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# Non-native species have higher consumption rates than their native counterparts

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## ABSTRACT

Non-native species can be major drivers of ecosystem alteration, especially through changes in trophic interactions. Successful non-native species have been predicted to have greater resource use efficiency relative to trophically analogous native species (the Resource Consumption Hypothesis), but rigorous evidence remains equivocal. Here, we tested this proposition quantitatively in a global meta-analysis of comparative functional response studies. We calculated the log response ratio of paired non-native and native species functional responses, using attack rate and maximum consumption rate parameters as response variables. Explanatory variables were consumer taxonomic group and functional feeding group, habitat, native assemblage latitude, and non-native species taxonomic distinctiveness. Maximum consumption rates for non-native species were 70% higher, on average, than those of their native counterparts; attack rates also tended to be higher, but not significantly so. The magnitude of maximum consumption rate effect sizes varied with consumer taxonomic group and functional feeding group, being highest in favour of non-natives for molluscs and herbivores. Consumption rate differences between non-native and native species tended to be greater for freshwater taxa, perhaps reflecting sensitivity of insular freshwater food webs to novel consumers; this pattern needs to be explored further as additional data are obtained from terrestrial and marine ecosystems. In general, our results support the Resource Consumption Hypothesis, which can partly explain how successful non-native species can reduce native resource populations and restructure food webs.

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

## CONTENTS

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## I. INTRODUCTION

Rates of introduction of non-native species into new environments are on the order of hundreds of species per year in many regions, with no sign of deceleration (Seebens *et al.*, 2021; IPBES, 2023; Briski *et al.*, 2024). Invasive non-native species (*sensu* Soto *et al.*, 2024) are among the main drivers of ecosystem alteration worldwide (Bellard, Cassey & Blackburn, 2016; Blackburn, Bellard & Ricciardi, 2019; Jaureguiberry *et al.*, 2022), causing negative impacts through various mechanisms – most notably through direct consumption *via* predation and herbivory (Lockwood, Hoopes & Marchetti, 2007). Overexploitation of resources by invasive non-native species and associated disruption of ecological networks is expected to become an increasingly prevalent extinction driver worldwide over the coming century (Strona & Bradshaw, 2022). Several examples of the potential for non-native species to extirpate natives are notorious, such as the introduction of Nile perch (*Lates niloticus*) to Lake Victoria that drove many dozens of endemic cichlids to extinction and caused the decline of other carnivore species (Kruuk & Goudswaard, 1990; Goudswaard, Witte & Katunzi, 2002). Another is the case of the peacock bass (*Cichla monoculus*) in South America, which reduced or extirpated native prey due to predation, and native piscivores due to competition (Pelicice & Agostinho, 2009; Pelicice, Latini & Agostinho, 2015; Franco, García-Berthou & Santos, 2021).

Many impactful non-native species are highly efficient in consuming available resources (Funk & Vitousek, 2007; Morrison & Hay, 2011). Potential underlying reasons for this pattern include release from parasites and predators (Enemy Release Hypothesis *sensu* Keane & Crawley, 2002) or a lack of evolutionary history of the native resource with the novel consumer [Prey Naïveté Hypothesis and/or non-native Novel Weapons Hypothesis (Ricciardi *et al.*, 2013; Buckley & Catford, 2016)]. If non-native species have a propensity to exploit resources at greater rates, it could lead to ramifying effects on resource populations and food webs – and offer a species trait to predict ecological impacts (Dick *et al.*, 2013).

