply it to different taxa and environments as well as to refine the experiments to consider more realistic contexts. This methodology holds promises as a practical and reliable prioritisation tool for NNS management and it could be included in formal assessment protocols. Evidently, the comparative FR approach cannot be understood as the Holy grail of invasion science because, as with any experiment, it is a simplification of reality. However, it can provide a valuable starting point when we are faced with emerging NNS with no history of invasion elsewhere or with many species to manage and limited resources to do so. I hope this thesis serves as a guide or a source of ideas for future research on the topic, hence contributing to improving the method.

REFERENCES

Ahmed, D. A., Hudgins, E. J., Cuthbert, R. N., Haubrock, P. J., Renault, D., Bonnaud, E., Diagne, C., & Courchamp, F. (2022). Modelling the damage costs of invasive alien species. *Biological Invasions*, *24*(7), 1949–1972. https://doi.org/10.1007/S10530-021-02586-5

Alexander, M. E., Dick, J. T. A., & O'Connor, N. E. (2013). Trait-mediated indirect interactions in a marine intertidal system as quantified by functional responses. *Oikos*, *122*(11), 1521–1531. https://doi.org/10.1111/j.1600-0706.2013.00472.x

Alexander, M. E., Dick, J. T. A., O'Connor, N. E., Haddaway, N. R., & Farnsworth, K. D. (2012). Functional responses of the intertidal amphipod *Echinogammarus marinus*: Effects of prey supply, model selection and habitat complexity. *Marine Ecology Progress Series*, *468*, 191–202. https://doi.org/10.3354/meps09978

Alexander, M. E., Dick, J. T. A., Weyl, O. L. F., Robinson, T. B., & Richardson, D. M. (2014). Existing and emerging high impact invasive species are characterized by higher functional responses than natives. *Biology Letters*, *10*, 20130946. https://doi.org/10.1098/rsbl.2013.0946

Alexander, M. E., Kaiser, H., Weyl, O. L. F., & Dick, J. T. A. (2015). Habitat simplification increases the impact of a freshwater invasive fish. *Environmental Biology of Fishes*, *98*(2), 477–486. https://doi.org/10.1007/s10641-014-0278-z

Angulo, E., Diagne, C., Ballesteros-Mejia, L., Adamjy, T., Ahmed, D. A., Akulov, E., Banerjee, A. K., Capinha, C., Dia, C. A. K. M., Dobigny, G., Duboscq-Carra, V. G., Golivets, M., Haubrock, P. J., Heringer, G., Kirichenko, N., Kourantidou, M., Liu, C., Nuñez, M. A., Renault, D., … Courchamp, F. (2021). Non-English languages enrich scientific knowledge: The example of economic costs of biological invasions. *Science of The Total Environment*, *775*, 144441. https://doi.org/10.1016/J.SCITOTENV.2020.144441

Anton, A., Geraldi, N. R., Ricciardi, A., & Dick, J. T. A. (2020). Global determinants of prey naiveté to exotic predators. *Proceedings of the Royal Society B*, *287*. https://doi.org/10.1098/rspb.2019.2978

Ball, S. L., Woodcock, B. A., Potts, S. G., & Heard, M. S. (2015). Size matters: Body size determines functional responses of ground beetle interactions. *Basic and Applied Ecology*, *16*(7), 621–628. https://doi.org/10.1016/j.baae.2015.06.001

Barrios-O'Neill, D., Dick, J. T. A., Emmerson, M. C., Ricciardi, A., & MacIsaac, H. J. (2015). Predator-free space, functional responses and biological invasions. *Functional Ecology*, *29*(3), 377–384. https://doi.org/10.1111/1365-2435.12347

Barrios-O'Neill, D., Dick, J. T. A., Emmerson, M. C., Ricciardi, A., MacIsaac, H. J., Alexander, M. E., & Bovy, H. C. (2014). Fortune favours the bold: A higher predator reduces the impact of a native but not an invasive intermediate predator. *Journal of Animal Ecology*, *83*(3), 693–701. https://doi.org/10.1111/1365-2656.12155

Barrios-O'Neill, D., Kelly, R., Dick, J. T. A., Ricciardi, A., MacIsaac, H. J., & Emmerson, M. C. (2016). On the context-dependent scaling of consumer feeding rates. *Ecology Letters*, *19*(6), 668–678. https://doi.org/10.1111/ele.12605

Beattie, M. C., & Moore, P. A. (2018). Predator recognition of chemical cues in crayfish: Diet and experience influence the ability to detect predation threats. *Behaviour*, *155*(6), 505–530. https://doi.org/10.1163/1568539X-00003501

Begon, M., Townsend, C. R., & Harper, J. L. (2006). *Ecology: From Individuals to Ecosystems* (4th ed.). Blackwell Publishing Ltd.

Bellard, C., Cassey, P., & Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology Letters*, *12*, 1–4. https://doi.org/10.1098/rsbl.2015.0623

Bellard, C., & Jeschke, J. (2016). A spatial mismatch between invader impacts and research publications. *Conservation Biology*, *30*(1), 230–232. https://doi.org/10.1111/cobi.12611

Benhadi-Marín, J., Pereira, J. A., Barreales, D., Sousa, J. P., & Santos, S. A. P. (2018). A simulation-based method to compare the pest suppression potential of predators: A case study with spiders. *Biological Control*, *123*, 87–96. https://doi.org/10.1016/j.biocontrol.2018.05.007

Bergström, U., & Englund, G. (2004). Spatial scale, heterogeneity and functional responses. *Journal of Animal Ecology*, *73*, 487–493. https://doi.org/10.1111/j.0021-8790.2004.00823.x

Blackburn, T. M., Bellard, C., & Ricciardi, A. (2019). Alien versus native species as drivers of recent extinctions. *Frontiers in Ecology and the Environment*, *17*(4), 203–207. https://doi.org/10.1002/fee.2020

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, *26*(7), 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Blake, M. A., & Hart, P. J. B. (1993). The behavioural responses of juvenile signal crayfish *Pacifastacus leniusculus* to stimuli from perch and eels. *Freshwater Biology*, *29*(1), 89–97. https://doi.org/10.1111/j.1365-2427.1993.tb00747.x

Blossey, B., & Nötzold, R. (1995). Evolution of increased competitive ability in invasive nonindigenous plants: A hypothesis. *Journal of Ecology*, *83*(5), 887–889. https://doi.org/10.2307/2261425

Blumenthal, D. M. (2006). Interactions between resource availability and enemy release in plant invasion. *Ecology Letters*, *9*(7), 887–895. https://doi.org/10.1111/j.1461-0248.2006.00934.x

Boets, P., Laverty, C., Fukuda, S., Verreycken, H., Green, K., Britton, R. J., Caffrey, J., Goethals, P. L. M., Pegg, J., Médoc, V., & Dick, J. T. A. (2019). Intra- and intercontinental variation in the functional responses of a high impact alien invasive fish. *Biological Invasions*, *21*, 1751–1762. https://doi.org/10.1007/s10530-019-01932-y

Bolker, B. (2008). *Ecological Models and Data in R*. Princeton University Press. https://doi.org/10.1086/644667

Bollache, L., Dick, J. T. A., Farnsworth, K. D., & Montgomery, W. I. (2008). Comparison of the functional responses of invasive and native amphipods. *Biology Letters*, *4*(2), 166–169. https://doi.org/10.1098/rsbl.2007.0554

Braga, R. R., Gómez-Aparicio, L., Heger, T., Vitule, J. R. S., & Jeschke, J. M. (2017). Structuring evidence for invasional meltdown: Broad support but with biases and gaps. *Biological Invasions*, *20*, 923–936. https://doi.org/10.1007/s10530-017-1582-2

Braga, R. R., Ribeiro, V. M., Padial, A. A., Thomaz, S. M., Affonso, I. P., Wojciechowski, J., Ribas, L. G. S., Cunha, E. R., Tiburcio, V. G., & Vitule, J. R. S. (2020). Invasional meltdown: An experimental test and a framework to distinguish synergistic, additive, and antagonistic effects. *Hydrobiologia*, *847*, 1603–1618. https://doi.org/10.1007/s10750-019-04107-x

Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, *7*(10), 999–1014. https://doi.org/10.1111/j.1461-0248.2004.00661.x

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, *80*(2), 385–399. https://doi.org/10.2307/1383287

Brown, T. G., Runciman, B., Pollard, S., & Grant, A. D. A. (2009). Biological synopsis of largemouth bass (*Micropterus salmoides*). *Canadian Manuscript Report of Fisheries and Aquatic Sciences,* 2884, 27p.

Buba, Y., DeLong, J. P., & Belmaker, J. (2022). Synthesizing drivers of fish functional responses across species. *Fish and Fisheries, 23*(2), 376–391. https://doi.org/10.1111/faf.12622

Buckley, Y. M., & Catford, J. A. (2016). Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *Journal of Ecology*, *104*(1), 4–17. https://doi.org/10.1111/1365-2745.12501

Bunke, M., Dick, J. T. A., Hatcher, M. J., & Dunn, A. M. (2019). Parasites influence cannibalistic and predatory interactions within and between native and invasive amphipods. *Diseases of Aquatic Organisms*, *136*(1), 79–86. https://doi.org/10.3354/dao03415

Caliman, A., Pires, A. F., Esteves, F. A., Bozelli, R. L., & Farjalla, V. F. (2010). The prominence of and biases in biodiversity and ecosystem functioning research.

Biodiversity and Conservation, *19*(3), 651–664. https://doi.org/10.1007/S10531-009-9725-0

Carreira, B. M., Segurado, P., Laurila, A., & Rebelo, R. (2017). Can heat waves change the trophic role of the world’s most invasive crayfish? Diet shifts in *Procambarus clarkii*. *PLOS ONE*, *12*(9), e0183108. https://doi.org/10.1371/journal.pone.0183108

Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, *15*(1), 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Catford, J. A., Wilson, J. R. U., Pyšek, P., Hulme, P. E., & Duncan, R. P. (2022). Addressing context dependence in ecology. *Trends in Ecology & Evolution*, *37*(2), 158–170. https://doi.org/10.1016/j.tree.2021.09.007

Chong, K. Y., Corlett, R. T., Nuñez, M. A., Chiu, J. H., Courchamp, F., Dawson, W., Kuebbing, S., Liebhold, A. M., Padmanaba, M., Souza, L., Andersen, K. M., Fei, S., Lee, B. P. Y.-H., Lum, S., Luskin, M. S., Ngo, K. M., & Wardle, D. A. (2021). Are terrestrial biological invasions different in the tropics? *Annual Review of Ecology, Evolution, and Systematics*, *52*(1), 291–314. https://doi.org/10.1146/annurev-ecolsys-012021-095454

Chucholl, F., & Chucholl, C. (2021). Differences in the functional responses of four invasive and one native crayfish species suggest invader-specific ecological impacts. *Freshwater Biology*, *66*(11), 2051–2063. https://doi.org/10.1111/fwb.13813

Coblentz, K. E., & DeLong, J. P. (2021). Estimating predator functional responses using the times between prey captures. *Ecology*, *102*(4). https://doi.org/10.1002/ecy.3307

Colautti, R. I., Ricciardi, A., Grigorovich, I. A., & MacIsaac, H. J. (2004). Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, *7*(8), 721–733. https://doi.org/10.1111/j.1461-0248.2004.00616.x

Correia, A. M. (2002). Niche breadth and trophic diversity: Feeding behaviour of the red swamp crayfish (*Procambarus clarkii*) towards environmental availability of aquatic macroinvertebrates in a rice field (Portugal). *Acta Oecologica*, *23*(6), 421–429. https://doi.org/10.1016/S1146-609X(02)01166-9

Correia, A. M. (2003). Food choice by the introduced crayfish *Procambarus clarkii*. *Annales Zoologici Fennici*, *40*(6), 517–528.

Cox, J. G., & Lima, S. L. (2006). Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology and Evolution*, *21*(12), 674–680. https://doi.org/10.1016/j.tree.2006.07.011

Crandall, K. A., & Buhay, J. E. (2008). Global diversity of crayfish (Astacidae, Cambaridae, and Parastacidae—Decapoda) in freshwater. *Hydrobiologia*, *595*(1), 295–301. https://doi.org/10.1007/s10750-007-9120-3

Crane, K., Cuthbert, R. N., Ricciardi, A., Kregting, L., Coughlan, N. E., MacIsaac, H. J., Reid, N., & Dick, J. T. A. (2021). Gimme Shelter: Differential utilisation and propagule creation of invasive macrophytes by native caddisfly larvae. *Biological Invasions*, *23*(1), 95–109. https://doi.org/10.1007/s10530-020-02358-7

Crystal-Ornelas, R., & Lockwood, J. L. (2020). The ‘known unknowns’ of invasive species impact measurement. *Biological Invasions*, *22*(4), 1513–1525. https://doi.org/10.1007/s10530-020-02200-0

Cunico, A. M., & Vitule, J. R. S. (2014). First records of the European catfish, *Silurus glanis* Linnaeus, 1758 in the Americas (Brazil). *BioInvasions Records*, *3*(2), 117–122. https://doi.org/10.3391/bir.2014.3.2.10

Cuthbert, R. N., Coughlan, N. E., Dickey, J. W. E., Rea, M., Laverty, C., South, J., Crane, K., McCard, M., & Dick, J. T. A. (2019). Shell shocked: High potential impacts on native prey by non-native turtles irrespective of benthic habitat context. *Aquatic Invasions*, *14*(4), 758–774. https://doi.org/10.3391/ai.2019.14.4.13

Cuthbert, R. N., Dickey, J. W. E., Coughlan, N. E., Joyce, P. W. S., & Dick, J. T. A. (2019). The Functional Response Ratio (FRR): Advancing comparative metrics for predicting the ecological impacts of invasive alien species. *Biological Invasions*, *21*(8), 2543–2547. https://doi.org/10.1007/s10530-019-02002-z

Cuthbert, R. N., Dickey, J. W. E., McMorrow, C., Laverty, C., & Dick, J. T. A. (2018). Resistance is futile: Lack of predator switching and a preference for native prey predict the success of an invasive prey species. *Royal Society Open Science*, *5*(8), 180339. https://doi.org/10.1098/rsos.180339

Cuthbert, R. N., Pattison, Z., Taylor, N. G., Verbrugge, L., Diagne, C., Ahmed, D. A., Leroy, B., Angulo, E., Briski, E., Capinha, C., Catford, J. A., Dalu, T., Essl, F., Gozlan, R. E., Haubrock, P. J., Kourantidou, M., Kramer, A. M., Renault, D., Wasserman, R. J., & Courchamp, F. (2021). Global economic costs of aquatic invasive alien species. *Science of the Total Environment*, *775*(April), 145238. https://doi.org/10.1016/j.scitotenv.2021.145238

Daehler, C. C. (2003). Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 183–211.

Dalal, A., Gallogly, J., Cuthbert, R. N., Laverty, C., Dickey, J. W. E., & Dick, J. T. A. (2021). Ecological impacts of an invasive predator are mediated by the reproductive cycle. *Biological Invasions*, *23*(3), 669–675. https://doi.org/10.1007/s10530-020-02414-2

Daly, E. Z., Chabrerie, O., Massol, F., Facon, B., Hess, M. C. M., Tasiemski, A., Grandjean, F., Chauvat, M., Viard, F., Forey, E., Folcher, L., Buisson, E., Boivin, T., Baltora-Rosset, S., Ulmer, R., Gibert, P., Thiébaut, G., Pantel, J. H., Heger, T., … Renault, D. (2023). A synthesis of biological invasion hypotheses associated with the introduction–naturalisation–invasion continuum. *Oikos*, e09645. https://doi.org/10.1111/oik.09645

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

DeLong, J. P. (2021). *Predator Ecology: Evolutionary ecology of the functional response*. Oxford University Press.

DeLong, J. P., Bachman, G., Gibert, J. P., Luhring, T. M., Montooth, K. L., Neyer, A., & Reed, B. (2018). Habitat, latitude and body mass influence the temperature dependence of metabolic rate. *Biology Letters*, *14*(8). https://doi.org/10.1098/rsbl.2018.0442

DeRoy, E. M., Scott, R., Hussey, N. E., & MacIsaac, H. J. (2020). Density dependence mediates the ecological impact of an invasive fish. *Diversity and Distributions*, *26*(7), 867–880. https://doi.org/10.1111/ddi.13063

Diagne, C., Leroy, B., Vaissière, A. C., Gozlan, R. E., Roiz, D., Jarić, I., Salles, J. M., Bradshaw, C. J. A., & Courchamp, F. (2021). High and rising economic costs of biological invasions worldwide. *Nature*, *592*(7855), 571–576. https://doi.org/10.1038/S41586-021-03405-6

Dick, J. T. A., Alexander, M. E., Jeschke, J., Ricciardi, A., MacIsaac, H. J., Robinson, T. B., Kumschick, S., Weyl, O. L. F., Dunn, A. M., Hatcher, M. J., Paterson, R. A., Farnsworth, K. D., & Richardson, D. M. (2014). Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions*, *16*(4), 735–753. https://doi.org/10.1007/s10530-013-0550-8

Dick, J. T. A., Alexander, M. E., & MacNeil, C. (2013). Natural born killers: An invasive amphipod is predatory throughout its life-history. *Biological Invasions*, *15*(2), 309–313. https://doi.org/10.1007/s10530-012-0287-9

Dick, J. T. A., Alexander, M. E., Ricciardi, A., Laverty, C., Downey, P. O., Xu, M., Jeschke, J., Saul, W.C., Hill, M. P., Wasserman, R., Barrios-O'Neill, D., Weyl, O. L. F., & Shaw, R. H. (2017). Functional responses can unify invasion ecology. *Biological Invasions*, *19*(5), 1667–1672. https://doi.org/10.1007/s10530-016-1355-3

Dick, J. T. A., Armstrong, M., Clarke, H. C., Farnsworth, K. D., Hatcher, M. J., Ennis, M., Kelly, A., & Dunn, A. M. (2010). Parasitism may enhance rather than reduce the predatory impact of an invader. *Biology Letters*, *6*(5), 636–638. https://doi.org/10.1098/rsbl.2010.0171

Dick, J. T. A., Gallagher, K., Avlijas, S., Clarke, H. C., Lewis, S. E., Leung, S., Minchin, D., Caffrey, J., Alexander, M. E., Maguire, C., Harrod, C., Reid, N., Haddaway, N. R., Farnsworth, K. D., Penk, M., & Ricciardi, A. (2013). Ecological impacts of an invasive predator explained and predicted by comparative functional responses. *Biological Invasions*, *15*(4), 837–846. https://doi.org/10.1007/s10530-012-0332-8

Dick, J. T. A., Laverty, C., Lennon, J. J., Barrios-O’Neill, D., Mensink, P. J., Britton, J. R., Médoc, V., Boets, P., Alexander, M. E., Taylor, N. G., Dunn, A. M., Hatcher, M. J., Rosewarne, P. J., Crookes, S., MacIsaac, H. J., Xu, M., Ricciardi, A., Wasserman, R. J., Ellender, B. R., … Caffrey, J. M. (2017). Invader Relative Impact Potential: A new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. *Journal of Applied Ecology*, *54*(4), 1259–1267. https://doi.org/10.1111/1365-2664.12849

Dickey, J. W. E., Arnott, G., McGlade, C. L. O., Moore, A., Riddell, G. E., & Dick, J. T. A. (2022). Threats at home? Assessing the potential ecological impacts and risks of commonly traded pet fishes. *NeoBiota*, *73*, 109–136. https://doi.org/10.3897/neobiota.73.80542

Dickey, J. W. E., Cuthbert, R. N., South, J., Britton, J. R., Caffrey, J., Chang, X., Crane, K., Coughlan, N. E., Fadaei, E., Farnsworth, K. D., Ismar-Rebitz, S. M. H., Joyce, P. W. S., Julius, M., Laverty, C., Lucy, F. E., MacIsaac, H. J., McCard, M., McGlade, C. L. O., Reid, N., … Dick, J. T. A. (2020). On the RIP: using Relative Impact Potential to assess the ecological impacts of invasive alien species. *NeoBiota*, *55*, 27–60. https://doi.org/10.3897/neobiota.55.49547

Dickey, J. W. E., Cuthbert, R. N., Steffen, G. T., Dick, J. T. A., & Briski, E. (2021). Sea freshening may drive the ecological impacts of emerging and existing invasive non-native species. *Diversity and Distributions*, *27*(1), 144–156. https://doi.org/10.1111/ddi.13178

Dodd, J. A., Dick, J. T. A., Alexander, M. E., MacNeil, C., Dunn, A. M., & Aldridge, D. C. (2014). Predicting the ecological impacts of a new freshwater invader: Functional responses and prey selectivity of the ‘killer shrimp’, *Dikerogammarus villosus*, compared to the native *Gammarus pulex*. *Freshwater Biology*, *59*, 337–352. https://doi.org/10.1111/fwb.12268

Dominguez Almela, V., South, J., & Britton, J. R. (2021). Predicting the competitive interactions and trophic niche consequences of a globally invasive fish with threatened native species. *Journal of Animal Ecology*, *90*, 2651–2662. https://doi.org/10.1111/1365-2656.13571

Dorn, N. J., & Wojdak, J. M. (2004). The role of omnivorous crayfish in littoral communities. *Oecologia*, *140*(1), 150–159. https://doi.org/10.1007/S00442-004-1548-9

Ebenhard, T. (1988). Introduced birds and mammals and their ecological effects. *Viltrevy (Swedish Wildlife Research)*, *13*(4), 1–107.

