

The rise of the Functional Response in invasion science: a systematic review

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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

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 Driessche 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).

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 \times Numerical Response; Holling 1959), as has been done with biological control (e.g. killing rate *per* individual agent \times number of agents)

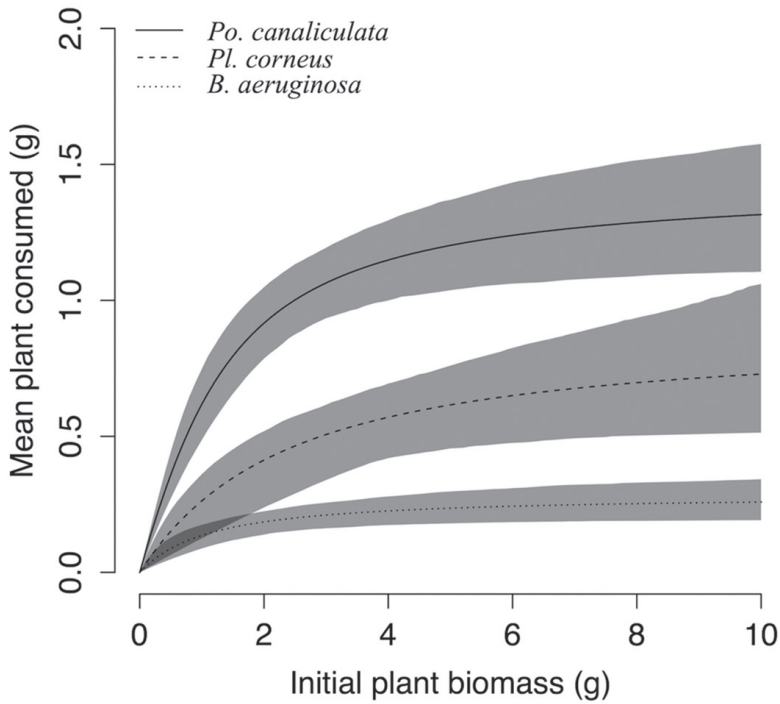


Figure 1. Functional Responses of known impactful invasive non-native species (NNS) are often higher when compared to those of native or non-invasive NNS trophic analogues, as shown for aquatic snails: the invasive NNS *Pomacea canaliculata*, the non-invasive NNS *Planorbis corneus*, and the native *Bellamya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

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 \times Abundance \times *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.

Methods

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 (Suppl. material 1). 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.

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 Suppl. material 2). 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):

$$AI = \left(\frac{CY}{CT} \right) / \left(\frac{TY}{TT} \right) \quad (1)$$

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* (Suppl. material 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).

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.

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 Suppl. material 4).

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 $\alpha = 0.05$.

Results

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 (Suppl. material 1; the list of all references included in the systematic review is available in Suppl. material 5).

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 Suppl. material 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 ($\chi^2 = 245.2$, $df = 4$, $n = 120$, $p < 0.001$), with predator-prey interactions predominantly featuring in impact assessment studies, and all studies of host-parasitoid interactions classified as biological