It has been claimed that per-capita rates of consumption, such as those quantified by functional responses (FRs; see Section II and Fig. 1), are useful for quantifying and predicting non-native species impacts in the field (Dick *et al.*, 2014; Faria *et al.*, 2023a). If efficient resource consumption is a general trait among invasive non-native species, it is expected that parameters of their FRs would be higher when compared to those of native analogues (Dick *et al.*, 2017a). By measuring consumption across a realistic gradient of resource densities, FR assessments allow the inference of density-dependent effects. At low resource densities, if non-native species are more efficient at consuming resources when the resources are scarce, then such consumers are more likely to extirpate resource populations. If resources are abundant and the non-native species displays higher consumption rates, this could in the long term drive increased non-native 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 ecological impacts (Faria *et al.*, 2023a). *Per-capita* effects quantified through laboratory experiments can be a proxy for field impacts and could thus support rapid

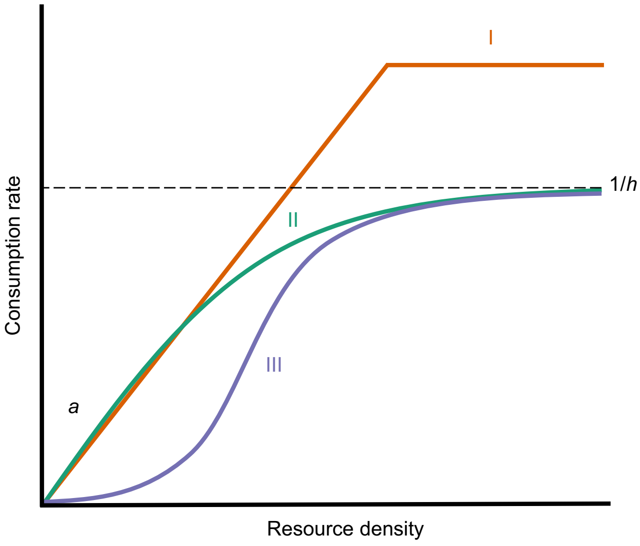

**Fig. 1.** General functional response types (linear I – orange; hyperbolic II – green; and sigmoidal III – violet). The attack rate parameter (*a*) determines the initial slope of the curve in Type I and II functional responses, whereas the inverse of handling time (1/*h*, dashed line) coincides with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

assessment and prioritisation of high-impact species for management (Ricciardi *et al.*, 2021; Faria *et al.*, 2023a). Although biotic and abiotic environmental factors have been shown substantially to mediate outcomes of FR studies (Faria *et al.*, 2023a), these contexts can be explicitly tested rather than viewed as nuisance factors (Dick *et al.*, 2014).

Despite the rapid accumulation of evidence across study systems using the CFR approach (Faria *et al.*, 2023a), the hypothesis that successful non-native species have higher FR parameters 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, DeLong & Belmaker, 2022); however, data used in that study were not matched with native comparators as was recommended by Dick *et al.* (2014).

Here, we perform the first global meta-analysis of published CFR studies to address the Resource Consumption Hypothesis (Ricciardi *et al.*, 2013; Dick *et al.*, 2014; Faria *et al.*, 2023a). We tested the following specific predictions: (*i*) differences in consumption rates are greater for freshwater than marine and terrestrial taxa, reflecting prey naïveté stemming from differences in insularity of their respective biota (Cox & Lima, 2006); (*ii*) differences in consumption 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 predator richness reduces the evolutionary mismatch created by a novel consumer (Schemske *et al.*, 2009); and (*iii*) non-native species that represent novel (unshared) genera in the region containing the native analogues to which they are compared will have higher impact than non-native species that belong to genera shared with the native biota (the Taxonomic Distinctiveness Hypothesis; Ricciardi & Atkinson, 2004).

## II. FUNCTIONAL RESPONSE IN ECOLOGY

The consumption rate of a species (such as a predator) as a function of the availability of a resource (prey) is known as the functional response (FR) (Solomon, 1949; Holling, 1959b). Generally, the FR describes how much an individual can consume across a gradient of resource densities in a specified amount of time. This relationship can be broadly described by at least three different FR types (Fig. 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 FR (Holling, 1959b). However, many consumers will be limited by the time they spend pursuing, subduing and consuming one resource item, decelerating the rate of consumption as resources become more abundant. This results in a hyperbolic relationship between resource availability and consumption rate that characterises a Type II FR (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 an alternative more abundant resource (driven by frequency-dependent predation such as prey switching). In these cases, a Type III FR 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 resource densities (DeLong, 2021). This can happen when there are swarming effects, such as consumer confusion or accumulation of toxic substances produced by dangerous prey (Jeschke, Kopp & Tollrian, 2004).