Eby, L. A., Rudstam, L. G., & Kitchell, J. F. (1995). Predator responses to prey population dynamics: An empirical analysis based on Lake Trout growth rates. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*, 1564–1571. https://doi.org/10.1139/f95-149

Eggleston, D. B., Johnson, E. G., Kellison, G. T., & Nadeau, D. A. (2003). Intense removal and non-saturating functional responses by recreational divers on spiny lobster *Panulirus argus*. *Marine Ecology Progress Series*, *257*, 197–207. https://doi.org/10.3354/meps257197

Elton, C. S. (1958). *The Ecology of Invasions by Animals and Plants*. Methuen.

Enders, M., Havemann, F., Ruland, F., Bernard-Verdier, M., Catford, J. A., Gómez-Aparicio, L., Haider, S., Heger, T., Kueffer, C., Kühn, I., Meyerson, L. A., Musseau, C., Novoa, A., Ricciardi, A., Sagouis, A., Schittko, C., Strayer, D. L., Vilà, M., Essl, F., … Jeschke, J. M. (2020). A conceptual map of invasion biology: Integrating hypotheses into a consensus network. *Global Ecology and Biogeography*, *29*(6), 978–991. https://doi.org/10.1111/geb.13082

Englund, G., Öhlund, G., Hein, C. L., & Diehl, S. (2011). Temperature dependence of the functional response. *Ecology Letters*, *14*(9), 914–921. https://doi.org/10.1111/j.1461-0248.2011.01661.x

Evangelista, H. B. A., Thomaz, S. M., & Umetsu, C. A. (2014). An analysis of publications on invasive macrophytes in aquatic ecosystems. *Aquatic Invasions*, *9*(4), 521–528. https://doi.org/10.3391/ai.2014.9.4.10

Faria, L., Cuthbert, R. N., Dickey, J. W. E., Jeschke, J. M., Ricciardi, A., Dick, J. T. A., & Vitule, J. R. S. (2023). The rise of the Functional Response in invasion science: A systematic review. *NeoBiota*, *85*, 43–79. https://doi.org/10.3897/neobiota.85.98902

Farnsworth, K. D., Focardi, S., & Beecham, J. A. (2002). Grassland-herbivore interactions: How do grazers coexist? *The American Naturalist*, *159*(1), 24–39. https://doi.org/10.1086/324114

Franco, A. C. S., García-Berthou, E., & Santos, L. N. (2021). Ecological impacts of an invasive top predator fish across South America. *Science of The Total Environment*, 761, 143296. https://doi.org/10.1016/j.scitotenv.2020.143296

Freestone, A. L., Torchin, M. E., Jurgens, L. J., Bonfim, M., López, D. P., Repetto, M. F., Schlöder, C., Sewall, B. J., & Ruiz, G. M. (2021). Stronger predation intensity and impact on prey communities in the tropics. *Ecology*, *102*(8), e03428. https://doi.org/10.1002/ecy.3428

Fridley, J. D., & Sax, D. F. (2014). The imbalance of nature: Revisiting a Darwinian framework for invasion biology. *Global Ecology and Biogeography*, *23*, 1157–1166. https://doi.org/10.1111/geb.12221

Funk, J. L., & Vitousek, P. M. (2007). Resource-use efficiency and plant invasion in low-resource systems. *Nature*, *446*(7139), 1079–1081. https://doi.org/10.1038/nature05719

Garvey, J. E., Stein, R. A., & Thomas, H. M. (1994). Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. *Ecology*, *75*(2), 532–547. https://doi.org/10.2307/1939556

Gebauer, R., Veselý, L., Kouba, A., Buric, M., & Drozd, B. (2018). Forecasting impact of existing and emerging invasive gobiids under temperature change using comparative functional responses. *Aquatic Invasions*, *13*(2), 289–297. https://doi.org/10.3391/ai.2018.13.2.09

Gherardi, F. (2007). *Biological invaders in inland waters: Profiles, distribution, and threats* (F. Gherardi, Ed.). Springer.

Gherardi, F., Acquistapace, P., Hazlett, B. A., & Whisson, G. (2002). Behavioural responses to alarm odours in indigenous and non-indigenous crayfish species: A case study from Western Australia. *Marine and Freshwater Research*, *53*(1), 93–98. https://doi.org/10.1071/mf00131

Gherardi, F., Aquiloni, L., Diéguez-Uribeondo, J., & Tricarico, E. (2011). Managing invasive crayfish: Is there a hope? *Aquatic Sciences*, *73*(2), 185–200. https://doi.org/10.1007/s00027-011-0181-z

Gherardi, F., Mavuti, K. M., Pacini, I. C., Tricarico, E., & Harper, D. M. (2011). The smell of danger: Chemical recognition of fish predators by the invasive crayfish *Procambarus clarkii*. *Freshwater Biology*, *56*, 1567–1578. https://doi.org/10.1111/j.1365-2427.2011.02595.x

Giacomini, H. C. (2022). Metabolic responses of predators to prey density. *Frontiers in Ecology and Evolution*, *10*. https://doi.org/10.3389/fevo.2022.980812

Gioria, M., & Osborne, B. A. (2014). Resource competition in plant invasions: Emerging patterns and research needs. *Frontiers in Plant Science*, *5*, 501. https://doi.org/10.3389/FPLS.2014.00501

Glon, M. G., Reisinger, L. S., & Pintor, L. M. (2018). Biogeographic differences between native and non-native populations of crayfish alter species coexistence and trophic interactions in mesocosms. *Biological Invasions*, *20*(12), 3475–3490. https://doi.org/10.1007/S10530-018-1788-y

Goss-Custard, J. D., West, A. D., Yates, M. G., Caldow, R. W. G., Stillman, R. A., Bardsley, L., Castilla, J., Castro, M., Dierschke, V., Durell, S. E. A. L. V. dit, Eichhorn, G., Ens, B. J., Exo, K.-M., Udayangani-Fernando, P. U., Ferns, P. N., Hockey, P. A. R., Gill, J. A., Johnstone, I., Kalejta-Summers, B., … Pettifor, R. A. (2006). Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. *Biological Reviews*, *81*(4), 501–529. https://doi.org/10.1111/J.1469-185X.2006.TB00216.X

Gotelli, N. J. (2008). *A Primer of Ecology* (4th ed.). Sinauer Associates, Inc.

Goudswaard, P. C., Witte, F., & Katunzi, E. F. B. (2002). The tilapiine fish stock of Lake Victoria before and after the Nile perch upsurge. *Journal of Fish Biology*, *60*(4), 838–856. https://doi.org/10.1111/j.1095-8649.2002.tb02413.x

Griffen, B. D. (2006). Detecting emergent effects of multiple predator species. *Oecologia*, *148*(4), 702–709. https://doi.org/10.1007/s00442-006-0414-3

Griffen, B. D. (2021). Considerations when applying the consumer functional response measured under artificial conditions. *Frontiers in Ecology and Evolution*, *9*, 713147. https://doi.org/10.3389/fevo.2021.713147

Griffen, B. D., van den Akker, D., DiNuzzo, E. R., Anderson, L., & Vernier, A. (2020). Comparing methods for predicting the impacts of invasive species. *Biological Invasions*, *23*, 491–505. https://doi.org/10.1007/s10530-020-02377-4

Grimm, J., Dick, J. T. A., Verreycken, H., Jeschke, J. M., Linzmaier, S. M., & Ricciardi, A. (2020). Context-dependent differences in the functional responses of conspecific native and non-native crayfishes. *NeoBiota*, *54*, 71–88. https://doi.org/10.3897/neobiota.54.38668

Haddaway, N. R., Wilcox, R. H., Heptonstall, R. E. A., Griffiths, H. M., Mortimer, R. J. G., Christmas, M., & Dunn, A. M. (2012). Predatory functional response and prey choice identify predation differences between native/invasive and parasitised/unparasitised crayfish. *PLoS ONE*, *7*(2), e32229. https://doi.org/10.1371/journal.pone.0032229

Hassell, M. P. (1978). *The Dynamics of Arthopod Predator-Prey Systems* (Vol. 13). Princeton University Press.

Hassell, M. P., & Waage, J. K. (1984). Host-parasitoid population interactions. *Annual Review of Entomology*, *29*(1), 89–114. https://doi.org/10.1146/annurev.en.29.010184.000513

Hazlett, B. A., Burba, A., Gherardi, F., & Acquistapace, P. (2003). Invasive species of crayfish use a broader range of predation-risk cues than native species. *Biological Invasions*, *5*(3), 223–228. https://doi.org/10.1023/A:1026114623612

Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, *80*(4), 1150–1156. https://doi.org/10.2307/177062

Heger, T., Pahl, A. T., Botta-Dukát, Z., Gherardi, F., Hoppe, C., Hoste, I., Jax, K., Lindström, L., Boets, P., Haider, S., Kollmann, J., Wittmann, M. J., & Jeschke, J. (2013). Conceptual frameworks and methods for advancing invasion ecology. *Ambio*, *42*(5), 527–540. https://doi.org/10.1007/s13280-012-0379-x

Heikinheimo, O. (2001). Effect of predation on the low-density dynamics of vendace: Significance of the functional response. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 1909–1923. https://doi.org/10.1139/cjfas-58-10-1909

Higgins, J. P. T., & Thompson, S. G. (2002). Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine*, *21*(11), 1539–1558. https://doi.org/10.1002/sim.1186

Hirvonen, H., Holopainen, S., Lempiäinen, N., Selin, M., & Tulonen, J. (2007). Sniffing the trade-off: Effects of eel odours on nocturnal foraging activity of native and introduced crayfish juveniles. *Marine and Freshwater Behaviour and Physiology*, *40*(3), 213–218. https://doi.org/10.1080/10236240701556919

Hodges, K. E. (2008). Defining the problem: Terminology and progress in ecology. *Frontiers in Ecology and the Environment*, *6*(1), 35–42. https://doi.org/10.1890/060108

Holling, C. S. (1959a). Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, *91*(7), 385–398. https://doi.org/10.4039/Ent91385-7

Holling, C. S. (1959b). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist*, *91*(5), 234–261. https://doi.org/10.4039/Ent91293-5

Hooff, R. C., & Bollens, S. M. (2004). Functional response and potential predatory impact of *Tortanus dextrilobatus*, a carnivorous copepod recently introduced to the San Francisco Estuary. *Marine Ecology Progress Series*, *277*, 167–179. https://doi.org/10.3354/meps277167

Howard, B. R., Barrios-O’Neill, D., Alexander, M. E., Dick, J. T. A., Therriault, T. W., Robinson, T. B., & Côté, I. M. (2018). Functional responses of a cosmopolitan invader demonstrate intraspecific variability in consumer-resource dynamics. *PeerJ*, *6*. https://doi.org/10.7717/peerj.5634

Hui, C., Richardson, D. M., Landi, P., Minoarivelo, H. O., Garnas, J., & Roy, H. E. (2016). Defining invasiveness and invasibility in ecological networks. *Biological Invasions*, *18*(4), 971–983. https://doi.org/10.1007/s10530-016-1076-7

Hulme, P. E. (2021). Unwelcome exchange: International trade as a direct and indirect driver of biological invasions worldwide. *One Earth*, *4*(5), 666–679. https://doi.org/10.1016/J.ONEEAR.2021.04.015

Iacarella, J. C., Dick, J. T. A., Alexander, M. E., & Ricciardi, A. (2015). Ecological impacts of invasive alien species along temperature gradients: Testing the role of environmental matching. *Ecological Applications*, *25*(3), 706–716. https://doi.org/10.1890/14-0545.1

Iacarella, J. C., Dick, J. T. A., & Ricciardi, A. (2015). A spatio-temporal contrast of the predatory impact of an invasive freshwater crustacean. *Diversity and Distributions*, *21*(7), 803–812. https://doi.org/10.1111/ddi.12318

Iacarella, J. C., Hudgins, E. J., Dick, J. T. A., & Ricciardi, A. (2018). Predatory behaviour of an invasive amphipod in response to varying conspecific densities under higher-order predation risk. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*, 131–140. https://doi.org/10.1139/cjfas-2016-0417

Iacarella, J. C., Mankiewicz, P. S., & Ricciardi, A. (2015). Negative competitive effects of invasive plants change with time since invasion. *Ecosphere*, *6*(7), art123. https://doi.org/10.1890/ES15-00147.1

Iacarella, J. C., & Ricciardi, A. (2015). Dissolved ions mediate body mass gain and predatory response of an invasive fish. *Biological Invasions*, *17*(11), 3237–3246. https://doi.org/10.1007/s10530-015-0949-5

IPBES. (2023). *Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Roy, H. E., Pauchard, A., Stoett, P., Renard Truong, T., Bacher, S., Galil, B. S., Hulme, P. E., Ikeda, T., Sankaran, K. V., McGeoch, M. A., Meyerson, L. A., Nuñez, M. A., Ordonez, A., Rahlao, S. J., Schwindt, E., Seebens, H., Sheppard, A. W., and Vandvik, V. https://doi.org/10.5281/zenodo.7430692

IPCC. (2021). Summary for Policymakers. In V. Masson-Delmotte, P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 3–32). Cambridge University Press. https://doi.org/10.1017/9781009157896.001

Jackson, M. C., Evangelista, C., Zhao, T., Lecerf, A., Britton, J. R., & Cucherousset, J. (2017). Between-lake variation in the trophic ecology of an invasive crayfish. *Freshwater Biology*, *62*(9), 1501–1510. https://doi.org/10.1111/fwb.12957

Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D. E., Coscieme, L., Golden, A. S., Guerra, C. A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., & Purvis, A. (2022). The direct drivers of recent global anthropogenic biodiversity loss. *Science Advances*, *8*(45), eabm9982. https://doi.org/10.1126/sciadv.abm9982

Jeschke, J. (2014). General hypotheses in invasion ecology. *Diversity and Distributions, 20*(11), 1229–1234. https://doi.org/10.1111/ddi.12258

Jeschke, J., Bacher, S., Blackburn, T. M., Dick, J. T. A., Essl, F., Evans, T., Gaertner, M., Hulme, P. E., Kuhn, I., Mrugala, A., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D. M., Sendek, A., Vilà, M., Winter, M., & Kumschick, S. (2014). Defining the impact of non-native species. *Conservation Biology*, *28*(5), 1188–1194. https://doi.org/10.1111/cobi.12299

Jeschke, J., Gómez Aparicio, L., Haider, S., Heger, T., Lortie, C., Pyšek, P., & Strayer, D. L. (2012). Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota, 14*, 1–20. https://doi.org/10.3897/neobiota.14.3435

Jeschke, J. M., & Heger, T. (2018). *Invasion Biology: Hypotheses and Evidence*. CABI.

Jeschke, J. M., Kopp, M., & Tollrian, R. (2002). Predator functional responses: Discriminating between handling and digesting prey. *Ecological Monographs*, *72*(1), 95–112. https://doi.org/10.2307/3100087

Jeschke, J. M., Kopp, M., & Tollrian, R. (2004). Consumer-food systems: Why type I functional responses are exclusive to filter feeders. *Biological Reviews*, *79*, 337–349. https://doi.org/10.1017/S1464793103006286

Jeschke, J. M., Lokatis, S., Bartram, I., & Tockner, K. (2019). Knowledge in the dark: Scientific challenges and ways forward. *FACETS*, *4*, 423–441. https://doi.org/10.1139/facets-2019-0007

Johnson, B. M., & Carpenter, S. R. (1994). Functional and numerical responses—A Framework for Fish-Angler Interactions. *Ecological Applications*, *4*(4), 808–821. https://doi.org/10.2307/1942010

Johnson, B. M., Martinez, P. J., Hawkins, J. A., & Bestgen, K. R. (2008). Ranking predatory threats by nonnative fishes in the Yampa River, Colorado, via bioenergetics modeling. *North American Journal of Fisheries Management*, *28*(6), 1941–1953. https://doi.org/10.1577/M07-199.1

Joyce, P. W. S., Dick, J. T. A., & Kregting, L. T. (2020). Lack of biotic resistance to an invasive bivalve irrespective of season or hydrodynamic disturbance. *Journal of Experimental Marine Biology and Ecology*, *528*, 151382. https://doi.org/10.1016/j.jembe.2020.151382

Juliano, S. A. (2001). Nonlinear curve fitting: Predation and functional response curves. In S. M. Scheiner & J. Gurevitch (Eds.), *Design and Analysis of Ecological Experiments* (pp. 178–196). Oxford University Press.

Kalinkat, G., Rall, B. C., Uiterwaal, S. F., & Uszko, W. (2023). Empirical evidence of type III functional responses and why it remains rare. *Frontiers in Ecology and Evolution*, *11*. https://doi.org/10.3389/fevo.2023.1033818

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, *17*(4), 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0

Kemp, J. S., & Aldridge, D. C. (2018). Comparative functional responses to explain the impact of sympatric invasive bivalves (*Dreissena* spp.) under different thermal regimes. *Journal of Molluscan Studies*, *84*, 175–181. https://doi.org/10.1093/mollus/eyy006

Kenison, E. K., Weldy, P. Y., & Williams, R. N. (2018). There must be something in the water: Assessing the behavioral responses of rusty crayfish (*Orconectes rusticus*) to fish and amphibian predator kairomones. *Journal of Ethology*, *36*(1), 77–84. https://doi.org/10.1007/s10164-017-0529-5

Kestrup, Å. M., & Ricciardi, A. (2009). Environmental heterogeneity limits the local dominance of an invasive freshwater crustacean. *Biological Invasions*, *11*(9), 2095–2105. https://doi.org/10.1007/S10530-009-9490-8

Keynes, R. D. (2001). *Charles Darwin's Beagle diary*. Cambridge University Press.