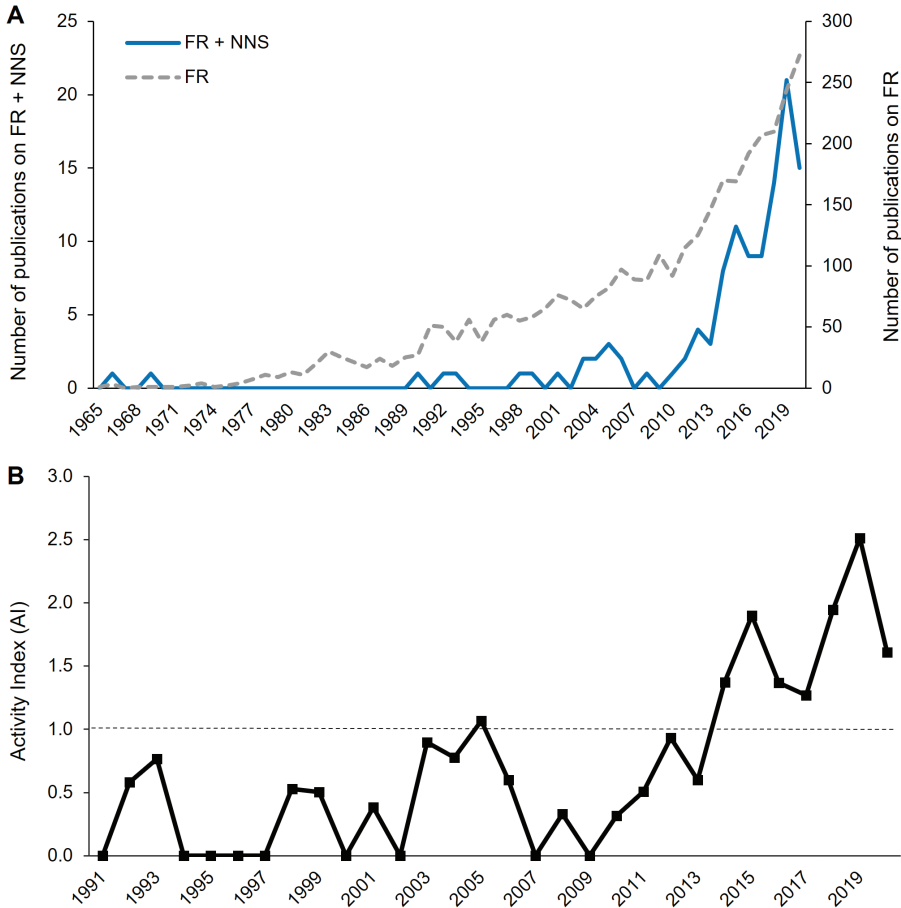


Figure 2. Temporal trends of papers using Functional Response in invasion science (i.e. FR + NNS) and Functional Response in general (FR) **A** number of published papers *per year* (please note the different scale on the right) **B** the Activity Index (AI) in research output that used Functional Response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

control ($\chi^2 = 47.1$, $df = 8$, $n = 120$, $p < 0.001$; 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).

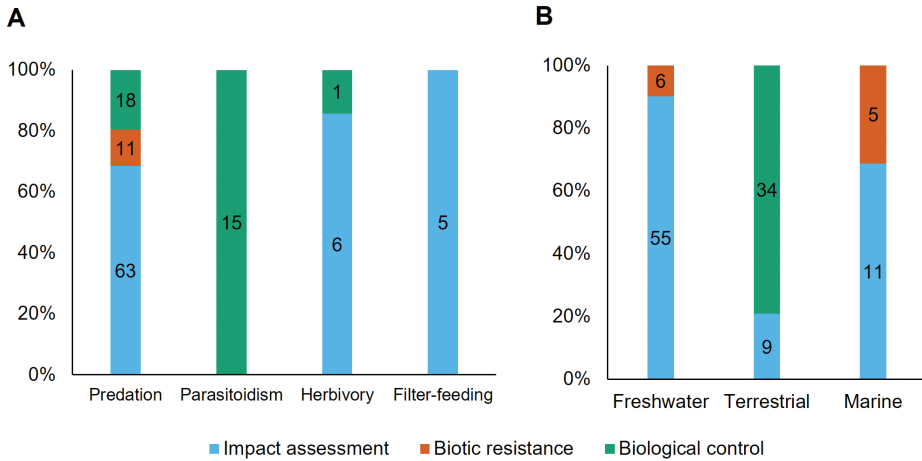


Figure 3. The proportion of studies *per category A* regarding type of interaction *B* regarding habitat type. The numbers inside the bars indicate the total number of papers. The plant-nutrient interaction type was omitted in plot **A** to facilitate visualisation (only one study in the freshwater environment).