FRs are typically derived through laboratory experiments (although field data can also be used, e.g. Smout *et al.*, 2014) consisting of a gradient of resources offered to a consumer for a prespecified experimental duration, and then quantifying how much has been consumed after the available time (DeLong, 2021). Consumption data are then modelled using the relevant equation according to the FR type (i.e. typically Type I, II, or III, alongside flexible models across types). The most important parameters in FR models are (*cf.* Jeschke, Kopp & Tollrian, 2002) the attack rate and the handling time (Holling, 1959a). Attack rate $a$ is also known as the attack constant, capture rate, maximum clearance rate, instantaneous rate of discovery, and related terms, and describes the space or volume containing resources that is effectively cleared by the consumer per unit of time (Holling, 1959a; DeLong, 2021). This parameter describes the initial slope of the FR curve (Fig. 1), 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 that are at 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 (Fig. 1; Holling, 1959a; DeLong, 2021). The shorter the handling time, the greater the number of resource items consumed. Therefore, the inverse of handling time ($1/h$) determines the highest consumption rate of a consumer when resources are not limiting, a parameter called maximum consumption rate (MCR; sometimes maximum predation rate, maximum feeding rate, and related terms) that corresponds to the asymptote of the Type II and Type III FR curves (DeLong, 2021). Furthermore, attack rate and handling time can be assimilated into the Functional Response Ratio (FRR), through deriving $a/h$ (Cuthbert *et al.*, 2019), which captures both parameters for a holistic metric of the FR.

Determining the type and magnitude of FR is relevant, as it directly influences population dynamics (DeLong, 2021; Kalinkat *et al.*, 2023). A Type II FR 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 FR is more stabilising, as consumption rates are low when resources are scarce, giving the resource population refugia to increase its abundance in the long term (Holling, 1959b; Murdoch & Oaten, 1975). It is important to note, however, that the FR 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). Moreover, FR parameters may change with several biotic and abiotic variables such as temperature, body size ratio, and parasite infection, and they vary among individual consumers within a given species and population (DeLong, 2021).

## III. METHODS

### (1) Selection of studies and observations

We systematically searched for a subset of CFR studies that compared the FRs of non-native and analogous native species consuming the same resource. This subset was taken from a previously published systematic review of FRs in invasion science (Faria *et al.*, 2023a), with the literature search updated in May 2023 following the same methodology as Faria *et al.* (2023a). We conducted our review according to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses for Ecology and Evolutionary Biology (PRISMA-EcoEvo) guidelines (see online Supporting Information, Appendix S1; O'Dea *et al.*, 2021).

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 FR models. Therefore, we sought studies that provided the FR parameters attack rate ($a$), handling time ($h$), and/or MCR comparably between non-native and native species (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 variable was consumption *via* feeding; thus omitting, for example, studies using parasitoids (response recorded as attacks or oviposition) from our analyses, which are generally rare in CFR studies (Faria *et al.*, 2023a).

We considered each pair of non-native and native species consuming the same resource within studies as a separate observation. As previously reviewed by Faria *et al.* (2023a), many studies perform more than one FR experiment for the same pair of consumers under different biotic and abiotic treatments. In these cases, we chose to retain data from the most context-realistic treatment (when this was explicit from the text) or from the treatment that was comparable between studies. For example, Dickey *et al.* (2021b) tested two salinities (10 and 16 ppt) and analysed data from consumption and consumption plus wounded prey. In this case, we decided to retain only observations from the ambient salinity (16 ppt) and excluded those that correspond to a potential future scenario of sea freshening (10 ppt, less representative currently). Likewise, we retained 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 for each consumer into a single composite sample (when provided, standard errors were propagated from individual estimates), to avoid pseudo-replication. Nonetheless, our final data set still contained more than one observation per study, particularly capturing unique non-native *versus* native pairs (e.g. the same pair of consumers feeding on a different resource, or different non-native species compared to the same native analogue). This non-independence within studies is accounted for statistically (see Section III.3). The screening of 209 observations was performed by one author (L.F.) and subsequently checked by two other authors (R.N.C. and J.W.E.D.) to ensure agreement. Observations that these authors assessed as equally realistic had their parameter estimates averaged into a single composite sample. Likewise, observations considered less realistic by these authors were excluded, and the remaining observations were kept for further analysis.