King, W. M., & Wilson, J. B. (2006). Differentiation between native and exotic plant species from a dry grassland: Fundamental responses to resource availability, and growth rates. *Austral Ecology*, *31*(8), 996–1004. https://doi.org/10.1111/j.1442-9993.2006.01693.x

Knauf, A., Litton, C., Cole, R., Sparks, J., Giardina, C., Gerow, K., & Quiñones-Santiago, M. (2021). Nutrient use strategy and not competition determines native and invasive species response to changes in soil nutrient availability. *Restoration Ecology*, *29*. https://doi.org/10.1111/rec.13374

Kreps, T. A., Baldridge, A. K., & Lodge, D. M. (2012). The impact of an invasive predator (*Orconectes rusticus*) on freshwater snail communities: Insights on habitat-specific effects from a multilake long-term study. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(7), 1164–1173. https://doi.org/10.1139/f2012-052

Kruuk, H., & Goudswaard, P. C. (1990). Effects of changes in fish populations in Lake Victoria on the food of otters (*Lutra maculicollis* Schinz and *Aonyx capensis* Lichtenstein). *African Journal of Ecology*, 28(4), 322–329. https://doi.org/10.1111/j.1365-2028.1990.tb01167.x

Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J., Pyšek, P., Ricciardi, A., Bacher, S., Blackburn, T. M., Dick, J. T. A., Evans, T., Hulme, P. E., Kühn, I., Mrugala, A., Pergl, J., Rabitsch, W., Richardson, D. M., Sendek, A., & Winter, M. (2015). Ecological impacts of alien species: Quantification, scope, caveats, and recommendations. *BioScience*, *65*(1), 55–63. https://doi.org/10.1093/biosci/biul93

Kushner, R. B., & Hovel, K. A. (2006). Effects of native predators and eelgrass habitat structure on the introduced Asian mussel *Musculista senhousia* (Benson in Cantor) in southern California. *Journal of Experimental Marine Biology and Ecology*, *332*(2), 166–177. https://doi.org/10.1016/j.jembe.2005.11.011

Lajeunesse, M. J. (2015). Bias and correction for the log response ratio in ecological meta-analysis. *Ecology*, *96*(8), 2056–2063. https://doi.org/10.1890/14-2402.1

Landi, P., McCoy, M. W., & Vonesh, J. R. (2022). Predicting invasive consumer impact via the comparative functional response approach: Linking application to ecological theory. *Biological Invasions*, *24*, 3565–3579. https://doi.org/10.1007/S10530-022-02862-Y

Larson, E. R., & Olden, J. D. (2011). The state of crayfish in the Pacific Northwest. *Fisheries*, *36*(2), 60–73. https://doi.org/10.1577/03632415.2011.10389069

Larson, E. R., & Olden, J. D. (2013). Crayfish occupancy and abundance in lakes of the Pacific Northwest, USA. *Freshwater Science*, *32*(1), 94–107. https://doi.org/10.1899/12-051.1

Larson, E. R., Twardochleb, L. A., & Olden, J. D. (2017). Comparison of trophic function between the globally invasive crayfishes *Pacifastacus leniusculus* and *Procambarus clarkii*. *Limnology*, *18*(3), 275–286. https://doi.org/10.1007/S10201-016-0505-8

Latombe, G., Catford, J. A., Essl, F., Lenzner, B., Richardson, D. M., Wilson, J. R. U., & McGeoch, M. A. (2022). GIRAE: a generalised approach for linking the total impact of invasion to species' range, abundance and per-unit effects. *Biological Invasions*, *24*, 3147–3167. https://doi.org/10.1007/S10530-022-02836-0

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: Ecological implications of being afraid. *The Open Ecology Journal*, *3*(3), 1–7. https://doi.org/10.2174/1874213001003030001

Laverty, C., Brenner, D., McIlwaine, C., Lennon, J. J., Dick, J. T. A., Lucy, F. E., & Christian, K. A. (2017). Temperature rise and parasitic infection interact to increase the impact of an invasive species. *International Journal for Parasitology*, *47*(5), 291–296. https://doi.org/10.1016/j.ijpara.2016.12.004

Leung, B., Lodge, D. M., Finnof, D., Shogren, J. F., Lewis, M. E., & Lamberti, G. (2002). An ounce of prevention or a pound of cure: Bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society B*, *269*, 2407–2413. https://doi.org/10.1098/rspb.2002.2179

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Liu, G., Liu, Z., Li, Y., Chen, F., Gu, B., & Smoak, J. M. (2009). Effects of fish introduction and eutrophication on the cladoceran community in Lake Fuxian, a deep oligotrophic lake in southwest China. Journal of Paleolimnology, 42, 427–435. https://doi.org/10.1007/s10933-008-9286-3

Liu, Y., He, L., Hilt, S., Wang, R., Zhang, H., & Ge, G. (2021). Shallow lakes at risk: Nutrient enrichment enhances top-down control of macrophytes by invasive herbivorous snails. *Freshwater Biology*, *66*(3), 436–446. https://doi.org/10.1111/fwb.13649

Lockwood, J. L., Hoopes, M., & Marchetti, M. (2007). *Invasion Ecology* (1st ed.). Blackwell Publishing.

Lodge, D. M., Deines, A., Gherardi, F., Yeo, D. C. J., Arcella, T., Baldridge, A. K., Barnes, M. A., Chadderton, W. L., Feder, J. L., Gantz, C. A., Howard, G. W., Jerde, C. L., Peters, B. W., Peters, J. A., Sargent, L. W., Turner, C. R., Wittmann, M. E., & Zeng, Y. (2012). Global introductions of crayfishes: Evaluating the impact of species invasions on ecosystem services. *Annual Review of Ecology, Evolution, and*

Systematics, *43*(1), 449–472. https://doi.org/10.1146/annurev-ecolsys-111511-103919

Luger, A. M., South, J., Alexander, M. E., Ellender, B. R., Weyl, O. L. F., & Nagelkerke, L. A. J. (2020). Ecomorphology of largemouth bass relative to a native trophic analogue explains its high invasive impact. *Biological Invasions*, *22*, 2223–2233. https://doi.org/10.1007/s10530-020-02252-2

Ma, C., Li, S., Pu, Z., Tan, J., Liu, M., Zhou, J., Li, H., & Jiang, L. (2016). Different effects of invader-native phylogenetic relatedness on invasion success and impact: A meta-analysis of Darwin's naturalization hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, 283(1838). https://doi.org/10.1098/rspb.2016.0663

MacNeil, C., Dick, J. T. A., Alexander, M. E., Dodd, J., & Ricciardi, A. (2013). Predators vs. Alien: Differential biotic resistance to an invasive species by two resident predators. *NeoBiota*, *19*, 1–19. https://doi.org/10.3897/neobiota.19.4839

Madadi, H., Mohajeri Parizi, E., Allahyari, H., & Enkegaard, A. (2011). Assessment of the biological control capability of *Hippodamia variegata* (Col.: Coccinellidae) using functional response experiments. *Journal of Pest Science*, *84*(4), 447–455. https://doi.org/10.1007/s10340-011-0387-9

Madzivanzira, T. C., South, J., & Weyl, O. L. F. (2021). Invasive crayfish outperform Potamonautid crabs at higher temperatures. *Freshwater Biology*, *66*(5), 978–991. https://doi.org/10.1111/fwb.13691

Manfrin, C., Souty-Grosset, C., Anastácio, P. M., Reynolds, J., & Giulianini, P. G. (2019). Detection and control of invasive freshwater crayfish: From traditional to innovative methods. *Diversity*, *11*(1), Article 1. https://doi.org/10.3390/d11010005

Marescaux, J., Falisse, E., Lorquet, J., Doninck, K. V., Beisel, J.-N., & Descy, J.-P. (2016). Assessing filtration rates of exotic bivalves: Dependence on algae concentration and seasonal factors. *Hydrobiologia*, *777*(1), 67–78. https://doi.org/10.1007/s10750-016-2764-0

Maselou, D. A., Perdikis, D. Ch., Sabelis, M. W., & Fantinou, A. A. (2014). Use of plant resources by an omnivorous predator and the consequences for effective predation. *Biological Control*, *79*, 92–100. https://doi.org/10.1016/j.biocontrol.2014.09.002

Matadha, D., Hamilton, G. C., Lashomb, J. H., & Zhang, J. (2005). Ovipositional preferences and functional response of parasitoids of euonymus scale, *Unaspis euonymi* (Comstock) and San Jose scale, *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae). *Biological Control*, *32*(3), 337–347. https://doi.org/10.1016/j.biocontrol.2004.12.005

Matsuzaki, S. I. S., Usio, N., Takamura, N., & Washitani, I. (2009). Contrasting impacts of invasive engineers on freshwater ecosystems: An experiment and meta-analysis. *Oecologia*, *158*(4), 673–686. https://doi.org/10.1007/s00442-008-1180-1

McCarthy, J. M., Hein, C. L., Olden, J. D., & Vander Zanden, M. J. (2006). Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. *Freshwater Biology*, *51*(2), 224–235. https://doi.org/10.1111/j.1365-2427.2005.01485.x

McGlade, C. L. O., Dickey, J. W. E., Kennedy, R., Donnelly, S., Nelson, C. A., Dick, J. T. A., & Arnott, G. (2022). Behavioural traits of rainbow trout and brown trout may help explain their differing invasion success and impacts. *Scientific Reports*, *12*, 1757. https://doi.org/10.1038/s41598-022-05484-5

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, *14*(11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

McKnight, E., García-Berthou, E., Srean, P., & Rius, M. (2016). Global meta-analysis of native and nonindigenous trophic traits in aquatic ecosystems. *Global Change Biology*, *23*(5), 1861–1870. https://doi.org/10.1111/gcb.13524

Médoc, V., Albert, H., & Spataro, T. (2015). Functional response comparisons among freshwater amphipods: Ratio-dependence and higher predation for *Gammarus pulex* compared to the non-natives *Dikerogammarus villosus* and *Echinogammarus berilloni*. *Biological Invasions*, *17*(12), 3625–3637. https://doi.org/10.1007/s10530-015-0984-2

Médoc, V., & Spataro, T. (2015). Predicting the impact of invasive species: A look forward on the comparative functional response approach. *Revue d’Ecologie (Terre et Vie)*, *70*(12), 114–126. https://doi.org/10.3406/revec.2015.1821

Médoc, V., Thuillier, L., & Spataro, T. (2018). Opportunistic omnivory impairs our ability to predict invasive species impacts from functional response comparisons. *Biological Invasions*, *20*, 1307–1319. https://doi.org/10.1007/s10530-017-1628-5

Melbourne, B. A., Cornell, H. V., Davies, K. F., Dugaw, C. J., Elmendorf, S., Freestone, A. L., Hall, R. J., Harrison, S., Hastings, A., Holland, M., Holyoak, M., Lambrinos, J., Moore, K., & Yokomizo, H. (2007). Invasion in a heterogeneous world: Resistance, coexistence or hostile takeover? *Ecology Letters*, *10*(1), 77–94. https://doi.org/10.1111/J.1461-0248.2006.00987.X

Mengersen, K., Jennions, M. D., & Schmid, C. H. (2013). Statistical Models for the Meta-analysis of Nonindependent Data. In *Handbook of Meta-analysis in Ecology and Evolution* (pp. 255–283). Princeton University Press.

Mistri, M. (2004). Predatory behavior and preference of a successful invader, the mud crab *Dyspanopeus sayi* (Panopeidae), on its bivalve prey. *Journal of Experimental Marine Biology and Ecology*, *312*(2), 385–398. https://doi.org/10.1016/j.jembe.2004.07.012

Mitchell, M. D., Bairos-Novak, K. R., & Ferrari, M. C. O. (2017). Mechanisms underlying the control of responses to predator odours in aquatic prey. *Journal of Experimental Biology*, *220*(11), 1937–1946. https://doi.org/10.1242/jeb.135137

Mofu, L., South, J., Wasserman, R. J., Dalu, T., Woodford, D. J., Dick, J. T. A., & Weyl, O. L. F. (2019). Inter-specific differences in invader and native fish functional responses illustrate neutral effects on prey but superior invader competitive ability. *Freshwater Biology*, *64*, 1655–1663. https://doi.org/10.1111/fwb.13361

Mook, L. J., & Davies, D. M. (1966). The European praying mantis (*Mantis religiosa* L.) as a predator of the red-legged grasshopper *(Melanoplus femurrubrum* (De Geer)). *The Canadian Entomologist*, *98*, 913–918. https://doi.org/10.4039/Ent98913-9

Morrison, W. E., & Hay, M. E. (2011). Feeding and growth of native, invasive and non-invasive alien apple snails (Ampullariidae) in the United States: Invasives eat more and grow more. *Biological Invasions*, *13*(4), 945–955. https://doi.org/10.1007/S10530-010-9881-X

Murdoch, W. W. (1969). Switching in General Predators: Experiments on Predator Specificity and Stability of Prey Populations. *Ecological Monographs*, *39*(4), 335–354. https://doi.org/10.2307/1942352

Murdoch, W. W., & Oaten, A. (1975). Predation and population stability. *Advances in Ecological Research*, *9*, 1–131. https://doi.org/10.1016/S0065-2504(08)60288-3

Murray, G. P. D., Stillman, R. A., & Britton, J. R. (2016). Habitat complexity and food item size modify the foraging behaviour of a freshwater fish. *Hydrobiologia*, *766*(1), 321–332. https://doi.org/10.1007/s10750-015-2465-0

Nakagawa, S., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W. A., Parker, T. H., Sánchez-Tójar, A., Yang, Y., & O'Dea, R. E. (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution*, *13*(1), 4–21. https://doi.org/10.1111/2041-210X.13724

Nakagawa, S., Lagisz, M., O'Dea, R. E., Pottier, P., Rutkowska, J., Senior, A. M., Yang, Y., & Noble, D. W. A. (2023). orchaRd 2.0: An R package for visualising meta-analyses with orchard plots. *Methods in Ecology and Evolution*, *14*(8), 2003–2010. https://doi.org/10.1111/2041-210X.14152

Nakagawa, S., Noble, D. W. A., Lagisz, M., Spake, R., Viechtbauer, W., & Senior, A. M. (2023). A robust and readily implementable method for the meta-analysis of response ratios with and without missing standard deviations. *Ecology Letters*, *26*(2), 232–244. https://doi.org/10.1111/ele.14144

Nakagawa, S., Yang, Y., Macartney, E. L., Spake, R., & Lagisz, M. (2023). Quantitative evidence synthesis: A practical guide on meta-analysis, meta-regression, and publication bias tests for environmental sciences. *Environmental Evidence*, *12*(1), 8. https://doi.org/10.1186/s13750-023-00301-6

Naranjo, S. E., & Hagler, J. R. (2001). Toward the quantification of predation with predator gut immunoassays: A new approach integrating functional response behavior. *Biological Control*, *20*(2), 175–189. https://doi.org/10.1006/bcon.2000.0892

Noble, D. W. A., Lagisz, M., O'dea, R. E., & Nakagawa, S. (2017). Nonindependence and sensitivity analyses in ecological and evolutionary meta-analyses. *Molecular Ecology*, *26*(9), 2410–2425. https://doi.org/10.1111/mec.14031

Norbury, G., & van Overmeire, W. (2019). Low structural complexity of nonnative grassland habitat exposes prey to higher predation. *Ecological Applications*, *29*(2), e01830. https://doi.org/10.1002/eap.1830

Novak, M., & Stouffer, D. B. (2021). Systematic bias in studies of consumer functional responses. *Ecology Letters*, *24*(3), 580–593. https://doi.org/10.1111/ele.13660

Novoa, A., Richardson, D. M., Pyšek, P., Meyerson, L. A., Bacher, S., Canavan, S., Catford, J. A., Čuda, J., Essl, F., Foxcroft, L. C., Genovesi, P., Hirsch, H., Hui, C., Jackson, M. C., Kueffer, C., Le Roux, J. J., Measey, J., Mohanty, N. P., Moodley, D., … Wilson, J. R. U. (2020). Invasion syndromes: A systematic approach for predicting biological invasions and facilitating effective management. *Biological Invasions*, *22*(5), 1801–1820. https://doi.org/10.1007/S10530-020-02220-W

Oaten, A., & Murdoch, W. W. (1975). Functional response and stability in predator-prey systems. *The American Naturalist*, *109*(967), 289–298. https://doi.org/10.1086/282998

Olden, J. D., Larson, E. R., & Mims, M. C. (2009). Home-field advantage: Native signal crayfish (*Pacifastacus leniusculus*) out consume newly introduced crayfishes for invasive Chinese mystery snail (*Bellamya chinensis*). *Aquatic Ecology*, *43*(4), 1073–1084. https://doi.org/10.1007/s10452-009-9244-9

Otturi, G., Reggi, P. E., Battini, M. Á., & Barriga, J. P. (2020). The effects of trophic interaction between the Patagonian native *Percichthys trucha* and the invasive *Oncorhynchus mykiss* during the juvenile period. *Biological Invasions*, *22*(11), 3293–3305. https://doi.org/10.1007/s10530-020-02324-3

Paolucci, E. M., MacIsaac, H. J., & Ricciardi, A. (2013). Origin matters: Alien consumers inflict greater damage on prey populations than do native consumers. *Diversity and Distributions*, *19*, 988–995. https://doi.org/10.1111/ddi.12073

Papanikolaou, N. E., Kypraios, T., Moffat, H., Fantinou, A., Perdikis, D. P., & Drovandi, C. (2021). Predators' Functional Response: Statistical Inference, Experimental Design, and Biological Interpretation of the Handling Time. *Frontiers in Ecology and Evolution*, *9*, 740848. https://doi.org/10.3389/FEVO.2021.740848

Parker, I. M., Simberloff, D., Lonsdale, W., Goodell, K., Wonham, M., Kareiva, P., Williamson, M., Von Holle, B., Moyle, P., Byers, J., & Goldwasser, L. (1999). Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, *1*, 3–19. https://doi.org/10.1023/A:1010034312781

Paterson, R. A., Dick, J. T. A., Pritchard, D. W., Ennis, M., Hatcher, M. J., & Dunn, A. M. (2015). Predicting invasive species impacts: A community module functional response approach reveals context dependencies. *Journal of Animal Ecology*, *84*, 453–463. https://doi.org/10.1111/1365-2656.12292

Paterson, R. A., Pritchard, D. W., Dick, J. T. A., Alexander, M. E., Hatcher, M. J., & Dunn, A. M. (2013). Predator cue studies reveal strong trait-mediated effects in communities despite variation in experimental designs. *Animal Behaviour*, *86*(6), 1301–1313. https://doi.org/10.1016/j.anbehav.2013.09.036

Peckarsky, B. L., Abrams, P. A., Bolnick, D. I., Dill, L. M., Grabowski, J. H., Luttbeg, B., Orrock, J. L., Peacor, S. D., Preisser, E. L., Schmitz, O. J., & Trussell, G. C. (2008). Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology*, *89*(9), 2416–2425. https://doi.org/10.1890/07-1131.1

Pelicice, F. M., & Agostinho, A. A. (2009). Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. *Biological Invasions*, 11, 1789–1801. https://doi.org/10.1007/s10530-008-9358-3

Pelicice, F. M., Latini, J. D., & Agostinho, A. A. (2015). Fish fauna disassembly after the introduction of a voracious predator: Main drivers and the role of the invader's demography. *Hydrobiologia*, 746(1), 271–283. https://doi.org/10.1007/s10750-014-1911-8

Pellan, L., Médoc, V., Renault, D., Spataro, T., & Piscart, C. (2016). Feeding choice and predation pressure of two invasive gammarids, *Gammarus tigrinus* and *Dikerogammarus villosus*, under increasing temperature. *Hydrobiologia*, *781*, 43–54. https://doi.org/10.1007/s10750-015-2312-3

Penk, M., Saul, W.C., Dick, J. T. A., Donohue, I., Alexander, M. E., Linzmaier, S., & Jeschke, J. M. (2017). A trophic interaction framework for identifying the invasive capacity of novel organisms. *Methods in Ecology and Evolution*, *8*(12), 1786–1794. https://doi.org/10.1111/2041-210X.12817

Pintor, L. M., & Sih, A. (2009). Differences in growth and foraging behavior of native and introduced populations of an invasive crayfish. *Biological Invasions*, *11*(8), 1895–1902. https://doi.org/10.1007/s10530-008-9367-2

Poley, K., Bahlai, C., & Grieshop, M. (2018). Functional response of generalist predators to *Halyomorpha halys* (Hemiptera: Pentatomidae) eggs. *Environmental Entomology*, *47*(5), 1117–1127. https://doi.org/10.1093/ee/nvy110

Pope, K. L., Garwood, J. M., Welsh, H. H., & Lawler, S. P. (2008). Evidence of indirect impacts of introduced trout on native amphibians via facilitation of a shared predator. *Biological Conservation, 141*(5), 1321–1331. https://doi.org/10.1016/j.biocon.2008.03.008

Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, *86*(2), 501–509. https://doi.org/10.1890/04-0719

Pritchard, D. W., Paterson, R. A., Bovy, H. C., & Barrios-O’Neill, D. (2017). frair: An R package for fitting and comparing consumer functional responses. *Methods in Ecology and Evolution*, *8*(11), 1528–1534. https://doi.org/10.1111/2041-210X.12784

Pustejovsky, J. E., & Tipton, E. (2022). Meta-analysis with Robust Variance Estimation: Expanding the Range of Working Models. *Prevention Science*, *23*(3), 425–438. https://doi.org/10.1007/s11121-021-01246-3

Pyšek, P., Bacher, S., Kühn, I., Novoa, A., Catford, J. A., Hulme, P. E., Pergl, J., Richardson, D. M., Wilson, J. R. U., & Blackburn, T. M. (2020). MAcroecological Framework for Invasive Aliens (MAFIA): Disentangling large-scale context dependence in biological invasions. *NeoBiota*, *62*, 407–461. https://doi.org/10.3897/neobiota.62.52787

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., … Richardson, D. M. (2020). Scientists’ warning on invasive alien species. *Biological Reviews*, *95*(6), 1511–1534. https://doi.org/10.1111/brv.12627

Pyšek, P., Richardson, D. M., Pergl, J., Jarošík, V., Sixtová, Z., & Weber, E. (2008). Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution*, *23*(5), 237–244. https://doi.org/10.1016/j.tree.2008.02.002

Radford, I. J. (2013). Fluctuating resources, disturbance and plant strategies: Diverse mechanisms underlying plant invasions. *Journal of Arid Land*, *5*(3), 284–297. https://doi.org/10.1007/s40333-013-0164-0

Radford, I. J., Dickinson, K. J. M., & Lord, J. M. (2007). Functional and performance comparisons of invasive *Hieracium lepidulum* and co-occurring species in New Zealand. *Austral Ecology*, *32*(3), 338–354. https://doi.org/10.1111/j.1442-9993.2007.01700.x

Ramberg-Pihl, N. C., & Yurewicz, K. L. (2020). Behavioral responses of northern crayfish (*Faxonius virilis*) to conspecific alarm cues and predator cues from smallmouth bass (*Micropterus dolomieu*). *Marine and Freshwater Behaviour and Physiology*, *53*(1), 1–16. https://doi.org/10.1080/10236244.2020.1717338

R Core Team. (2021). *R: A language and environment for statistical computing* [Computer software]. R Foundation for Statistical Computing. https://www.r-project.org/

R Core Team. (2023). *R: A language and environment for statistical computing* [Computer software]. R Foundation for Statistical Computing. https://www.r-project.org/

Reisinger, L. S., Elgin, A. K., Towle, K. M., Chan, D. J., & Lodge, D. M. (2017). The influence of evolution and plasticity on the behavior of an invasive crayfish. *Biological Invasions*, *19*(3), 815–830. https://doi.org/10.1007/s10530-016-1346-4

Reynolds, J., Souty-Grosset, C., & Richardson, A. (2013). Ecological roles of crayfish in freshwater and terrestrial habitats. *Freshwater Crayfish*, *19*, 197–218. https://doi.org/10.5869/fc.2013.v19-2.197

Ricciardi, A., & Atkinson, S. K. (2004). Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecology Letters*, *7*, 781–784. https://doi.org/10.1111/j.1461-0248.2004.00642.x

Ricciardi, A., & Cohen, J. (2007). The invasiveness of an introduced species does not predict its impact. *Biological Invasions*, *9*(3), 309–315. https://doi.org/10.1007/s10530-006-9034-4

Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs*, *83*(3), 263–282. https://doi.org/10.1890/13-0183.1

Ricciardi, A., Iacarella, J. C., Aldridge, D. C., Blackburn, T. M., Carlton, J. T., Catford, J. A., Dick, J. T. A., Hulme, P. E., Jeschke, J. M., Liebhold, A. M., Lockwood, J. L., MacIsaac, H. J., Meyerson, L. A., Pyšek, P., Richardson, D. M., Ruiz, G. M., Simberloff, D., Vilà, M., & Wardle, D. A. (2021). Four priority areas to advance invasion science in the face of rapid environmental change. *Environmental Reviews*, *29*(2), 119–141. https://doi.org/10.1139/er-2020-0088

Ricciardi, A., & Kipp, R. (2008). Predicting the number of ecologically harmful exotic species in an aquatic system. *Diversity and Distributions*, *14*(2), 374–380. https://doi.org/10.1111/j.1472-4642.2007.00451.x

Ricciardi, A., & MacIsaac, H. J. (2008). The book that began invasion ecology. *Nature*, *452*, 34.