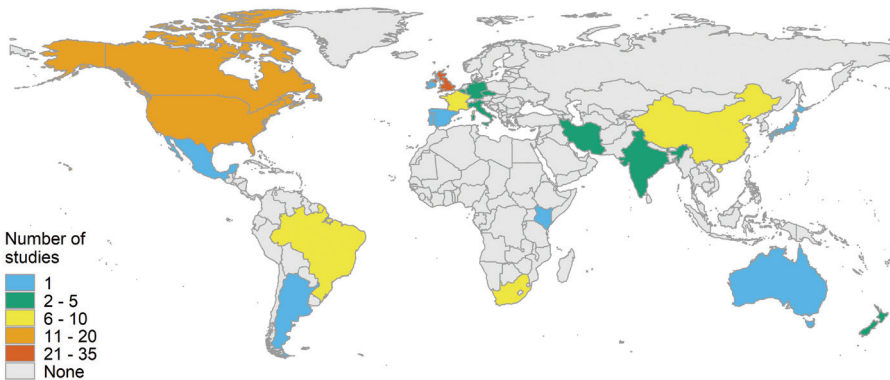


Figure 4. World map showing the number of studies conducted *per country* included in this review. Antarctica is omitted from the map but there are no studies conducted in this region.

Taxonomic trends

In general, insects and crustaceans were the most studied taxonomic groups, both as consumers ($\chi^2 = 98.1$, $df = 7$, $n = 122$, $p < 0.001$) and as resource ($\chi^2 = 176.5$, $df = 7$, $n = 134$, $p < 0.001$), 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

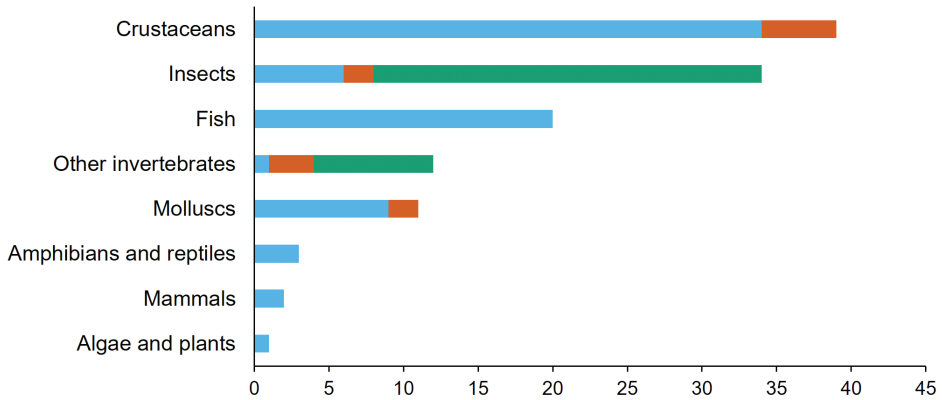
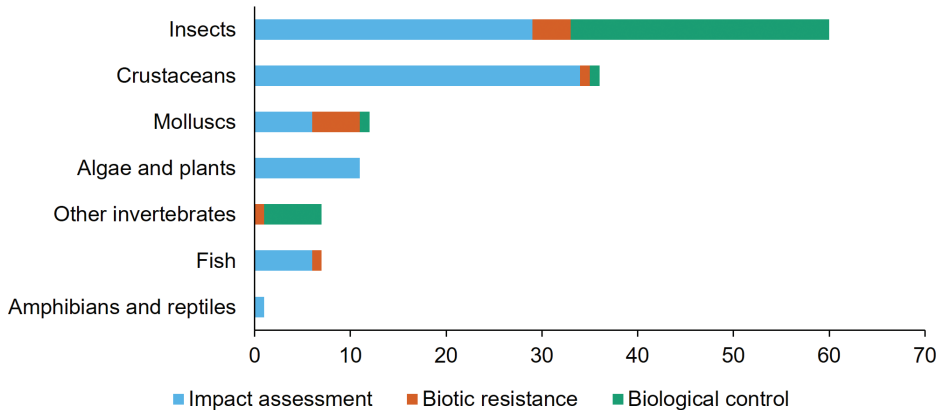
A**B**

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.