### (2) Data extraction

When available, we extracted $a$, $h$, and MCR parameters estimated from FR models and their corresponding standard errors (S.E.) 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 S.E. Input data used to model FR parameters (i.e. the sum of replicates of all initial densities used in the experiment) were recorded as the sample size, except when S.E. from estimates were obtained through bootstrapping (in these cases, we considered the number of bootstraps as the sample size). Sample size and S.E. (when available) were used to calculate standard deviations (S.D.) for each consumer.

We used the $h$ parameter estimate to calculate the MCR for each consumer species as $1/h$, to standardise it as units of resource consumed per consumer, per experiment. The corresponding MCR S.E. was propagated from the S.E. of $h$. When $h$ was not provided, we extracted the MCR as calculated by the study. All data were extracted by the same author (L.F.).

Information on consumer taxonomic group, functional feeding group, habitat, native species sampling site, resource origin and resource source were also recorded as provided by authors or searched for in the relevant literature (see Table 1 for definitions). From the native species sampling site, we obtained coordinates to categorise the latitude of native assemblages as tropical/sub-tropical (0° to 35° N and S) or temperate (>35° N and S). We also used the native species sampling site to check in the available literature if the native community shared any species from the same genus as the non-native species, considering the finest spatial scale possible, thereby inferring taxonomic distinctiveness. For example, in a study where the native species was sampled at River Lagan, Northern Ireland, *Dikerogammarus villosus* was the non-native species studied (Bollache *et al.*, 2008). The genus *Dikerogammarus* belongs to the Ponto-Caspian faunistic complex and was thus classified as a distinctive genus for Northern Ireland, where it is

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

| Variable | Definition |
|---|---|
| Consumer taxonomic group | Taxonomic group of the consumer defined as per Pyšek *et al.* (2008). |
| Consumer functional feeding group | Functional feeding group of the consumer defined as carnivore, herbivore or omnivore, according to the focal study or relevant literature. |
| Habitat | Type of habitat where consumer and resource interact, that is freshwater, marine (including brackish) or terrestrial, according to the focal study. |
| Native species sampling site | Where native species specimens were collected for use in experiments, according to the study methods. |
| Resource origin | Origin of the resource species (native or non-native) according to the focal study or relevant literature. In some cases, resources were not specified as species and therefore origin was not identified. |
| Resource source | Origin from where resource specimens used in experiments were sourced (wild or cultivated). |

not yet present (Özbek & Özkan, 2011). References used for this classification are provided in Dataset S1. Taxonomic distinctiveness between non-native species and the native recipient community was only tested for observations where the resource was a native species sourced in the wild to ensure they were ecologically relevant.

### (3) Meta-analysis

Considering that FR parameters are usually estimated from the same model (and thus likely correlated), we performed a meta-analysis for each response variable ($a$ and MCR) separately. As many studies did not provide S.E. to allow us to calculate S.D. (72% of studies without in the $a$ data set, and 61% of studies without in the MCR data set), we employed the "Missing Cases" method, as proposed by Nakagawa *et al.* (2023b), where sampling variances of observations with missing S.D. are estimated by imputing the pooled coefficient of variation (CV) from the subset of studies that report S.D. We decided to handle missing data in this way because alternatively we would have needed to rely on an unweighted meta-analysis, which, given the low number of complete case observations, would significantly decrease the sample size ($k$) of our analysis.