Richardson, D. M., & Pyšek, P. (2007). Elton, C.S. 1958: The ecology of invasions by animals and plants. London: Methuen. *Progress in Physical Geography: Earth and Environment*, *31*(6), 539–667. https://doi.org/10.1177/0309133307087089

Richardson, D. M., & Pyšek, P. (2008). Fifty years of invasion ecology – the legacy of Charles Elton. *Diversity and Distributions*, *14*(2), 161–168. https://doi.org/10.1111/J.1472-4642.2007.00464.X

Richardson, D. M., & Ricciardi, A. (2013). Misleading criticisms of invasion science: A field guide. *Diversity and Distributions*, *19*(12), 1461–1467. https://doi.org/10.1111/ddi.12150

Robertson, P. A., Mill, A., Novoa, A., Jeschke, J. M., Essl, F., Gallardo, B., Geist, J., Jarić, I., Lambin, X., Musseau, C., Pergl, J., Pyšek, P., Rabitsch, W., von Schmalensee, M., Shirley, M., Strayer, D. L., Stefansson, R. A., Smith, K., & Booy, O. (2020). A proposed unified framework to describe the management of biological invasions. *Biological Invasions*, *22*(9), 2633–2645. https://doi.org/10.1007/S10530-020-02298-2

Rodríguez Valido, C. A., Johnson, M. F., Dugdale, S. J., Cutts, V., Fell, H. G., Higgins, E. A., Tarr, S., Templey, C. M., & Algar, A. C. (2021). Thermal sensitivity of feeding and burrowing activity of an invasive crayfish in UK waters. *Ecohydrology*, *14*(1), e2258. https://doi.org/10.1002/eco.2258

Rogers, D. (1972). Random search and insect population models. *Journal of Animal Ecology*, *41*(2), 369–383. https://doi.org/10.2307/3474

Romanuk, T. N., Zhou, Y., Brose, U., Berlow, E. L., Williams, R. J., & Martinez, N. D. (2009). Predicting invasion success in complex ecological networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1524), 1743–1754. https://doi.org/10.1098/rstb.2008.0286

Rosenbaum, B., & Rall, B. C. (2018). Fitting functional responses: Direct parameter estimation by simulating differential equations. *Methods in Ecology and Evolution*, *9*(10), 2076–2090. https://doi.org/10.1111/2041-210X.13039

Rosewarne, P. J., Mortimer, R. J. G., Newton, R. J., Grocock, C., Wing, C. D., & Dunn, A. M. (2016). Feeding behaviour, predatory functional responses and trophic interactions of the invasive Chinese mitten crab (*Eriocheir sinensis*) and signal crayfish (*Pacifastacus leniusculus*). *Freshwater Biology*, *61*, 426–443. https://doi.org/10.1111/fwb.12717

Rossiter-Rachor, N. A., Setterfield, S. A., Douglas, M. M., Hutley, L. B., Cook, G. D., & Schmidt, S. (2009). Invasive *Andropogon gayanus* (gamba grass) is an ecosystem transformer of nitrogen relations in Australian savanna. *Ecological Applications*, *19*(6), 1546–1560. https://doi.org/10.1890/08-0265.1

Rubio-Aparicio, M., López-López, J. A., Viechtbauer, W., Marín-Martínez, F., Botella, J., & Sánchez-Meca, J. (2020). Testing Categorical Moderators in Mixed-Effects Meta-analysis in the Presence of Heteroscedasticity. *The Journal of Experimental Education*, *88*(2), 288–310. https://doi.org/10.1080/00220973.2018.1561404

Ruokonen, T. J., & Karjalainen, J. (2022). Divergent temperature-specific metabolic and feeding rates of native and invasive crayfish. *Biological Invasions*, *24*(3), 787–799. https://doi.org/10.1007/s10530-021-02687-1

Salo, P., Korpimäki, E., Banks, P. B., Nordström, M., & Dickman, C. R. (2007). Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B*, *274*, 1237–1243. https://doi.org/10.1098/rspb.2006.0444

Santos, D. A., Affonso, I. P., Message, H. J., Okada, E. K., Gomes, L. C., Bornatowski, H., & Vitule, J. R. S. (2019). Societal perception, impacts and judgment values about invasive freshwater stingrays. *Biological Invasions*, *21*(12), 3593–3606. https://doi.org/10.1007/s10530-019-02071-0

Saul, W. C., & Jeschke, J. (2015). Eco-evolutionary experience in novel species interactions. *Ecology Letters*, *18*(3), 236–245. https://doi.org/10.1111/ele.12408

Saul, W. C., Jeschke, J., & Heger, T. (2013). The role of eco-evolutionary experience in invasion success. *NeoBiota, 17*, 57–74. https://doi.org/10.3897/neobiota.17.5208

Savino, V., Coviella, C. E., & Luna, M. G. (2012). Reproductive biology and functional response of *Dineulophus phtorimaeae*, a natural enemy of the tomato moth, *Tuta absoluta*. *Journal of Insect Science*, *12*, 153. https://doi.org/10.1673/031.012.15301

Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecology Letters*, *7*(2), 153–163. https://doi.org/10.1111/J.1461-0248.2003.00560.X

Seebens, H., Bacher, S., Blackburn, T. M., Capinha, C., Dawson, W., Dullinger, S., Genovesi, P., Hulme, P. E., van Kleunen, M., Kühn, I., Jeschke, J. M., Lenzner, B., Liebhold, A. M., Pattison, Z., Pergl, J., Pyšek, P., Winter, M., & Essl, F. (2021). Projecting the continental accumulation of alien species through to 2050. *Global Change Biology*, *27*(5), 970–982. https://doi.org/10.1111/GCB.15333

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435. https://doi.org/10.1038/ncomms14435

Sher, A. A., & Hyatt, L. A. (1999). The Disturbed Resource-Flux Invasion Matrix: A New Framework for Patterns of Plant Invasion. *Biological Invasions*, *1*(2), 107–114. https://doi.org/10.1023/A:1010050420466

Sih, A., Bolnick, D. I., Luttbeg, B., Orrock, J. L., Peacor, S. D., Pintor, L. M., Preisser, E., Rehage, J. S., & Vonesh, J. R. (2010). Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos*, *119*(4), 610–621. https://doi.org/10.1111/j.1600-0706.2009.18039.x

Simberloff, D. (2006a). Invasional meltdown 6 years later: Important phenomenon, unfortunate metaphor, or both? *Ecology Letters*, *9*(8), 912–919. https://doi.org/10.1111/j.1461-0248.2006.00939.x

Simberloff, D. (2006b). Risk assessments, blacklists, and white lists for introduced species: Are predictions good enough to be useful? *Agricultural and Resource Economics Review*, *35*(1), 1–10. https://doi.org/10.1017/S1068280500010005

Simberloff, D. (2011). Charles Elton: Neither Founder Nor Siren, But Prophet. In D. M. Richardson (Ed.), *Fifty Years of Invasion Ecology: The Legacy of Charles Elton* (pp. 11–24). Blackwell Publishing.

Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions*, *1*, 21–32. https://doi.org/10.1023/A:1010086329619

Simberloff, D., Martin, J. L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., & Vilà, M. (2013). Impacts of biological invasions: What's what and the way forward. *Trends in Ecology and Evolution*, *28*(1), 58–66. https://doi.org/10.1016/j.tree.2012.07.013

Simberloff, D., & Rejmanek, M. (2011). *Encyclopedia of Biological Invasions*. University of California Press.

Simberloff, D., Souza, L., Nũnez, M. A., Barrios-Garcia, M. N., & Bunn, W. (2012). The natives are restless, but not often and mostly when disturbed. *Ecology*, *93*(3), 598–607. https://doi.org/10.1890/11-1232.1

Simberloff, D., & Vitule, J. R. S. (2014). A call for an end to calls for the end of invasion biology. *Oikos*, *123*, 408–413. https://doi.org/10.1111/j.1600-0706.2013.01228.x

Sinclair, A. R. E., Olsen, P. D., & Redhead, T. D. (1990). Can predators regulate small mammal populations? Evidence from house mouse outbreaks in Australia. *Oikos*, *59*(3), 382–392. https://doi.org/10.2307/3545150

Sinclair, A. R. E., Pech, R. P., Dickman, C. R., Hik, D., Mahon, P., & Newsome, A. E. (1998). Predicting effects of predation on conservation of endangered prey. *Conservation Biology*, *12*(3), 564–575. https://doi.org/10.1046/j.1523-1739.1998.97030.x

Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S., Thirgood, S., & Harwood, J. (2010). The functional response of a generalist predator. *PLoS ONE*, *5*(5). https://doi.org/10.1371/journal.pone.0010761

Smout, S., Rindorf, A., Wanless, S., Daunt, F., Harris, M. P., & Matthiopoulos, J. (2013). Seabirds maintain offspring provisioning rate despite fluctuations in prey abundance: A multi-species functional response for guillemots in the North Sea. *Journal of Applied Ecology*, *50*(4), 1071–1079. https://doi.org/10.1111/1365-2664.12095

Solomon, M. E. (1949). The natural control of animal populations. *Journal of Animal Ecology*, *18*(1), 1–35. https://doi.org/10.2307/1578

Sorte, C. J. B., Ibáñez, I., Blumenthal, D. M., Molinari, N. A., Miller, L. P., Grosholz, E. D., Diez, J. M., D'Antonio, C. M., Olden, J. D., Jones, S. J., & Dukes, J. S. (2013). Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. *Ecology Letters*, *16*(2), 261–270. https://doi.org/10.1111/ele.12017

South, J., Dick, J. T. A., McCard, M., Barrios-O'Neill, D., & Anton, A. (2017). Predicting predatory impact of juvenile invasive lionfish (*Pterois volitans*) on a crustacean prey using functional response analysis: Effects of temperature, habitat complexity and light regimes. *Environmental Biology of Fishes*, *100*, 1155–1165. https://doi.org/10.1007/s10641-017-0633-y

South, J., Madzivanzira, T. C., Tshali, N., Measey, J., & Weyl, O. L. F. (2020). In a pinch: Mechanisms behind potential biotic resistance toward two invasive crayfish by native African freshwater crabs. *Frontiers in Ecology and Evolution*, *8*, 72. https://doi.org/10.3389/fevo.2020.00072

South, J., McCard, M., Khosa, D., Mofu, L., Madzivanzira, T. C., Dick, J. T. A., & Weyl, O. L. F. (2019). The effect of prey identity and substrate type on the functional response of a globally invasive crayfish. *NeoBiota*, *52*, 9–24. https://doi.org/10.3897/neobiota.52.39245

Stebbing, P. D., Watson, G. J., & Bentley, M. G. (2010). The response to disturbance chemicals and predator odours of juvenile and adult signal crayfish *Pacifastacus leniusculus* (Dana). *Marine and Freshwater Behaviour and Physiology*, *43*(3), 183–195. https://doi.org/10.1080/10236244.2010.487301

Stein, J. N. (1970). *A study of the largemouth bass population in Lake Washington* [Master's thesis]. University of Washington, Seattle.

Strayer, D. L. (2010). Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology*, *55*, 152–174. https://doi.org/10.1111/j.1365-2427.2009.02380.x

Strayer, D. L., D'Antonio, C. M., Essl, F., Fowler, M. S., Geist, J., Hilt, S., Jarić, I., Jöhnk, K., Jones, C. G., Lambin, X., Latzka, A. W., Pergl, J., Pyšek, P., Robertson, P., Von Schmalensee, M., Stefansson, R. A., Wright, J., & Jeschke, J. M. (2017). Boom-bust dynamics in biological invasions: Towards an improved application of the concept. *Ecology Letters, 20*(10), 1337–1350. https://doi.org/10.1111/ele.12822

Strayer, D. L., Eviner, V. T., Jeschke, J. M., & Pace, M. L. (2006). Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution*, *21*(11), 645–651. https://doi.org/10.1016/j.tree.2006.07.007

Swanepoel, L. H., Somers, M. J., & Dalerum, F. (2015). Functional responses of retaliatory killing versus recreational sport hunting of leopards in South Africa. *PLoS ONE*, *10*(4), 1–11. https://doi.org/10.1371/journal.pone.0125539

Tanner-Smith, E. E., & Tipton, E. (2014). Robust variance estimation with dependent effect sizes: Practical considerations including a software tutorial in Stata and SPSS: Robust variance estimation. *Research Synthesis Methods*, *5*(1), 13–30. https://doi.org/10.1002/jrsm.1091

Taylor, N. G., & Dunn, A. M. (2018). Predatory impacts of alien decapod Crustacea are predicted by functional responses and explained by differences in metabolic rate. *Biological Invasions*, *20*(10), 2821–2837. https://doi.org/10.1007/s10530-018-1735-y

Thomsen, M. S., Olden, J. D., Wernberg, T., Griffin, J. N., & Silliman, B. R. (2011). A broad framework to organize and compare ecological invasion impacts. *Environmental Research*, *111*(7), 899–908. https://doi.org/10.1016/j.envres.2011.05.024

Tilman, D. (1977). Resource competition between plankton algae: An experimental and theoretical approach. *Ecology*, *58*(2), 338–348. https://doi.org/10.2307/1935608

Tilves, U., Purcell, J. E., Marambio, M., Canepa, A., Olariaga, A., & Fuentes, V. (2013). Predation by the scyphozoan *Pelagia noctiluca* on *Mnemiopsis leidyi* ctenophores in the NW Mediterranean Sea. *Journal of Plankton Research*, *35*(1), 218–224. https://doi.org/10.1093/plankt/fbs082

Toscano, B. J., & Griffen, B. D. (2013). Predator size interacts with habitat structure to determine the allometric scaling of the functional response. *Oikos*, *122*(3), 454–462. https://doi.org/10.1111/j.1600-0706.2012.20690.x

Toscano, B. J., Newsome, B., & Griffen, B. D. (2014). Parasite modification of predator functional response. *Oecologia*, *175*(1), 345–352. https://doi.org/10.1007/s00442-014-2905-y

Turner, A. M., & Mittelbach, G. G. (1990). Predator avoidance and community structure: Interactions among piscivores, planktivores, and plankton. *Ecology*, *71*(6), 2241–2254. https://doi.org/10.2307/1938636

Twardochleb, L. A., Novak, M., & Moore, J. W. (2012). Using the functional response of a consumer to predict biotic resistance to invasive prey. *Ecological Applications*, *22*(4), 1162–1171. https://doi.org/10.1890/11-0871.1

Twardochleb, L. A., Olden, J. D., & Larson, E. R. (2013). A global meta-analysis of the ecological impacts of nonnative crayfish. *Freshwater Science*, *32*(4), 1367–1382. https://doi.org/10.1899/12-203.1

Uiterwaal, S. F., Dell, A. I., & Delong, J. P. (2019). Arena size modulates functional responses via behavioral mechanisms. *Behavioral Ecology*, *30*(2), 483–489. https://doi.org/10.1093/BEHECO/ARY188

Uiterwaal, S. F., & DeLong, J. P. (2020). Functional responses are maximized at intermediate temperatures. *Ecology*, *101*(4), 1–10. https://doi.org/10.1002/ecy.2975

Uiterwaal, S. F., Lagerstrom, I. T., Lyon, S. R., & DeLong, J. P. (2022). FoRAGE database: A compilation of functional responses for consumers and parasitoids. *Ecology*, *103*, e3706. https://doi.org/10.1002/ECY.3706

Usio, N., Kamiyama, R., Saji, A., & Takamura, N. (2009). Size-dependent impacts of invasive alien crayfish on a littoral marsh community. *Biological Conservation*, *142*(7), 1480–1490. https://doi.org/10.1016/j.biocon.2009.02.016

Usio, N., Nakata, K., Kawai, T., & Kitano, S. (2007). Distribution and control status of the invasive signal crayfish (*Pacifastacus leniusculus*) in Japan. *Japanese Journal of Limnology*, *68*(3), 471–482. https://doi.org/10.3739/rikusui.68.471

Uszko, W., Diehl, S., & Wickman, J. (2020). Fitting functional response surfaces to data: A best practice guide. *Ecosphere*, *11*(4), e03051. https://doi.org/10.1002/ECS2.3051

Vaeßen, S., & Hollert, H. (2015). Impacts of the North American signal crayfish (*Pacifastacus leniusculus*) on European ecosystems. *Environmental Sciences Europe*, *27*, 33. https://doi.org/10.1186/S12302-015-0065-2

Valéry, L., Fritz, H., Lefeuvre, J.-C. C., & Simberloff, D. (2008). In search of a real definition of the biological invasion phenomenon itself. *Biological Invasions*, *10*(8), 1345–1351. https://doi.org/10.1007/s10530-007-9209-7

Van Driesche, R., Bellows, T. S., & Van Driesche, R. (1996). *Biological Control*. Chapman & Hall [u.a.].

Vatland, S., & Budy, P. (2007). Predicting the invasion success of an introduced omnivore in a large, heterogeneous reservoir. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(10), 1329–1345. https://doi.org/10.1139/f07-100

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*(3), 1–48.