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%).

Context-dependencies and FR types

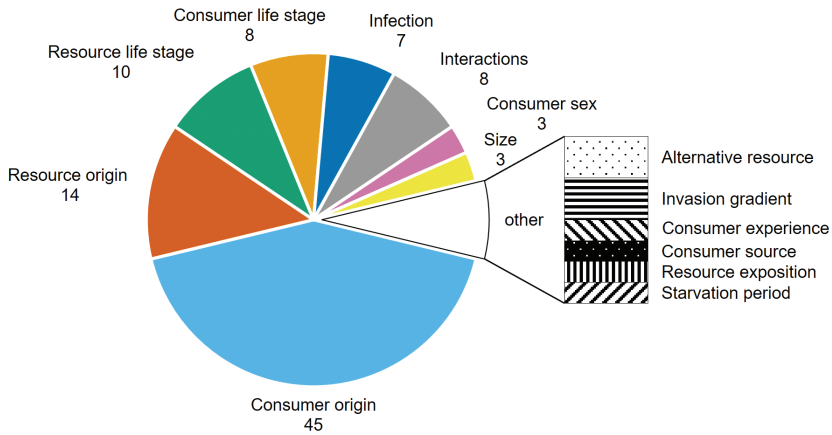
Most studies (81.7%) considered context-dependency in their experimental design by modelling the FR under different biotic and abiotic treatments. From these, the majority tested biotic contexts (65.7%), followed by studies testing different abiotic contexts (20.2%), while just 14.1% used both biotic 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).

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 ($\chi^2 = 243.3$, $df = 6$, $n = 717$, $p < 0.001$). Type II was also the most common type of FR regardless of the type of habitat studied ($\chi^2 = 33.2$, $df = 4$, $n = 717$, $p < 0.001$).

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

A



B

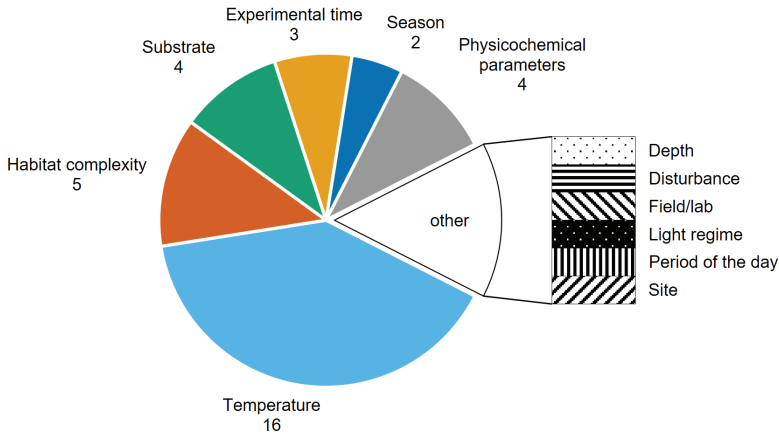


Figure 6. Different contexts used in experiments of the studies which derived Functional Responses under more than one treatment **A** regarding biotic contexts **B** regarding abiotic contexts. For biotic contexts, treatments used in two or fewer studies (alternative resource 2, invasion gradient 2, 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”.

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; Coblenz 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 (Lavery 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).