Vollmer, K. L., & Gall, B. G. (2014). Complex predator–prey interactions between the rusty crayfish (*Orconectes rusticus*) and invertebrate and vertebrate prey within their native range. *Journal of Freshwater Ecology*, *29*(2), 267–277. https://doi.org/10.1080/02705060.2014.888688

Vonesh, J., McCoy, M., Altwegg, R., Landi, P., & Measey, J. (2017). Functional responses can't unify invasion ecology. *Biological Invasions*, *19*(5), 1673–1676. https://doi.org/10.1007/s10530-016-1356-2

Vucic-Pestic, O., Rall, B. C., Kalinkat, G., & Brose, U. (2010). Allometric functional response model: Body masses constrain interaction strengths. *Journal of Animal Ecology*, *79*, 249–256. https://doi.org/10.1111/j.1365-2656.2009.01622.x

Wagner, M. J., & Moore, P. A. (2022). Are you scared yet? Variations to cue indices elicit differential prey behavioral responses even when gape-limited predators are relatively small. *Canadian Journal of Zoology*, *100*, 583–595. https://doi.org/10.1139/cjz-2022-0050

Wang, X., Biondi, A., & Daane, K. M. (2020). Functional responses of three candidate asian larval parasitoids evaluated for classical biological control of *Drosophila suzukii* (Diptera: Drosophilidae). *Journal of Economic Entomology*, *113*(1), 73–80. https://doi.org/10.1093/jee/toz265

Werner, E. E., & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, *15*(1), 393–425. https://doi.org/10.1146/annurev.es.15.110184.002141

Werner, E. E., & Peacor, S. D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, *84*(5), 1083–1100. https://doi.org/10.1890/0012-9658

Westhoff, J. T., & Rosenberger, A. E. (2016). A global review of freshwater crayfish temperature tolerance, preference, and optimal growth. *Reviews in Fish Biology and Fisheries*, *26*(3), 329–349. https://doi.org/10.1007/s11160-016-9430-5

Wood, T. C., Kelley, R. E., & Moore, P. A. (2018). Feeding in fear: Indirect effects of predatory fish on macrophyte communities mediated by altered crayfish foraging behaviour. *Freshwater Biology*, *63*(12), 1523–1533. https://doi.org/10.1111/fwb.13181

Wood, T. C., & Moore, P. A. (2020a). Big and bad: How relative predator size and dietary information influence rusty crayfish (*Faxonius rusticus*) behavior and resource-use decisions. *Canadian Journal of Zoology*, *98*(1), 62–72. https://doi.org/10.1139/cjz-2019-0089

Wood, T. C., & Moore, P. A. (2020b). Fine-tuned responses to chemical landscapes: Crayfish use predator odors to assess threats based on relative sizes. *Ecosphere*, *11*(9), e03188. https://doi.org/10.1002/ecs2.3188

Xu, M., Mu, X., Dick, J. T. A., Fang, M., Gu, D., Luo, D., Zhang, J., Luo, J., & Hu, Y. (2016). Comparative functional responses predict the invasiveness and ecological impacts of alien herbivorous snails. *PLoS ONE*, *11*(1), e0147017. https://doi.org/10.1371/journal.pone.0147017

Yodzis, P. (1994). Predator-prey theory and management of multispecies fisheries. *Ecological Applications*, *4*(1), 51–58. https://doi.org/10.2307/1942114

Zanette, L. Y., & Clinchy, M. (2019). Ecology of fear. *Current Biology*, *29*(9), R309–R313. https://doi.org/10.1016/j.cub.2019.02.042

Závorka, L., Buoro, M., & Cucherousset, J. (2018). The negative ecological impacts of a globally introduced species decrease with time since introduction. *Global Change Biology*, *24*(9), 4428–4437. https://doi.org/10.1111/gcb.14323

APPENDIX 1 – SUPPLEMENTARY MATERIAL FROM CHAPTER 1 “THE RISE OF THE FUNCTIONAL RESPONSE IN INVASION SCIENCE: A SYSTEMATIC REVIEW”

Supplementary material 1

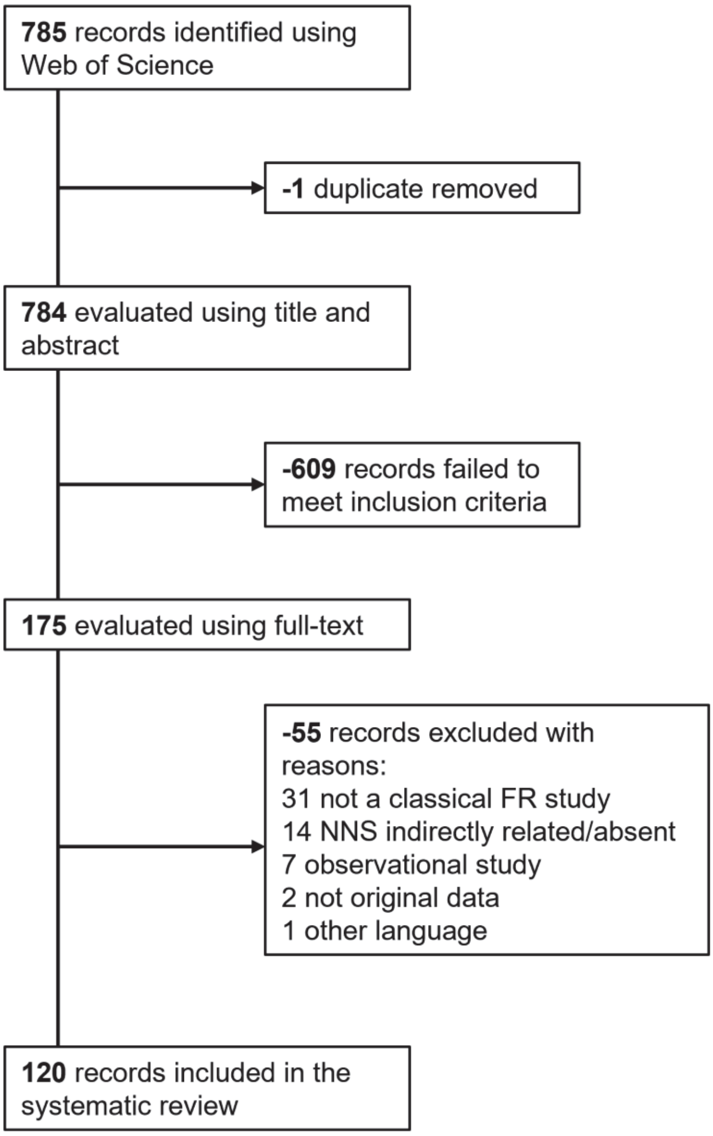


Figure S1. Flow chart showing the steps followed to evaluate studies that used the Functional Response (FR) related to non-native species (NNS) included in the systematic review.

Supplementary material 2

Table S1. List of the data extracted from publications included in the systematic review.

Field	Description
Publication year	Publication year in issue[a]
Journal	Journal name
Country	Country of the corresponding author
Study category	Biological control, biotic resistance, or impact assessment
Type of interaction	Predation, parasitism, herbivory or filter-feeding
Habitat	Freshwater, marine/brackish water or terrestrial
Consumer origin	Native, non-native, both or non-identified
Resource origin	Native, non-native, both or non-identified
Consumer taxonomic group	Algae and plants, amphibians and reptiles, crustaceans, fishes, insects, mammals, molluscs, or other invertebrates
Consumer(s) species	Consumer species Latin name
Resource taxonomic group	Algae and plants, amphibians and reptiles, crustaceans, fishes, insects, mammals, molluscs, or other invertebrates
Resource(s) species	Resource species Latin name
Contexts	Biotic, abiotic, both or none
Number of treatments	Number of different contexts tested
Treatment type	Description of the contexts (e.g. temperature, life stage, etc)
FR type	I, II, III, or not defined (for each Functional Response curve)

[a] Note that even limiting our search in the Web of Science up to 2020, some papers published in issue in 2021 were included because they were indexed in the database as Early View papers. However, we recorded the year of publication in issue (2021).

Supplementary material 3

Journal trends analysis

We recorded the number of publications *per* journal. As each journal publishes variable numbers of papers *per* year, it is necessary to account for this bias (journals that publish more papers *per* year are likely to have published more papers on any given subject). To do that, a formula for relative weight was used (Braga et al. 2012, Frehse et al. 2016):

$$w = \left(\frac{n}{p \times e \times y}\right) \times 1000$$

where *p* is the average number of papers published in the journal's first edition of each year, *e* is the average number of editions *per* year, *y* is the total number of years that the journal has published papers within the period of this review, and *n* is the number of resulting papers of this review for each journal. To create a proxy of the number of editions and papers published *per* journal, we used a subset of six years (1966, 1976, 1986, 1996, 2006, and 2016) to calculate the formula. This was done only for journals that were more relevant in the review, i.e. had more than one published paper.

In total, 50 different journals published papers about FR and NNS. Of these, only 24 published more than one paper. The most relevant sources were: *Biological Invasions* (n = 19), followed by *Biological Control* and *Freshwater Biology* (n = 6 each), *Environmental Entomology* and *NeoBiota* (n = 5 each). Together, these five journals published 34% of the papers in this review. *NeoBiota* and *Biological Invasions* were the journals with the highest calculated weight (i.e. highest number of publications in this review relative to the total number of publications) (Fig. S2).

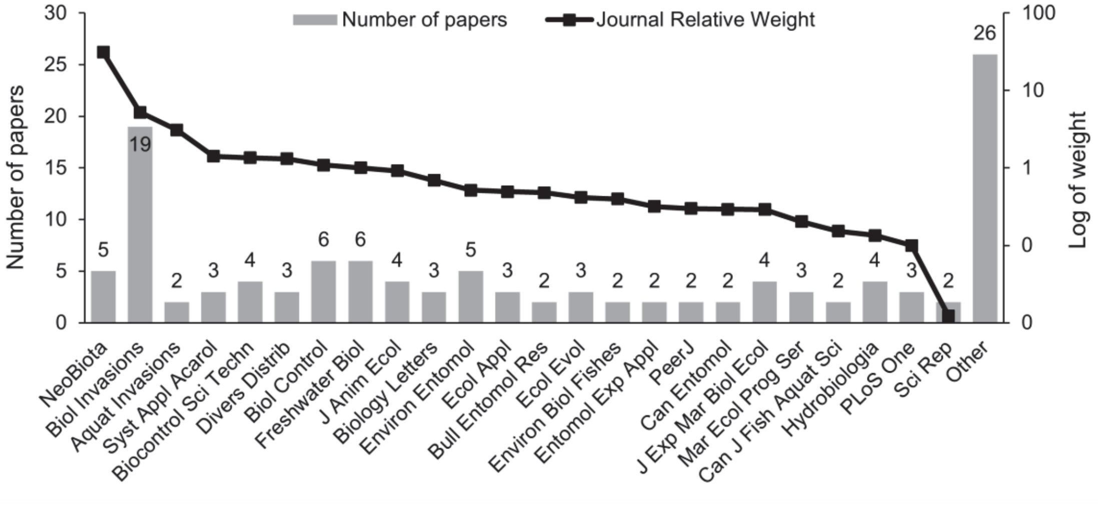


Figure S2. The weighted pattern of journals that published studies using Functional Response in invasion science, ordered by relative weight. Bars represent the raw number of resulting papers for each journal. The light grey line represents the relative weight of each journal. Relative weight was log transformed to facilitate visualisation (please note the different scale on the right).

References

Braga RR, Bornatowski H, Vitule JRS (2012) Feeding ecology of fishes: An overview of worldwide publications. Reviews in Fish Biology and Fisheries 22(4): 915–929. https://doi.org/10.1007/s11160-012-9273-7

Frehse FA, Braga RR, Nocera GA, Vitule JRS (2016) Non-native species and invasion biology in a megadiverse country: Scientometric analysis and ecological interactions in Brazil. Biological Invasions 18(12): 3713–3725. https://doi.org/10.1007/s10530-016-1260-9

Supplementary material 4

Table S2. List of treatments used by the studies deriving Functional Response (FR) curves under different biotic and abiotic contexts. The list of references can be found in Supplementary material 5.

Context	Treatment	Description	References
Abiotic			
	Depth	The study analysed the FR in different depths in the aquatic environment.	Barrios-O'Neill et al. 2014b
	Disturbance	The study analysed the FR in different hydrodynamic disturbance levels (e.g. high vs low).	Joyce et al. 2020
	Experimental time	The study derived FR curves using different total experimental periods.	Ruscoe et al. 2005, Bollache et al. 2008, Kestrup et al. 2011
	Field vs. laboratory	The study derived FR curves in the laboratory and in the field using cage enclosures.	Sallam et al. 1999
	Habitat complexity	The study analysed the FR in different levels of habitat complexity (e.g. none, low, medium, high).	Kushner & Hovel 2006, Alexander et al. 2015a, Barrios-O'Neill et al. 2015, South et al. 2017, Norbury et al. 2019

	Light regime	The study performed FR trials under different light experimental treatments.	South et al. 2017
	Physicochemical parameters	The study performed FR trials under different treatments of water physicochemical parameters (e.g. conductivity, salinity or dissolved oxygen).	Kestrup et al. 2011, Laverty et al. 2015, Iacarella & Ricciardi 2015, Dickey et al. 2021
	Period of the day	The study analysed the FR in different periods of the day (e.g. daytime and night).	Barrios-O'Neill et al. 2014b
	Season	The study repeated the same FR procedure in at least two different seasons (e.g. summer and winter). It was not simply a temperature variation, but performing the FR trial in different periods of the year.	Greenwood et al. 2020, Joyce et al. 2020
	Site	The study analysed the FR in different sites in the aquatic environment (e.g. shallow or deep).	Barrios-O'Neill et al. 2014b
	Substrate	The study analysed the FR using different substrates in the experimental arena (e.g. none, sandy, gravel)	Dodd et al. 2014, Gebauer et al. 2019, Cuthbert et al. 2019b, South et al. 2019
	Temperature	The study performed FR trials under different temperatures.	Wang & Ferro 1998, Jones et al. 2003, Hooff & Bollens 2004, Mahdian et al. 2006, Iacarella et al. 2015a, Marescaux et al. 2016, Pellan et al. 2016, Xu et al. 2016a, Laverty et al. 2017a, South et al. 2017, Kemp & Aldridge 2018, Gebauer et al. 2018, Benhadi-Marín et al. 2018, Mu et al. 2019, Mofu et al. 2019a, Haubrock et al. 2020
Biotic			
	Alternative resource	The study tested the FR of the consumer offering just one resource and the	Médoc et al. 2018, Crane et al. 2021

		same resource plus an alternative one.	
	Size	The study tested the FR of different consumer size classes or assessed the effect of variations in predator–prey body size ratios (combinations of predator and prey size classes).	Dodd et al. 2014, Taylor & Dunn 2017, Cuthbert et al. 2020
	Interactions	The study investigated the effect of other ecological interactions on the FR of a focal consumer. Includes studies that used more than one consumer *per* trial (in intra- or interspecific combinations), studies that used a higher-order predator, and studies that investigated cannibalism (offering juveniles of the predator species as prey) and intraguild predation (offering juveniles of other species of the same trophic guild as prey). In competition arrangements some studies kept the competitor enclosed and some studies allowed them to feed together.	Barrios-O'Neill et al. 2014a, Paterson et al. 2015, Slaughter et al. 2016, Bunke et al. 2019, Mofu et al. 2019b, Grimm et al. 2020, DeRoy et al. 2020a, Otturi et al. 2020
	Consumer experience	The study investigated the effect of the consumer's previous experience with the resource (e.g experienced consumer and naïve consumer).	Mendes et al. 2018
	Consumer life stage	The study tested the FR of the consumer while varying its developmental life stage (e.g. juveniles and adults).	Koch et al. 2003, Tilves et al. 2013, Mu et al. 2019, Seyfollahi et al. 2019, Fincham et al. 2019, Haubrock et al. 2020, Ren et al. 2020, Dalal et al. 2021
	Consumer origin (population)	The study compared the FR of different origins (native and non-native) of the same species using	Bollache et al. 2008, Howard et al. 2018, Boets et al. 2019, Grimm et al. 2020

		populations from its native and introduced ranges.	
	Consumer origin (species)	The study compared the FR of different origins (native and non-native) using different consumer species of the same location.	Sallam et al. 1999, Jones et al. 2003, Bollache et al. 2008, Kestrup et al. 2011, Farazmand et al. 2012, Haddaway et al. 2012, Kögel et al. 2013, Dick et al. 2013, Alexander et al. 2014, Dodd et al. 2014, Hoki et al. 2014, Barrios-O'Neill et al. 2014a, Barrios-O'Neill et al. 2014b, Bovy et al. 2015, Paterson et al. 2015, Barrios-O'Neill et al. 2015, Laverty et al. 2015, Médoc et al. 2015, Xu et al. 2016b, Rosewarne et al. 2016, Taylor & Dunn 2017, Laverty et al. 2017b, Guo et al. 2017, Iltis et al. 2018, Médoc et al. 2018, Poley et al. 2018, Hoxha et al. 2018, Taylor & Dunn 2018, Kemp et al. 2018, Bunke et al. 2019, Crookes et al. 2019, Paton et al. 2019, Hoxha et al. 2019, Britton et al. 2019, Mofu et al. 2019b, Mofu et al. 2019a, Fincham et al. 2019, Faria et al. 2019, DeRoy et al. 2020b, Otturi et al. 2020, Carvalho et al. 2020, Dickey et al. 2021
	Consumer sex	The study analysed the FR of both sexes of the consumer.	Li et al. 2017, Poley et al. 2018, Linzmaier & Jeschke 2020
	Consumer source	The study analysed the FR of the same species from different sources (e.g. wild and commercial stock).	Linzmaier & Jeschke 2020
	Infection	The study investigated the effect of an infection/parasitism on the FR of the consumer (e.g. healthy and infected, unparasitised and parasitised). Some studies used naturally infected individuals, whereas other	Dick et al. 2010, Haddaway et al. 2012, Paterson et al. 2015, Laverty et al. 2017a, Iltis et al. 2018, Bunke et al. 2019, Fincham et al. 2019

		infected them in the laboratory.	
	Invasion gradient	The study compared the FR of different populations of the same species, collected in several locations along the invasion pathway gradient (e.g. invasion front and well-established/low- or high density sites).	Iacarella et al. 2015b, Paton et al. 2019
	Resource exposition	The study used a resource species that builds a defensive structure around its body (e.g. tubeless individuals and individuals in mud tube).	Bovy et al. 2015
	Resource life stage	The study tested the FR of the consumer while varying the developmental life stage of the resource (e.g. eggs, larvae, adults).	Koch et al. 2003, Farazmand et al. 2012, Renkema et al. 2015, Slaughter et al. 2016, Li et al. 2017, Patel & Zhang 2017, Rios-Velasco et al. 2017, Seyfollahi et al. 2019, Viteri Jumbo et al. 2019, Guleria et al. 2021
	Resource origin (species)	The study compared the FR of different origins (native and non-native) using different resource species of the same location.	Sallam et al. 1999, Hooff & Bollens 2004, Griswold & Lounibos 2005, Kestrup et al. 2011, Zuharah & Lester 2011, Bovy et al. 2015, Alexander et al. 2015b, Giacoletti et al. 2016, Cuthbert et al. 2018c, Bunke et al. 2019, Joyce et al. 2019, Cuthbert et al. 2019a, Pacheco et al. 2020, Joyce et al. 2020
	Starvation time	The study varied the total period of starvation of the consumer prior the trials.	Gonçalves et al. 2016

Supplementary material 5

List of publications included in the systematic review:

Alexander ME, Dick JTA, Weyl OLF, Robinson TB, Richardson DM (2014) Existing and emerging high impact invasive species are characterized by higher functional responses than natives. Biology Letters 10: 20130946. https://doi.org/10.1098/rsbl.2013.0946

Alexander ME, Kaiser H, Weyl OLF, Dick JTA (2015) Habitat simplification increases the impact of a freshwater invasive fish. Environmental Biology of Fishes 98: 477–486. https://doi.org/10.1007/s10641-014-0278-z

Alexander ME, Raven HJ, Robinson TB (2015) Foraging decisions of a native whelk, *Trochia cingulata* Linnaeus, and the effects of invasive mussels on prey choice. Journal of Experimental Marine Biology and Ecology 470: 26–33. https://doi.org/10.1016/j.jembe.2015.04.023

Barrios-O'Neill D, Dick JTA, Emmerson MC, Ricciardi A, MacIsaac HJ (2015) Predator-free space, functional responses and biological invasions. Functional Ecology 29: 377–384. https://doi.org/10.1111/1365-2435.12347

Barrios-O'Neill D, Dick JTA, Emmerson MC, Ricciardi A, MacIsaac HJ, Alexander ME, Bovy HC (2014) Fortune favours the bold: A higher predator reduces the impact of a native but not an invasive intermediate predator. Journal of Animal Ecology 83: 693–701. https://doi.org/10.1111/1365-2656.12155

Barrios-O'Neill D, Dick JTA, Ricciardi A, MacIsaac HJ, Emmerson MC (2014) Deep impact: *in situ* functional responses reveal context-dependent interactions between vertically migrating invasive and native mesopredators and shared prey. Freshwater Biology 59: 2194–2203. https://doi.org/10.1111/fwb.12423

Benhadi-Marín J, Pereira JA, Barreales D, Sousa JP, Santos SAP (2018) A simulation-based method to compare the pest suppression potential of predators: a case study with spiders. Biological Control 123: 87–96. https://doi.org/10.1016/j.biocontrol.2018.05.007

Bezemer TM, Mills NJ (2001) Host density responses of *Mastrus ridibundus*, a parasitoid of the codling moth, *Cydia pomonella*. Biological Control 22: 169–175. https://doi.org/10.1006/bcon.2001.0963

Bodino N, Ferracini C, Tavella L (2019) Functional response and age-specific foraging behaviour of *Necremnus tutae* and *N. cosmopterix*, native natural enemies of the invasive pest *Tuta absoluta* in Mediterranean area. Journal of Pest Science 92: 1467–1478. https://doi.org/10.1007/s10340-018-1025-6

Boets P, Laverty C, Fukuda S, Verreycken H, Green K, Britton RJ, Caffrey J, Goethals PLM, Pegg J, Médoc V, Dick JTA (2019) Intra- and intercontinental variation in the functional responses of a high impact alien invasive fish. Biological Invasions 21: 1751–1762. https://doi.org/10.1007/s10530-019-01932-y

Bollache L, Dick JTA, Farnsworth KD, Montgomery WI (2008) Comparison of the functional responses of invasive and native amphipods. Biology Letters 4: 166–169. https://doi.org/10.1098/rsbl.2007.0554

Bovy HC, Barrios-O’Neill D, Emmerson MC, Aldridge DC, Dick JTA (2015) Predicting the predatory impacts of the “demon shrimp” *Dikerogammarus haemobaphes*, on native and previously introduced species. Biological Invasions 17: 597–607. https://doi.org/10.1007/s10530-014-0751-9

Britton JR, Roberts CG, Trigo FA, Nolan ET, De Santis V (2019) Predicting the ecological impacts of an alien invader: Experimental approaches reveal the trophic consequences of competition. Journal of Animal Ecology 88: 1066–1078. https://doi.org/10.1111/1365-2656.12996

Bunke M, Dick JTA, Hatcher MJ, Dunn AM (2019) Parasites influence cannibalistic and predatory interactions within and between native and invasive amphipods. Diseases of Aquatic Organisms 136: 79–86. https://doi.org/10.3354/dao03415

Carrillo D, Peña JE (2012) Prey-stage preferences and functional and numerical responses of *Amblyseius largoensis* (Acari: Phytoseiidae) to *Raoiella indica* (Acari: Tenuipalpidae). Experimental and Applied Acarology 57: 361–372. https://doi.org/10.1007/s10493-011-9488-7

Carvalho TL, Ferreira EA, Pelicice FM, Fernandes R (2021) Comparative functional responses predict the predatory impact of the highly invasive fish *Cichla kelberi*. Hydrobiologia 848: 2203–2211. https://doi.org/10.1007/s10750-020-04440-6

Crane K, Cuthbert RN, Ricciardi A, Kregting L, Coughlan NE, MacIsaac HJ, Reid N, Dick JTA (2021) Gimme Shelter: differential utilisation and propagule creation of invasive macrophytes by native caddisfly larvae. Biological Invasions 23: 95–109. https://doi.org/10.1007/s10530-020-02358-7

Crookes S, DeRoy EM, Dick JTA, MacIsaac HJ (2019) Comparative functional responses of introduced and native ladybird beetles track ecological impact through predation and competition. Biological Invasions 21: 519–529. https://doi.org/10.1007/s10530-018-1843-8

Cuthbert RN, Callaghan A, Dick JTA (2019) A novel metric reveals biotic resistance potential and informs predictions of invasion success. Scientific Reports 9: 15314. https://doi.org/10.1038/s41598-019-51705-9

Cuthbert RN, Coughlan NE, Dickey JWE, Rea M, Laverty C, South J, Crane K, McCard M, Dick JTA (2019) Shell shocked: high potential impacts on native prey by non-native turtles irrespective of benthic habitat context. Aquatic Invasions 14: 758–774. https://doi.org/ 10.3391/ai.2019.14.4.13

Cuthbert RN, Dickey JWE, McMorrow C, Laverty C, Dick JTA (2018) Resistance is futile: lack of predator switching and a preference for native prey predict the success of an invasive prey species. Royal Society Open Science 5: 180339. https://doi.org/10.1098/rsos.180339

Cuthbert RN, Wasserman RJ, Dalu T, Kaiser H, Weyl OLF, Dick JTA, Sentis A, McCoy MW, Alexander ME (2020) Influence of intra- and interspecific variation in predator–prey body size ratios on trophic interaction strengths. Ecology and Evolution 10: 5946–5962. https://doi.org/10.1002/ece3.6332

Dalal A, Gallogly J, Cuthbert RN, Laverty C, Dickey JWE, Dick JTA (2021) Ecological impacts of an invasive predator are mediated by the reproductive cycle. Biological Invasions 23: 669–675. https://doi.org/10.1007/s10530-020-02414-2

DeRoy EM, Scott R, Hussey N, MacIsaac H (2020) High predatory efficiency and abundance drive expected ecological impacts of a marine invasive fish. Marine Ecology Progress Series 637: 195–208. https://doi.org/10.3354/meps13251

DeRoy EM, Scott R, Hussey NE, MacIsaac HJ (2020) Density dependence mediates the ecological impact of an invasive fish. Diversity and Distributions 26: 867–880. https://doi.org/10.1111/ddi.13063

Dick JTA, Armstrong M, Clarke HC, Farnsworth KD, Hatcher MJ, Ennis M, Kelly A, Dunn AM (2010) Parasitism may enhance rather than reduce the predatory impact of an invader. Biology Letters 6: 636–638. https://doi.org/10.1098/rsbl.2010.0171

Dick JTA, Gallagher K, Avlijas S, Clarke HC, Lewis SE, Leung S, Minchin D, Caffrey J, Alexander ME, Maguire C, Harrod C, Reid N, Haddaway NR, Farnsworth KD, Penk M, Ricciardi A (2013) Ecological impacts of an invasive predator explained and predicted by comparative functional responses. Biological Invasions 15: 837–846. https://doi.org/10.1007/s10530-012-0332-8

Dickey JWE, Cuthbert RN, Rea M, Laverty C, Crane K, South J, Briski E, Chang X, Coughlan NE, MacIsaac HJ, Ricciardi A, Riddell GE, Xu M, Dick JTA (2018) Assessing the relative potential ecological impacts and invasion risks of emerging and future invasive alien species. NeoBiota 20: 1–24. https://doi.org/10.3897/neobiota.40.28519

Dickey JWE, Cuthbert RN, Steffen GT, Dick JTA, Briski E (2021) Sea freshening may drive the ecological impacts of emerging and existing invasive non-native species. Diversity and Distributions 27: 144–156. https://doi.org/10.1111/ddi.13178

Dodd JA, Dick JTA, Alexander ME, MacNeil C, Dunn AM, Aldridge DC (2014) Predicting the ecological impacts of a new freshwater invader: functional responses and prey selectivity of the “killer shrimp”, *Dikerogammarus villosus*, compared to the native *Gammarus pulex*. Freshwater Biology 59: 337–352. https://doi.org/10.1111/fwb.12268

Farazmand A, Fathipour Y, Kamali K (2012) Functional response and mutual interference of *Neoseiulus californicus* and *Typhlodromus bagdasarjani* (Acari: Phytoseiidae) on *Tetranychus urticae* (Acari: Tetranychidae). International Journal of Acarology 38: 369–376. https://doi.org/10.1080/01647954.2012.655310

Faria L, Alexander ME, Vitule JRS (2019) Assessing the impacts of the introduced channel catfish *Ictalurus punctatus* using the comparative functional response approach. Fisheries Management and Ecology 26: 570–577. https://doi.org/10.1111/fme.12353

Faria LDB, Tuller J, Maia LF, Reigada C, Godoy WAC (2014) Alternative prey and abundance covariance switches an intraguild predator's functional response. Journal of Insect Behavior 27: 503–513. https://doi.org/10.1007/s10905-014-9445-5

Feng DD, Li P, Zhou ZS, Xu ZF (2014) Parasitism potential of *Aenasius bambawalei* on the invasive mealybug *Phenacoccus solenopsis*. Biocontrol Science and Technology 24: 1333–1338. https://doi.org/10.1080/09583157.2014.939946

Filgueiras RMC, Mendes JDA, Silva FWB, Sousa Neto EP, Melo JWS (2020) Prey stage preference and functional and numerical responses of *Neoseiulus barkeri* Hughes (Acari: Phytoseiidae) to eggs of *Raoiella indica* Hirst (Acari: Tenuipalpidae). Systematic and Applied Acarology 25: 1147–1157. https://doi.org/10.11158/saa.25.6.16

Fincham WNW, Dunn AM, Brown LE, Hesketh H, Roy HE (2019) Invasion success of a widespread invasive predator may be explained by a high predatory efficacy but may be influenced by pathogen infection. Biological Invasions 21: 3545–3560. https://doi.org/10.1007/s10530-019-02067-w

Gebauer R, Veselý L, Kouba A, Buric M, Drozd B (2018) Forecasting impact of existing and emerging invasive gobiids under temperature change using comparative functional responses. Aquatic Invasions 13: 289–297. https://doi.org/10.3391/ai.2018.13.2.09

Gebauer R, Veselý L, Vanina T, Bur M (2019) Prediction of ecological impact of two alien gobiids in habitat structures of differing complexity. Canadian Journal of Fisheries and Aquatic Sciences 76: 1954–1961. https://doi.org/10.1139/cjfas-2018-0346

Giacoletti A, Rinaldi A, Mercurio M, Mirto S, Sarà G (2016) Local consumers are the first line to control biological invasions: a case of study with the whelk *Stramonita haemastoma* (Gastropoda: Muricidae). Hydrobiologia 772: 117–129. https://doi.org/10.1007/s10750-016-2645-6

Gonçalves V, Gherardi F, Rebelo R (2016) Modelling the predation effects of invasive crayfish, *Procambarus clarkii* (Girard, 1852), on invasive zebra mussel, *Dreissena polymorpha* (Pallas, 1771), under laboratory conditions. Italian Journal of Zoology 83: 59–67. https://doi.org/10.1080/11250003.2016.1138558

Greenwood DJ, Hall Jr RO, Tibbets TM, Krist AC (2020) A precipitous decline in an invasive snail population cannot be explained by a native predator. Biological Invasions 22: 363–378. https://doi.org/10.1007/s10530-019-02093-8

Griffiths KJ (1969) The importance of coincidence on functional and numerical responses of two parasites of the European pine sawfly, *Neodiprion sertifer*. The Canadian Entomologist 101: 673–713. https://doi.org/10.4039/Ent101673-7

Grimm J, Dick JTA, Verreycken H, Jeschke JM, Linzmaier SM, Ricciardi A (2020) Context-dependent differences in the functional responses of conspecific native and non-native crayfishes. NeoBiota 54: 71–88. https://doi.org/10.3897/neobiota.54.38668

Griswold MW, Lounibos LP (2005) Does differential predation permit invasive and native mosquito larvae to coexist in Florida? Ecological Entomology 30: 122–127. https://doi.org/10.1111/j.0307-6946.2005.00671.x

Guleria P, Sharma PL, Verma SC, Chandel RS, Sharma N (2020) Functional response of *Neochrysocharis formosa* to *Tuta absoluta*. Biocontrol Science and Technology 31: 252–264. https://doi.org/10.1080/09583157.2020.1846163

Guo Z, Sheath D, Amat Trigo F, Britton JR (2017) Comparative functional responses of native and high-impacting invasive fishes: Impact predictions for native prey populations. Ecology of Freshwater Fish 26: 533–540. https://doi.org/10.1111/eff.12297

Haddaway NR, Wilcox RH, Heptonstall REA, Griffiths HM, Mortimer RJG, Christmas M, Dunn AM (2012) Predatory functional response and prey choice identify predation differences between native/invasive and parasitised/unparasitised crayfish. PLoS ONE 7. https://doi.org/10.1371/journal.pone.0032229

Haubrock PJ, Cuthbert RN, Veselý L, Balzani P, Baker NJ, Dick JTA, Kouba A (2020) Predatory functional responses under increasing temperatures of two life stages of an invasive gecko. Scientific Reports 10: 10119. https://doi.org/10.1038/s41598-020-67194-0

Hogg BN, Wang XG, Mills NJ, Daane KM (2014) Resident spiders as predators of the recently introduced light brown apple moth, *Epiphyas postvittana*. Entomologia Experimentalis et Applicata 151: 65–74. https://doi.org/10.1111/eea.12168

Hoki E, Losey J, Ugine TA (2014) Comparing the consumptive and non-consumptive effects of a native and introduced lady beetle on pea aphids (*Acyrthosiphon pisum*). Biological Control 70: 78–84. https://doi.org/10.1016/j.biocontrol.2013.12.007

Hooff RC, Bollens SM (2004) Functional response and potential predatory impact of *Tortanus dextrilobatus*, a carnivorous copepod recently introduced to the San Francisco Estuary. Marine Ecology Progress Series 277: 167–179. https://doi.org/10.3354/meps277167

Howard BR, Barrios-O’Neill D, Alexander ME, Dick JTA, Therriault TW, Robinson TB, Côté IM (2018) Functional responses of a cosmopolitan invader demonstrate intraspecific variability in consumer-resource dynamics. PeerJ 6. https://doi.org/10.7717/peerj.5634

Hoxha T, Crookes S, Lejeusne C, Dick JTA, Chang X, Bouchemousse S, Cuthbert RN, MacIsaac HJ (2018) Comparative feeding rates of native and invasive ascidians. Marine Pollution Bulletin 135: 1067–1071. https://doi.org/10.1016/j.marpolbul.2018.08.039

Hoxha T, Crookes S, MacIsaac I, Chang X, Johansson M, Dick JTA, Nicolai A, MacIsaac HJ (2019) Comparative feeding behaviour of native and introduced terrestrial snails tracks their ecological impacts. NeoBiota 47: 81–94. https://doi.org/10.3897/neobiota.47.35000

Hughes RD, Woolcock LT, Hughes MA (1992) Laboratory evaluation of parasitic hymenoptera used in attempts to biologically control aphid pests of crops in Australia. Entomologia Experimentalis et Applicata 63: 177–185. https://doi.org/10.1111/j.1570-7458.1992.tb01572.x

Iacarella JC, Dick JTA, Alexander ME, Ricciardi A (2015) Ecological impacts of invasive alien species along temperature gradients: testing the role of environmental matching. Ecological Applications 25: 706–716. https://doi.org/10.1890/14-0545.1

Iacarella JC, Dick JTA, Ricciardi A (2015) A spatio-temporal contrast of the predatory impact of an invasive freshwater crustacean. Diversity and Distributions 21: 803–812. https://doi.org/10.1111/ddi.12318

Iacarella JC, Ricciardi A (2015) Dissolved ions mediate body mass gain and predatory response of an invasive fish. Biological Invasions 17: 3237–3246. https://doi.org/10.1007/s10530-015-0949-5

Iacarella JC, Hudgins EJ, Dick JTA, Ricciardi A (2018) Predatory behaviour of an invasive amphipod in response to varying conspecific densities under higher-order predation risk. Canadian Journal of Fisheries and Aquatic Sciences 75: 131–140. https://doi.org/10.1139/cjfas-2016-0417

Iltis C, Spataro T, Wattier R, Médoc V (2018) Parasitism may alter functional response comparisons: a case study on the killer shrimp *Dikerogammarus villosus* and two non-invasive gammarids. Biological Invasions 20: 619–632. https://doi.org/10.1007/s10530-017-1563-5

Ingegno BL, Bodino N, Leman A, Messelink GJ, Tavella L (2017) Predatory efficacy of *Dicyphus errans* on different prey. Acta Horticulturae 1164: 425–430. https://doi.org/10.17660/ActaHortic.2017.1164.55

Jones DB, Giles KL, Berberet RC, Royer TA, Elliott NC, Payton ME (2003) Functional responses of an introduced parasitoid and an indigenous parasitoid on greenbug at four temperatures. Environmental Entomology 32: 425–432. https://doi.org/https://doi.org/10.1603/0046-225X-32.3.425

Joyce PWS, Dick JTA, Kregting LT (2020) Lack of biotic resistance to an invasive bivalve irrespective of season or hydrodynamic disturbance. Journal of

Experimental Marine Biology and Ecology 528: 151382. https://doi.org/10.1016/j.jembe.2020.151382

Joyce PWS, Dickey JWE, Cuthbert RN, Dick JTA, Kregting L (2019) Using functional responses and prey switching to quantify invasion success of the Pacific oyster, *Crassostrea gigas*. Marine Environmental Research 145: 66–72. https://doi.org/10.1016/j.marenvres.2019.02.010

Kemp JS, Aldridge DC (2018) Comparative functional responses to explain the impact of sympatric invasive bivalves (*Dreissena* spp.) under different thermal regimes. Journal of Molluscan Studies 84: 175–181. https://doi.org/10.1093/mollus/eyy006

Kemp JS, Tang F, Aldridge DC (2018) Quantifying invader impact: Applying functional response metrics to a rapidly spreading non-native species. Freshwater Biology 63: 1514–1522. https://doi.org/10.1111/fwb.13180

Kestrup ÅM, Dick JTA, Ricciardi A (2011) Interactions between invasive and native crustaceans: differential functional responses of intraguild predators towards juvenile hetero-specifics. Biological Invasions 13: 731–737. https://doi.org/10.1007/s10530-010-9863-z

Koch RL, Hutchison WD, Venette RC, Heimpel GE (2003) Susceptibility of immature monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae: Danainae), to predation by *Harmonia axyridis* (Coleoptera: Coccinellidae). Biological Control 28: 265–270. https://doi.org/10.1016/S1049-9644(03)00102-6

Kögel S, Schieler M, Hoffmann C (2013) The ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) as a possible predator of grape phylloxera *Daktulosphaira vitifoliae* (Hemiptera: Phylloxeridae). European Journal of Entomology 110: 123–128. https://doi.org/10.14411/eje.2013.017

Kushner RB, Hovel KA (2006) Effects of native predators and eelgrass habitat structure on the introduced Asian mussel *Musculista senhousia* (Benson in Cantor) in southern California. Journal of Experimental Marine Biology and Ecology 332: 166–177. https://doi.org/10.1016/j.jembe.2005.11.011

Laverty C, Brenner D, McIlwaine C, Lennon JJ, Dick JTA, Lucy FE, Christian KA (2017) Temperature rise and parasitic infection interact to increase the impact of an invasive species. International Journal for Parasitology 47: 291–296. https://doi.org/10.1016/j.ijpara.2016.12.004

Laverty C, Dick JTA, Alexander ME, Lucy FE (2015) Differential ecological impacts of invader and native predatory freshwater amphipods under environmental change are revealed by comparative functional responses. Biological Invasions 17: 1761–1770. https://doi.org/10.1007/s10530-014-0832-9

Laverty C, Green KD, Dick JTA, Barrios-O’Neill D, Mensink PJ, Médoc V, Spataro T, Caffrey JM, Lucy FE, Boets P, Britton JR, Pegg J, Gallagher C (2017) Assessing the ecological impacts of invasive species based on their functional responses and abundances. Biological Invasions 19: 1653–1665. https://doi.org/10.1007/s10530-017-1378-4

Li M, Yang N, Wan F, Liu L, Chen Y, Li J, Fu J (2017) Functional response of *Neoseiulus cucumeris* (Oudemans) (Acari: Phytoseiidae) to *Bemisia tabaci* (Gennadius) on tomato leaves. Biocontrol Science and Technology 27: 677–685. https://doi.org/10.1080/09583157.2017.1328484

Linzmaier SM, Jeschke JM (2019) Towards a mechanistic understanding of individual-level functional responses: invasive crayfish as model organisms. Freshwater Biology: 1–17. https://doi.org/10.1111/fwb.13456

Mahdian K, Vantornhout I, Tirry L, De Clercq P (2006) Effects of temperature on predation by the stinkbugs *Picromerus bidens* and *Podisus maculiventris* (Heteroptera: Pentatomidae) on noctuid caterpillars. Bulletin of Entomological Research 96: 489–96. https://doi.org/10.1079/ber2006450

Manohar TN, Sharma PL, Verma SC, Sharma KC, Chandel RS (2019) Functional response of indigenous *Trichogramma* spp. to invasive tomato leafminer, *Tuta absoluta* (Meyrick) under laboratory conditions. International Journal of Tropical Insect Science 40: 101–107. https://doi.org/10.1007/s42690-019-00057-y

Marescaux J, Falisse E, Lorquet J, Doninck K Van, Beisel JN, Descy JP (2016) Assessing filtration rates of exotic bivalves: dependence on algae concentration and seasonal factors. Hydrobiologia 777: 67–78. https://doi.org/10.1007/s10750-016-2764-0