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 ecological impacts of NNS	As the FR can be a phenomenological approach, integrating ecomorphological traits (e.g. body size, feeding structures), metabolic rate measurements, or immunoassay analysis can provide mechanistic explanations for differences in consumption impacts, thus improving predictive capacity.	Naranjo and Hagler 2001; Taylor and Dunn 2018; Luger et al. 2020; Giacomini 2022
Spatiotemporal variation in the impacts of NNS	Impact prediction based on estimates from single populations can be misleading if <i>per capita</i> effects vary greatly across space and time. Studies comparing variation in FRs across conspecific populations have tested the importance of the 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 invasive. 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 <i>per capita</i> 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	<i>Successful NNS are often more efficient at exploiting key resources than functionally-similar native species.</i> Invasive and non-invasive NNS and trophically analogous native species could be compared with respect to <i>per capita</i> 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	<i>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.</i> 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	<i>NNS can facilitate one another in various ways to increase colonisation success, abundance, or performance, thereby causing an acceleration in the rate of invasion and increasing the likelihood of synergistic impacts.</i> 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

Hypothesis	Prediction (in italics) and application	Key references
Ecological Naïveté	<i>NNS will be more impactful if the recipient community do not share an eco-evolutionary experience with functionally similar species, being naive to the novel species.</i> One can use the FR to test the prediction that prey exposed to novel generalist predators would be more likely to be destabilised 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	<i>A NNS co-evolved enemy has a stronger negative effect on resident native species, thereby reducing biotic resistance.</i> The effect of parasites on <i>per capita</i> 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	<i>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.</i> 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	<i>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.</i> This hypothesis could be tested through a comparison of FR <i>per capita</i> effects of conspecific populations in invaded and native ranges.	Blossey and Nötzold 1995
Evolutionary Imbalance	<i>Successful and more competitive NNS are likely originating from geographic regions of high phylogenetic diversity.</i> FRs can compare <i>per capita</i> effects, and thus competitive abilities, of functionally or phylogenetically similar consumers from regions of contrasting diversity.	Fridley and Sax 2014
Environmental Heterogeneity	<i>Spatiotemporal heterogeneity creates refugia against the impacts of NNS on native resources, thereby facilitating coexistence.</i> 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	<i>The impact of a NNS is inversely correlated with the distance of the novel habitat conditions from the species' environmental optimum.</i> FRs can be used to measure variation in <i>per capita</i> 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	<i>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.</i> The comparative FR approach could be applied to test intraspecific differences in <i>per capita</i> effects across an expanding population to account for variation in impact across space and time.	Iacarella et al. 2015b
Taxonomic Distinctiveness	<i>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).</i> 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 to a novel genus.	Ricciardi and Atkinson 2004

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).

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Supplementary material I

Flow chart

Authors: Larissa Faria, Ross N. Cuthbert, James W. E. Dickey, Jonathan M. Jeschke, Anthony Ricciardi, Jaimie T. A. Dick, Jean R. S. Vitule

Data type: figure (.docx file)

Explanation note: 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.

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Link: <https://doi.org/10.3897/neobiota.85.98902.suppl1>

Supplementary material 2

List of the data extracted from publications included in the systematic review

Authors: Larissa Faria, Ross N. Cuthbert, James W. E. Dickey, Jonathan M. Jeschke, Anthony Ricciardi, Jaimie T. A. Dick, Jean R. S. Vitule

Data type: table (.docx file)

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Supplementary material 3

Journal trends analysis

Authors: Larissa Faria, Ross N. Cuthbert, James W. E. Dickey, Jonathan M. Jeschke, Anthony Ricciardi, Jaimie T. A. Dick, Jean R. S. Vitule

Data type: figure (.docx file)

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Link: <https://doi.org/10.3897/neobiota.85.98902.suppl3>

Supplementary material 4

List of treatments used by the studies deriving Functional Response (FR) curves under different biotic and abiotic contexts

Authors: Larissa Faria, Ross N. Cuthbert, James W. E. Dickey, Jonathan M. Jeschke, Anthony Ricciardi, Jaimie T. A. Dick, Jean R. S. Vitule

Data type: table (.docx file)

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Link: <https://doi.org/10.3897/neobiota.85.98902.suppl4>

Supplementary material 5

List of publications included in the systematic review

Authors: Larissa Faria, Ross N. Cuthbert, James W. E. Dickey, Jonathan M. Jeschke, Anthony Ricciardi, Jaimie T. A. Dick, Jean R. S. Vitule

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