Matadha D, Hamilton GC, Lashomb JH, Zhang J (2005) Ovipositional preferences and functional response of parasitoids of euonymus scale, *Unaspis euonymi* (Comstock) and San Jose scale, *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae). Biological Control 32: 337–347. https://doi.org/10.1016/j.biocontrol.2004.12.005

Médoc V, Albert H, Spataro T (2015) Functional response comparisons among freshwater amphipods: ratio-dependence and higher predation for *Gammarus pulex* compared to the non-natives *Dikerogammarus villosus* and *Echinogammarus berilloni*. Biological Invasions 17: 3625–3637. https://doi.org/10.1007/s10530-015-0984-2

Médoc V, Thuillier L, Spataro T (2018) Opportunistic omnivory impairs our ability to predict invasive species impacts from functional response comparisons. Biological Invasions 20: 1307–1319. https://doi.org/10.1007/s10530-017-1628-5

Mendes JA, Lima DB, Sousa Neto EP, Gondim Jr MGC, Melo JWS (2018) Functional response of *Amblyseius largoensis* to *Raoiella indica* eggs is mediated by previous feeding experience. Systematic and Applied Acarology 23: 1907–1914. https://doi.org/10.11158/saa.23.10.3

Mistri M (2004) Predatory behavior and preference of a successful invader, the mud crab *Dyspanopeus sayi* (Panopeidae), on its bivalve prey. Journal of

Experimental Marine Biology and Ecology 312: 385–398. https://doi.org/10.1016/j.jembe.2004.07.012

Mofu L, Cuthbert RN, Dalu T, Woodford DJ, Wasserman RJ, Dick JTA, Weyl OLF (2019) Impacts of non-native fishes under a seasonal temperature gradient are forecasted using functional responses and abundances. NeoBiota 49: 57–75. https://doi.org/10.3897/neobiota.49.34986

Mofu L, South J, Wasserman RJ, Dalu T, Woodford DJ, Dick JTA, Weyl OLF (2019) Inter-specific differences in invader and native fish functional responses illustrate neutral effects on prey but superior invader competitive ability. Freshwater Biology 64: 1655–1663. https://doi.org/10.1111/fwb.13361

Mook LJ, Davies DM (1966) The European praying mantis (*Mantis religiosa* L.) as a predator of the red-legged grasshopper (*Melanoplus femurrubrum* (De Geer)). The Canadian Entomologist 98: 913–918. https://doi.org/10.4039/Ent98913-9

Mu X, Xu M, Ricciardi A, Dick JTA, Luo D, Wei H, Hu Y, Wei Q (2019) The influence of warming on the biogeographic and phylogenetic dependence of herbivore – plant interactions. Ecology and Evolution 9: 2231–2241. https://doi.org/10.1002/ece3.4918

Norbury G, van Overmeire W (2019) Low structural complexity of nonnative grassland habitat exposes prey to higher predation. Ecological Applications 29: e01830. https://doi.org/10.1002/eap.1830

Otturi G, Reggi PE, Battini MÁ, Barriga JP (2020) The effects of trophic interaction between the Patagonian native *Percichthys trucha* and the invasive *Oncorhynchus mykiss* during the juvenile period. Biological Invasions 22: 3293–3305. https://doi.org/10.1007/s10530-020-02324-3

Overholt WA, Smith Jr JW (1990) Comparative evaluation of three exotic insect parasites (Hymenoptera: Braconidae) against the southwestern corn borer (Lepidoptera: Pyralidae) in corn. Environmental Entomology 19: 1155–1162. https://doi.org/10.1093/ee/19.4.1155

Pacheco HM, Vanlaerhoven SL, García MÁM (2020) Functional response and switching behaviour of *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) to the native host *Trichoplusia ni* and the non-native host *Chrysodeixis chalcites* mediating host range expansion. Biocontrol Science and Technology 30: 462–479. https://doi.org/10.1080/09583157.2020.1734185

Patel K, Zhang Z-Q (2017) Functional and numerical responses of *Amblydromalus limonicus* and *Neoseiulus cucumeris* to eggs and first instar nymph of tomato/potato psyllid (*Bactericera cockerelli*). Systematic & Applied Acarology 22: 1476–1488. https://doi.org/10.11158/saa.22.9.12

Paterson RA, Dick JTA, Pritchard DW, Ennis M, Hatcher MJ, Dunn AM (2015) Predicting invasive species impacts: a community module functional response approach reveals context dependencies. Journal of Animal Ecology 84: 453–463. https://doi.org/10.1111/1365-2656.12292

Paton RA, Gobin J, Rooke AC, Fox MG (2019) Population density contributes to the higher functional response of an invasive fish. Biological Invasions 21: 1737–1749. https://doi.org/10.1007/s10530-019-01931-z

Pellan L, Médoc V, Renault D, Spataro T, Piscart C (2016) Feeding choice and predation pressure of two invasive gammarids, *Gammarus tigrinus* and *Dikerogammarus villosus*, under increasing temperature. Hydrobiologia 781: 43–54. https://doi.org/10.1007/s10750-015-2312-3

Poley K, Bahlai C, Grieshop M (2018) Functional response of generalist predators to *Halyomorpha halys* (Hemiptera: Pentatomidae) eggs. Environmental Entomology 47: 1117–1127. https://doi.org/10.1093/ee/nvy110

Ren Q, Haseeb M, Fan J, Wu P, Tian T, Zhang R (2020) Functional response and intraspecific competition in the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Insects 11: 806. https://doi.org/10.3390/insects11110806

Renkema JM, Telfer Z, Gariepy T, Hallett RH (2015) *Dalotia coriaria* as a predator of *Drosophila suzukii*: functional responses, reduced fruit infestation and molecular diagnostics. Biological Control 89: 1–10. https://doi.org/10.1016/j.biocontrol.2015.04.024

Rios-Velasco C, Nájera-Miramontes D, Jacobo-Cuellar JL, Berlanga-Reyes DI, Ruiz-Cisneros MF, Zamudio-Flores PB, Ornelas-Paz JJ, Acosta-Muñiz CH, Romo-Chacón A, Marina MÁS, Ordaz-Silva S (2017) Predation capability and functional response of *Chrysoperla carnea* to *Choristoneura rosaceana* under laboratory conditions. Southwestern Entomologist 42: 677–690. https://doi.org/10.3958/059.042.0306

Rosewarne PJ, Mortimer RJG, Newton RJ, Grocock C, Wing CD, Dunn AM (2016) Feeding behaviour, predatory functional responses and trophic interactions of the invasive Chinese mitten crab (*Eriocheir sinensis*) and signal crayfish (*Pacifastacus leniusculus*). Freshwater Biology 61: 426–443. https://doi.org/10.1111/fwb.12717

Ruscoe WA, Elkinton JS, Choquenot D, Allen RB (2005) Predation of beech seed by mice: effects of numerical and functional responses. Journal of Animal Ecology 74: 1005–1019. https://doi.org/10.1111/j.1365-2656.2005.00998.x

Sallam MN, Overholt WA, Kairu E (1999) Comparative evaluation of *Cotesia flavipes* and *C. sesamiae* (Hymenoptera: Braconidae) for the management of *Chilo partellus* (Lepidoptera: Pyralidae) in Kenya. Bulletin of Entomological Research 89: 185–191. https://doi.org/10.1017/S0007485399000279

Sarkar SC, Wang E, Zhang Z, Wu S, Lei Z (2019) Laboratory and glasshouse evaluation of the green lacewing, *Chrysopa pallens* (Neuroptera: Chrysopidae) against the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae). Applied Entomology and Zoology 54: 115–121. https://doi.org/10.1007/s13355-018-0601-9

Seyfollahi F, Esfandiari M, Mossadegh MS, Rasekh A (2019) Functional response of *Hyperaspis polita* (Coleoptera, Coccinellidae) to the recently invaded mealybug *Phenacoccus solenopsis* (Hemiptera, Pseudococcidae). Neotropical Entomology 48: 484–495. https://doi.org/10.1007/s13744-018-0666-8

Slaughter AM, Ignoffo TR, Kimmerer W (2016) Predation impact of *Acartiella sinensis*, an introduced predatory copepod in the San Francisco Estuary, USA. Marine Ecology Progress Series 547: 47–60. https://doi.org/10.3354/meps11640

South J, Dick JTA, McCard M, Barrios-O'Neill D, Anton A (2017) Predicting predatory impact of juvenile invasive lionfish (*Pterois volitans*) on a crustacean prey using functional response analysis: effects of temperature, habitat complexity and light regimes. Environmental Biology of Fishes 100: 1155–1165. https://doi.org/10.1007/s10641-017-0633-y

South J, McCard M, Khosa D, Mofu L, Madzivanzira TC, Dick JTA, Weyl OLF (2019) The effect of prey identity and substrate type on the functional response of a globally invasive crayfish. NeoBiota 52: 9–24. https://doi.org/10.3897/neobiota.52.39245

Taylor NG, Dunn AM (2018) Predatory impacts of alien decapod Crustacea are predicted by functional responses and explained by differences in metabolic rate. Biological Invasions 20: 2821–2837. https://doi.org/10.1007/s10530-018-1735-y

Taylor NG, Dunn AM (2017) Size matters: predation of fish eggs and larvae by native and invasive amphipods. Biological Invasions 19: 89–107. https://doi.org/10.1007/s10530-016-1265-4

Tilves U, Purcell JE, Marambio M, Canepa A, Olariaga A, Fuentes V (2013) Predation by the scyphozoan *Pelagia noctiluca* on *Mnemiopsis leidyi* ctenophores in the NW Mediterranean Sea. Journal of Plankton Research 35: 218–224. https://doi.org/10.1093/plankt/fbs082

Twardochleb LA, Novak M, Moore JW (2012) Using the functional response of a consumer to predict biotic resistance to invasive prey. Ecological Applications 22: 1162–1171. https://doi.org/10.1890/11-0871.1

Van Echelpoel W, Boets P, Goethals PLM (2016) Functional Response (FR) and Relative Growth Rate (RGR) do not show the known invasiveness of *Lemna minuta* (Kunth). PLoS ONE 11: 1–18. https://doi.org/10.1371/journal.pone.0166132

Viteri Jumbo LO, Teodoro A V., Rêgo AS, Haddi K, Galvão AS, Oliveira EE (2019) The lacewing *Ceraeochrysa caligata* as a potential biological agent for controlling the red palm mite *Raoiella indica*. PeerJ 7: e7123. https://doi.org/10.7717/peerj.7123

Wang B, Ferro DN (1998) Functional responses of *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae) to *Ostrinia nubilalis* (Lepidoptera: Pyralidae) under laboratory and field conditions. Environmental Entomology 27: 752–758. https://doi.org/10.1093/ee/27.3.752

Wang X, Biondi A, Daane KM (2020) Functional responses of three candidate asian larval parasitoids evaluated for classical biological control of *Drosophila suzukii* (Diptera: Drosophilidae). Journal of Economic Entomology 113: 73–80. https://doi.org/10.1093/jee/toz265

Wiedenmann RN, Smith Jr JW (1993) Functional response of the parasite *Cotesia flavipes* (Hymenoptera: Braconidae) at low densities of the host *Diatraea saccharalis* (Lepidoptera: Pyralidae). Environmental Entomology 22: 849–858. https://doi.org/10.1093/ee/22.4.849

Xia Z, Cao X, Hoxha T, Zhan A, Haffner GD, MacIsaac HJ (2020) Functional response and size-selective clearance of suspended matter by an invasive mussel. Science of the Total Environment 711: 134679. https://doi.org/10.1016/j.scitotenv.2019.134679

Xu M, Dick JTA, Ricciardi A, Fang M, Zhang C, Gu D, Mu X, Luo D, Wei H, Hu Y (2016) Warming mediates the relationship between plant nutritional properties and herbivore functional responses. Ecology and Evolution 6: 8777–8784. https://doi.org/10.1002/ece3.2602

Xu M, Mu X, Dick JTA, Fang M, Gu D, Luo D, Zhang J, Luo J, Hu Y (2016) Comparative functional responses predict the invasiveness and ecological impacts of alien herbivorous snails. PLoS ONE 11: e0147017. https://doi.org/10.1371/journal.pone.0147017

Zuharah WF, Lester PJ (2011) Are exotic invaders less susceptible to native predators? A test using native and exotic mosquito species in New Zealand. Population Ecology 53: 307–317. https://doi.org/10.1007/s10144-010-0244-3

APPENDIX 2 – SUPPLEMENTARY MATERIAL FROM CHAPTER 3 “PREDATION RISK BY LARGEMOUTH BASS MODULATES FEEDING FUNCTIONAL RESPONSES OF NATIVE AND NON-NATIVE CRAYFISH”

Supplementary material 1

Data from functional response trials for each crayfish species under predator treatment and control.

replicate	treatment	species	density	alive	dead	eaten	temperature	sex	mass_g	CL_mm
1	control	redswamp	2	1	0	1	18.1	M	23.8	44.3
2	control	redswamp	2	1	0	1	18.1	M	23.1	49.7
3	control	redswamp	2	2	0	0	15.6	M	50.6	58.5
4	control	redswamp	2	2	0	0	15.7	M	50	58.4
5	control	redswamp	2	1	0	1	13.9	M	60.4	64.2
6	control	redswamp	2	1	0	1	12.8	M	20.1	42.2
7	control	redswamp	2	0	0	2	13	M	31.9	52.2
1	control	redswamp	4	0	0	4	18	F	44.3	59
2	control	redswamp	4	4	0	0	16.3	F	28.9	49.5
3	control	redswamp	4	4	0	0	14.9	F	39.5	52.5
4	control	redswamp	4	3	0	1	14.8	M	27.2	47.9
5	control	redswamp	4	3	0	1	13.9	M	34.6	49.5
6	control	redswamp	4	3	0	1	13.2	M	64.4	62.6
7	control	redswamp	4	1	0	3	13.1	M	19.3	40.7
1	control	redswamp	8	7	0	1	18	M	53.2	57.1
2	control	redswamp	8	4	0	4	15.6	M	27.5	49.7
3	control	redswamp	8	5	2	1	14.3	M	34.8	53.4
4	control	redswamp	8	6	0	2	13.5	M	25.2	47.5
5	control	redswamp	8	6	0	2	12.5	M	39.5	54.9
6	control	redswamp	8	5	0	3	12.8	M	54.5	56.9
7	control	redswamp	8	4	0	4	12.9	M	31.3	58.3
1	control	redswamp	12	11	0	1	18	M	23.9	45.4
2	control	redswamp	12	9	0	3	17.9	F	39.9	56.8
3	control	redswamp	12	9	0	3	15.9	M	28.1	46.8

4	control	redswamp	12	0	0	12	15.9	F	40.6	55.8
5	control	redswamp	12	7	0	5	12.7	M	60.9	61
6	control	redswamp	12	5	0	7	12.5	F	19	44.7
7	control	redswamp	12	10	0	2	13.2	M	17.5	41.8
1	control	redswamp	16	15	0	1	17.8	M	33	45.9
2	control	redswamp	16	2	0	14	17.9	M	49.2	60.2
3	control	redswamp	16	9	0	7	14.9	M	64.6	59.7
4	control	redswamp	16	13	0	3	14.2	M	35.1	52.6
5	control	redswamp	16	13	0	3	13.9	M	21	45.9
6	control	redswamp	16	14	0	2	13.4	M	53.1	56.8
7	control	redswamp	16	14	0	2	12.5	M	26.7	45.6
1	control	redswamp	24	21	0	3	15.6	M	28.3	49.1
2	control	redswamp	24	12	0	12	15.6	F	28.6	49.9
3	control	redswamp	24	21	0	3	15.9	F	31.2	53.6
4	control	redswamp	24	2	0	22	15.8	F	31.5	51.8
5	control	redswamp	24	5	0	19	14.9	M	42	52.8
6	control	redswamp	24	22	1	1	12.9	F	28.4	50.2
7	control	redswamp	24	22	1	1	12.9	M	34.3	48.7
1	control	redswamp	40	40	0	0	15.6	M	29.1	48.2
2	control	redswamp	40	10	0	30	16.1	M	43.2	54.7
3	control	redswamp	40	15	1	24	15.3	F	47.5	58.6
4	control	redswamp	40	39	0	1	15.2	M	23.4	44.6
5	control	redswamp	40	35	0	5	14.9	M	27.6	48.8
6	control	redswamp	40	31	3	6	14.7	M	49.9	54.8
7	control	redswamp	40	35	0	5	13.9	F	33.8	52.4
1	control	rusty	2	0	0	2	18.5	M	19.6	38
2	control	rusty	2	1	0	1	18	F	18.3	39.1
3	control	rusty	2	1	0	1	16.1	M	23.3	41.2
4	control	rusty	2	0	0	2	15.9	M	31.6	41.7
5	control	rusty	2	2	0	0	14.3	M	32.9	45.5
6	control	rusty	2	1	0	1	14.5	M	23	39.4
7	control	rusty	2	1	0	1	12.9	M	24.9	40.7
1	control	rusty	4	0	0	4	18.5	M	22.1	40.8

2	control	rusty	4	2	0	2	18	M	17.9	36.2
3	control	rusty	4	0	0	4	17.8	M	22.9	39.4
4	control	rusty	4	2	0	2	15.9	M	27.8	42
5	control	rusty	4	1	0	3	15.7	M	27.5	43.4
6	control	rusty	4	0	0	4	14.9	M	30.8	43.8
7	control	rusty	4	2	0	2	13.5	M	22.5	40.8
1	control	rusty	8	1	0	7	18	M	19.1	37.3
2	control	rusty	8	7	0	1	17.9	M	31.9	38.9
3	control	rusty	8	3	0	5	17.8	M	19.7	36.4
4	control	rusty	8	8	0	0	14.8	M	17.9	36
5	control	rusty	8	0	0	8	14.4	M	23	40.7
6	control	rusty	8	0	0	8	14.5	M	34	46
7	control	rusty	8	2	0	6	13.3	M	19.8	38
1	control	rusty	12	2	0	10	18	M	27.9	43
2	control	rusty	12	3	0	9	17.9	M	18	36.6
3	control	rusty	12	0	0	12	17.8	M	18	37.1
4	control	rusty	12	1	0	11	15.6	M	35.8	47.6
5	control	rusty	12	8	0	4	15.9	M	22.9	39.5
6	control	rusty	12	1	0	11	14.9	M	30.2	43.8
7	control	rusty	12	12	0	0	13.3	M	21.2	36.8
1	control	rusty	16	4	0	12	17.8	M	33	47.3
2	control	rusty	16	0	0	16	18	M	21.3	38.9
3	control	rusty	16	2	0	14	15.6	M	33.6	45.8
4	control	rusty	16	3	0	13	15.7	M	35.8	48.8
5	control	rusty	16	1	0	15	16.3	M	25.8	41
6	control	rusty	16	2	0	14	15.9	M	21.6	40.2
7	control	rusty	16	12	0	4	12.6	M	17.5	36.8
1	control	rusty	24	1	0	23	16.4	M	27.1	42.6
2	control	rusty	24	15	0	9	16.1	M	23.1	39.4
3	control	rusty	24	10	0	14	15.1	M	29.1	45
4	control	rusty	24	20	0	4	14.8	M	30.5	44.2
5	control	rusty	24	19	0	5	14.4	M	27.2	41.4
6	control	rusty	24	20	0	4	14.4	M	24.8	40.8

7	control	rusty	24	7	0	17	13.6	M	22.8	38.5
1	control	rusty	40	11	0	29	17.9	M	20.5	38.2
2	control	rusty	40	15	0	25	16.3	M	28.8	43.2
3	control	rusty	40	15	0	25	15.6	M	22.1	40
4	control	rusty	40	6	0	34	16.1	M	24.6	39.6
5	control	rusty	40	19	0	21	15.5	M	30.8	44.6
6	control	rusty	40	26	0	14	15.3	M	24.6	40.8
7	control	rusty	40	16	0	24	13.3	M	25.8	40.7
1	control	signal	2	0	0	2	18	F	20.3	42.1
2	control	signal	2	1	0	1	18	F	21.3	41.9
3	control	signal	2	0	0	2	17.9	M	24.3	44.7
4	control	signal	2	0	0	2	15.8	M	21.4	42.8
5	control	signal	2	0	0	2	15.4	F	43.5	54.6
6	control	signal	2	1	0	1	14.5	M	46.8	55.2
7	control	signal	2	0	0	2	13.5	F	25.4	45
1	control	signal	4	2	0	2	18.5	F	33.5	48.8
2	control	signal	4	2	0	2	18.5	F	35.7	52.7
3	control	signal	4	1	0	3	17.9	M	29.3	47.8
4	control	signal	4	0	0	4	15.6	M	30.6	47.9
5	control	signal	4	0	0	4	14.9	M	36.4	49.5
6	control	signal	4	0	0	4	14.5	M	48.7	55.9
7	control	signal	4	0	0	4	13.2	M	21.4	42.7
1	control	signal	8	5	0	3	18.1	F	24.6	44.8
2	control	signal	8	0	0	8	18.1	M	20.7	42.5
3	control	signal	8	4	0	4	15.8	F	31.5	48.9
4	control	signal	8	0	0	8	15.6	M	47.8	57
5	control	signal	8	2	1	5	15.5	M	30.1	48.6
6	control	signal	8	0	0	8	13.4	M	29.5	48.7
7	control	signal	8	0	0	8	12.9	M	48.8	56.1
1	control	signal	12	5	0	7	17.9	M	32	47.5
2	control	signal	12	2	0	10	15.9	M	38	52.9
3	control	signal	12	1	0	11	14.9	F	27.5	48.1
4	control	signal	12	0	1	11	14.3	M	50.7	59.4

5	control	signal	12	1	0	11	12.9	F	25	47
6	control	signal	12	2	0	10	14.1	M	39.2	51.1
7	control	signal	12	0	0	12	12.8	M	31.7	52.1
1	control	signal	16	11	0	5	17.9	F	29.8	48.1
2	control	signal	16	1	0	15	17.8	M	40.6	53.8
3	control	signal	16	4	0	12	15.9	M	40.5	52
4	control	signal	16	0	0	16	15.6	M	35.6	51
5	control	signal	16	1	0	15	16.2	M	44.8	52.4
6	control	signal	16	2	0	14	14.4	F	37.1	49.7
7	control	signal	16	0	0	16	13.7	M	71.2	61.3
1	control	signal	24	14	1	9	18	M	37.2	50.9
2	control	signal	24	7	3	14	17.8	M	40.8	53.1
3	control	signal	24	5	0	19	18	M	34.4	49.4
4	control	signal	24	8	0	16	15.6	M	41.9	50.5
5	control	signal	24	16	0	8	16.1	F	36.9	50.9
6	control	signal	24	10	0	14	13.6	M	29.6	45.6
7	control	signal	24	8	0	16	13.1	M	36.7	50.6
1	control	signal	40	4	0	36	15.9	M	45.1	53
2	control	signal	40	19	4	17	14.9	M	36.9	47.4
3	control	signal	40	21	0	19	15.6	F	32.1	49.5
4	control	signal	40	13	1	26	14.3	M	40.2	51.6
5	control	signal	40	18	0	22	14.9	F	33.3	48.3
6	control	signal	40	3	1	36	14.3	M	45.5	49.2
7	control	signal	40	28	1	11	13.5	M	47.9	55.3
1	control	virile	2	1	0	1	18	F	26.3	45.9
2	control	virile	2	1	0	1	18	F	36.8	50.9
3	control	virile	2	0	0	2	18.1	M	28.7	43.5
4	control	virile	2	2	0	0	15.6	M	35.2	46.7
5	control	virile	2	1	0	1	15.6	M	34.1	45.8
6	control	virile	2	0	0	2	14.7	F	41.7	50.3
7	control	virile	2	2	0	0	13.3	M	23.9	42.2
1	control	virile	4	1	0	3	18.1	M	30.2	44.2
2	control	virile	4	4	0	0	17.8	M	30.4	44.9

3	control	virile	4	1	0	3	17.9	M	32.5	44.8
4	control	virile	4	3	0	1	18.1	M	41.6	49.3
5	control	virile	4	4	0	0	15.7	M	26.9	42.8
6	control	virile	4	0	0	4	16	F	24.5	43.5
7	control	virile	4	0	0	4	12.9	F	23.8	43.5
1	control	virile	8	1	0	7	18.1	F	33.4	49.9
2	control	virile	8	2	0	6	18	M	38	46.2
3	control	virile	8	0	0	8	18.1	F	41.1	51.4
4	control	virile	8	4	0	4	15.6	F	22.5	42.8
5	control	virile	8	2	0	6	15.6	F	38.8	49.4
6	control	virile	8	1	0	7	14.9	M	28	44.2
7	control	virile	8	0	0	8	14	F	23	41.8
1	control	virile	12	0	0	12	17.8	M	35.7	50.2
2	control	virile	12	6	0	6	15.7	M	37	45.7
3	control	virile	12	6	0	6	14.5	M	34.1	44.8
4	control	virile	12	3	0	9	15.2	M	27.7	42.7
5	control	virile	12	0	0	12	14.3	F	27.4	45.5
6	control	virile	12	12	0	0	15.4	F	28.2	43.9
7	control	virile	12	4	0	8	12.8	F	20.3	39.3
1	control	virile	16	0	0	16	17.8	M	39.7	47.6
2	control	virile	16	4	0	12	15.6	M	41.9	45.5
3	control	virile	16	1	0	15	15.9	M	35.4	49.3
4	control	virile	16	3	0	13	15.7	M	27.2	42.4
5	control	virile	16	9	0	7	14.8	M	32.2	46.1
6	control	virile	16	3	0	13	14.3	F	27.1	45.7
7	control	virile	16	4	0	12	12.8	M	22.4	41.6
1	control	virile	24	3	0	21	18	M	33.9	45.5
2	control	virile	24	1	0	23	15.6	F	34.8	48.6
3	control	virile	24	5	0	19	16.3	M	33.1	46.5
4	control	virile	24	6	0	18	16.5	F	29.5	46.3
5	control	virile	24	8	2	14	15.1	M	51.7	51.5
6	control	virile	24	12	0	12	14.2	F	26.8	43.9
7	control	virile	24	23	0	1	13.9	M	24.5	41.7

1	control	virile	40	20	0	20	18	M	33.6	47.1
2	control	virile	40	14	0	26	15.7	M	37.8	47.8
3	control	virile	40	17	0	23	15.9	M	54.5	54.5
4	control	virile	40	31	1	8	15.8	M	33.8	45.7
5	control	virile	40	8	3	29	14.5	F	27.1	45.7
6	control	virile	40	21	0	19	14.6	F	28.1	43.9
7	control	virile	40	19	1	20	13.1	F	21.1	42.1
1	predator	redswamp	2	2	0	0	18.5	F	45.6	56.8
2	predator	redswamp	2	2	0	0	17.8	F	41.5	55.1
3	predator	redswamp	2	1	0	1	17.9	M	25.4	43.5
4	predator	redswamp	2	2	0	0	17.9	M	29.3	49
5	predator	redswamp	2	2	0	0	16.1	M	36.4	51.3
6	predator	redswamp	2	1	0	1	16	M	30.6	50.8
7	predator	redswamp	2	1	0	1	13.2	M	46.8	56.6
1	predator	redswamp	4	4	0	0	17.9	M	29.1	46.7
2	predator	redswamp	4	4	0	0	16.1	F	29.1	50.9
3	predator	redswamp	4	2	0	2	14.9	M	51.4	58.3
4	predator	redswamp	4	3	0	1	15.6	M	48.7	54.3
5	predator	redswamp	4	3	0	1	15.9	M	31.3	48.7
6	predator	redswamp	4	4	0	0	13	F	44.6	60
7	predator	redswamp	4	4	0	0	13.5	F	26.1	49.5
1	predator	redswamp	8	7	0	1	17.8	F	30	52.1
2	predator	redswamp	8	3	0	5	18.5	M	50.3	58.5
3	predator	redswamp	8	8	0	0	17.8	M	37.3	54.5
4	predator	redswamp	8	6	0	2	16.2	M	56.4	60.5
5	predator	redswamp	8	1	0	7	15.9	F	42.3	56.1
6	predator	redswamp	8	8	0	0	14.7	F	40.5	55.1
7	predator	redswamp	8	8	0	0	13	M	21	43.7
1	predator	redswamp	12	1	0	11	17.8	M	54.9	56
2	predator	redswamp	12	9	0	3	15.9	F	47.1	58.5
3	predator	redswamp	12	9	0	3	15.9	M	37.9	53.1
4	predator	redswamp	12	12	0	0	14.9	M	73.4	65
5	predator	redswamp	12	11	0	1	15.9	M	60.9	61.3

6	predator	redswamp	12	11	0	1	13.2	M	60.8	64.1
7	predator	redswamp	12	7	0	5	13.3	F	29.9	51.1
1	predator	redswamp	16	16	0	0	17.9	M	26.9	49.6
2	predator	redswamp	16	14	0	2	17.8	M	51.8	61.1
3	predator	redswamp	16	12	0	4	15.6	M	56.7	58.8
4	predator	redswamp	16	16	0	0	15.6	M	39.2	52.9
5	predator	redswamp	16	13	2	1	15.7	M	44.2	55.4
6	predator	redswamp	16	14	0	2	13.3	M	76.4	63.4
7	predator	redswamp	16	12	0	4	13.2	M	47.3	56.7
1	predator	redswamp	24	19	0	5	17.8	F	30.4	51
2	predator	redswamp	24	23	0	1	16.1	F	42.2	58.6
3	predator	redswamp	24	16	0	8	16.9	F	64.3	64.7
4	predator	redswamp	24	20	0	4	17	F	46.2	60.1
5	predator	redswamp	24	23	0	1	16	F	45.8	56.8
6	predator	redswamp	24	21	0	3	15.6	M	38.5	52.6
7	predator	redswamp	24	18	0	6	13.5	M	56.6	56
1	predator	redswamp	40	29	0	11	16.1	F	50.7	63.1
2	predator	redswamp	40	18	0	22	16.3	F	43.5	58.5
3	predator	redswamp	40	34	0	6	15.8	M	46.6	55.1
4	predator	redswamp	40	39	0	1	14.5	M	52.2	56.7
5	predator	redswamp	40	39	1	0	14.9	M	31.2	49.5
6	predator	redswamp	40	37	0	3	15.6	M	35.7	51.4
7	predator	redswamp	40	34	0	6	13.6	M	29.9	49.8
1	predator	rusty	2	0	0	2	17.9	M	21.6	37.5
2	predator	rusty	2	1	0	1	17.8	M	17.6	36.9
3	predator	rusty	2	2	0	0	17	M	21.9	36.5
4	predator	rusty	2	2	0	0	15.9	M	20.5	37.5
5	predator	rusty	2	1	0	1	15.2	M	27.5	42.7
6	predator	rusty	2	2	0	0	15.9	M	25	36.9
7	predator	rusty	2	2	0	0	13.9	M	24.5	39.7
1	predator	rusty	4	1	0	3	17.8	M	22.3	38.1
2	predator	rusty	4	3	0	1	17.9	M	24.8	42.6
3	predator	rusty	4	3	0	1	17.9	M	25.7	42.5

4	predator	rusty	4	0	0	4	16	M	38.9	45.6
5	predator	rusty	4	1	0	3	16.2	M	25.1	40.9
6	predator	rusty	4	1	0	3	15.5	M	25	41.1
7	predator	rusty	4	3	0	1	13.4	M	21.3	41.4
1	predator	rusty	8	4	0	4	18	M	21.1	37.5
2	predator	rusty	8	2	0	6	17.8	M	28.4	41.8
3	predator	rusty	8	2	0	6	18.5	M	19.2	38.9
4	predator	rusty	8	3	0	5	14.7	M	24.4	41.5
5	predator	rusty	8	3	0	5	15.9	M	26.1	41.8
6	predator	rusty	8	3	0	5	15.9	M	32.5	44.3
7	predator	rusty	8	5	0	3	13.2	M	28.6	41.1
1	predator	rusty	12	0	0	12	18	M	29.6	42.5
2	predator	rusty	12	2	0	10	17.8	M	27.8	43.4
3	predator	rusty	12	4	0	8	17.9	M	27.3	43.8
4	predator	rusty	12	4	0	8	16	M	30.2	44.8
5	predator	rusty	12	2	0	10	15.9	M	32.8	47
6	predator	rusty	12	9	0	3	15.5	M	25.8	40.3
7	predator	rusty	12	9	0	3	13.4	M	20	38.8
1	predator	rusty	16	2	0	14	17.9	M	34.9	46.1
2	predator	rusty	16	3	0	13	18	M	29.4	46.6
3	predator	rusty	16	2	0	14	15.9	M	37	47.1
4	predator	rusty	16	5	0	11	16.2	M	31.1	42.9
5	predator	rusty	16	16	0	0	16.9	M	20.9	41.1
6	predator	rusty	16	8	0	8	16	M	34.3	40.5
7	predator	rusty	16	1	0	15	13.6	M	17	37.1
1	predator	rusty	24	11	0	13	16.1	M	30.1	42.5
2	predator	rusty	24	9	0	15	16.2	M	38.5	47.2
3	predator	rusty	24	7	0	17	15.7	M	30.4	39.9
4	predator	rusty	24	16	0	8	14.7	M	22.9	43
5	predator	rusty	24	13	0	11	14.6	M	25.6	39.9
6	predator	rusty	24	10	0	14	15.9	M	23.8	40.2
7	predator	rusty	24	18	0	6	13	M	23.3	36.7
1	predator	rusty	40	25	0	15	18	M	27.6	42.3

2	predator	rusty	40	17	0	23	15.9	M	26.8	41.3
3	predator	rusty	40	15	0	25	16	M	27.5	41.9
4	predator	rusty	40	32	0	8	16	M	25.9	37.2
5	predator	rusty	40	29	0	11	15.4	M	28.8	41.5
6	predator	rusty	40	24	0	16	14.5	M	31.1	42.9
7	predator	rusty	40	28	0	12	13.3	M	17.7	36.8
1	predator	signal	2	0	0	2	18.5	F	28.7	47.4
2	predator	signal	2	2	0	0	17.8	M	29.9	45.4
3	predator	signal	2	2	0	0	17.9	F	30.3	47.1
4	predator	signal	2	0	0	2	16.5	F	29	49.3
5	predator	signal	2	1	0	1	15.8	M	43.6	53.8
6	predator	signal	2	0	0	2	15.9	F	30.7	47.5
7	predator	signal	2	2	0	0	13.3	F	24.3	46
1	predator	signal	4	2	0	2	18.5	M	31.9	48.3
2	predator	signal	4	3	0	1	17.9	F	28.9	48.1
3	predator	signal	4	3	0	1	17.8	F	26.1	45.8
4	predator	signal	4	1	0	3	16.4	F	28.2	46.8
5	predator	signal	4	1	0	3	15.6	M	33.7	49.7
6	predator	signal	4	0	0	4	14.6	M	45.1	51.6
7	predator	signal	4	3	0	1	12.9	M	35.6	50.9
1	predator	signal	8	0	0	8	17.9	M	25.9	47
2	predator	signal	8	0	0	8	17.8	M	33.8	53.3
3	predator	signal	8	2	0	6	15.9	M	32.4	46.3
4	predator	signal	8	0	0	8	16.9	M	44.9	54.7
5	predator	signal	8	0	0	8	15.3	F	31.5	49.6
6	predator	signal	8	0	0	8	15.6	M	44	53.2
7	predator	signal	8	1	0	7	13.2	M	25.9	43.9
1	predator	signal	12	4	0	8	18	F	28.3	46
2	predator	signal	12	0	0	12	16.2	M	30.4	47.3
3	predator	signal	12	5	0	7	15.9	M	36.4	51
4	predator	signal	12	1	0	11	16	M	49.9	58.9
5	predator	signal	12	0	0	12	14.4	M	39.8	51.7
6	predator	signal	12	3	0	9	14.5	M	53.4	55.3

7	predator	signal	12	6	0	6	13.3	M	25.8	45.1
1	predator	signal	16	2	0	14	17.9	M	44.7	51.9
2	predator	signal	16	8	0	8	17.9	M	38.8	49
3	predator	signal	16	3	0	13	16.1	M	52.3	55.6
4	predator	signal	16	2	0	14	16.2	M	47.5	55.1
5	predator	signal	16	3	0	13	15.9	F	25.3	45.9
6	predator	signal	16	0	0	16	15.9	M	45.9	52.5
7	predator	signal	16	1	0	15	13.6	M	68.8	61.3
1	predator	signal	24	9	0	15	17.8	M	54.7	55
2	predator	signal	24	7	0	17	17.9	M	35.6	46.6
3	predator	signal	24	0	0	24	17.9	M	45	50.5
4	predator	signal	24	10	0	14	16.5	M	35.6	49.5
5	predator	signal	24	12	0	12	16.2	M	30.6	47.1
6	predator	signal	24	0	0	24	15.1	M	58.4	55.8
7	predator	signal	24	0	0	24	13.2	M	63.4	59.8
1	predator	signal	40	33	0	7	16.8	F	42.4	52.9
2	predator	signal	40	37	0	3	15.8	M	46.9	54.6
3	predator	signal	40	22	0	18	14.3	F	28.8	43.4
4	predator	signal	40	23	2	15	15.9	M	47.7	54.2
5	predator	signal	40	19	1	20	15.8	M	33.5	48.8
6	predator	signal	40	16	1	23	15.9	M	26.5	46.1
7	predator	signal	40	16	2	22	13.3	M	43.9	53.4
1	predator	virile	2	0	0	2	17.8	F	30.2	46.5
2	predator	virile	2	1	0	1	17.9	F	37.1	49.7
3	predator	virile	2	1	0	1	17.9	F	34.3	48.7
4	predator	virile	2	0	0	2	15.9	M	32.5	45
5	predator	virile	2	0	0	2	16.1	F	34.3	40.6
6	predator	virile	2	2	0	0	14.4	F	28.9	46.2
7	predator	virile	2	2	0	0	13.1	F	24.5	41.1
1	predator	virile	4	0	0	4	18.5	M	44.4	47.8
2	predator	virile	4	4	0	0	17.9	F	33.5	51.3
3	predator	virile	4	2	0	2	18	F	46.9	51
4	predator	virile	4	0	0	4	17.9	M	34.8	46.1

5	predator	virile	4	2	0	2	16.3	F	25.7	44.2
6	predator	virile	4	1	0	3	15.9	F	26.3	45.3
7	predator	virile	4	0	0	4	13.9	F	23.9	37.6
1	predator	virile	8	1	0	7	17.8	F	32.7	45.6
2	predator	virile	8	1	0	7	17.9	M	32.7	44.6
3	predator	virile	8	2	0	6	17.9	M	35.9	48.3
4	predator	virile	8	0	0	8	16.3	F	38	49.8
5	predator	virile	8	1	0	7	15.9	F	31.1	48.1
6	predator	virile	8	2	1	5	15.6	F	39.8	50.3
7	predator	virile	8	1	0	7	13.5	F	23.5	43.8
1	predator	virile	12	10	0	2	17.9	F	34.8	47.8
2	predator	virile	12	0	0	12	16.5	M	43.5	48
3	predator	virile	12	1	0	11	14.6	M	49	54.5
4	predator	virile	12	8	0	4	14.6	F	24.3	43.1
5	predator	virile	12	5	1	6	15.4	F	29.5	48
6	predator	virile	12	3	0	9	15.5	M	21.9	39.9
7	predator	virile	12	1	0	11	13	F	25.1	43.4
1	predator	virile	16	0	0	16	17.9	M	36.6	47.5
2	predator	virile	16	4	0	12	16.2	F	37.2	44.4
3	predator	virile	16	4	0	12	16	M	26.4	41.6
4	predator	virile	16	11	0	5	15.8	M	55.8	52.5
5	predator	virile	16	5	0	11	14.4	F	34.8	49.5
6	predator	virile	16	12	2	2	15.6	M	39	48.1
7	predator	virile	16	9	0	7	13.3	F	21.6	41.5
1	predator	virile	24	10	0	14	17.9	M	39.4	47.9
2	predator	virile	24	17	0	7	16.1	M	42.5	50
3	predator	virile	24	4	0	20	15.9	F	26.3	44.8
4	predator	virile	24	23	0	1	16.5	F	25.2	44.4
5	predator	virile	24	13	1	10	15.6	M	24	42.2
6	predator	virile	24	15	0	9	14.7	M	26.6	41.5
7	predator	virile	24	11	1	12	13.1	M	21.1	39.2
1	predator	virile	40	13	0	27	17.9	F	38.9	49.1
2	predator	virile	40	12	0	28	16.1	F	41.5	53.2

3	predator	virile	40	35	0	5	16.5	M	34.8	45.7
4	predator	virile	40	35	0	5	15.4	M	46.9	51.1
5	predator	virile	40	34	1	5	15.9	M	33.6	46.6
6	predator	virile	40	18	0	22	15.8	M	33.6	45.7
7	predator	virile	40	27	0	13	12.9	F	22.7	42.3