For complete observations (i.e. those with S.D. data), we calculated the effect size and sampling variance ($v$) based on the log response ratio (lnRR), as originally proposed by Hedges, Gurevitch & Curtis (1999), with the bias correction recommended by Lajeunesse (2015):

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

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

where $m_{\mathrm{NN}}$ is the mean FR parameter ($a$ or MCR) of the non-native species, $m_{\mathrm{N}}$ is the corresponding mean parameter estimated for the native comparator, CV (S.D./$m$) is the coefficient of variation for each consumer and $n$ is the sample size. For observations with missing S.D., we calculated the effect size (lnRR) and the sampling variance using the equations proposed by Nakagawa *et al.* (2023b):

$$\mathrm{lnRR} = \ln\left(\frac{m_{\mathrm{NN}}}{m_{\mathrm{N}}}\right) + \frac{1}{2}\left(\frac{\left[\sum_{i=1}^{K}\left(n_{\mathrm{NN}i}\mathrm{CV}_{\mathrm{NN}i}\right)/\sum_{i=1}^{K} n_{\mathrm{NN}i}\right]^2}{n_{\mathrm{NN}}} - \frac{\left[\sum_{i=1}^{K}\left(n_{\mathrm{N}i}\mathrm{CV}_{\mathrm{N}i}\right)/\sum_{i=1}^{K} n_{\mathrm{N}i}\right]^2}{n_{\mathrm{N}}}\right) \tag{3}$$

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

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 FR parameters of non-native species are greater than those of native species, 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 species have higher consumption rates than trophically analogous native species.

Given the dependence of our data set (more than one observation per study and multiple non-native species compared to the same native analogue – "shared control"), we applied a multilevel meta-analysis model with "study" as a random effect (Mengersen, Jennions & Schmid, 2013; Noble *et al.*, 2017; Nakagawa *et al.*, 2023c). To account for shared-sampling variance between effect sizes due to a common native comparator species, we used Robust Variance Estimators (RVE) (Pustejovsky & Tipton, 2022; Nakagawa *et al.*, 2023c). First, a null multilevel model was fitted using restricted maximum likelihood for each data set 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 *et al.*, 2023a). Given the resulting high levels of $I^2$ total (>98% for both data sets) (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 and consumer functional feeding group (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 after setting struct = "HCS" to assume a heteroscedastic compound symmetry (heterogeneous variances). Results were visualised through forest-like plots with the *orchard_plot* function in the "orchaRd" package (Nakagawa *et al.*, 2023a). All analyses and plots were performed in the R environment v. 4.3.1 (R Core Team, 2023).

### (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 Lajeunesse (2015). We employed the "Missing Cases" method given the large proportion of missing data in our data set (which exceeded the 55% previously assessed by Nakagawa *et al.* (2023b)). However, it has been suggested that the "All Cases" method may perform better under several situations (Nakagawa *et al.*, 2023b). 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 this, 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 (Noble *et al.*, 2017; Nakagawa *et al.*, 2022).

## IV. 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 observation pairs of non-native *versus* native species (Fig. 2) that had either data on *a*, MCR or both response variables. Each study yielded an average of 2.4 ± 2.3 (mean ± S.D.) effect sizes, with a range of 1–12. Many observations involved comparisons from studies that compared more than one non-native to the same native species (56% of effect sizes).

Most observations came from omnivores (74%)—mainly crustaceans and fishes (89%)—from freshwater habitats (86%) in temperate locations (72%). 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 species.

Overall, we found higher maximum consumption rates for non-native species compared to native trophic analogues ($\text{lnRR}_{\text{MCR}} = 0.285$, 95% CI = 0.1–0.47; Fig. 3B). Attack rates also tended to be higher in non-native species, but this difference was not significant ($\text{lnRR}_a = 0.209$, 95% CI = −0.02–0.44; Fig. 3A). From total heterogeneity ($I^2$), the study random effect explained 41% of heterogeneity in the *a* data set, and 30% in the MCR data set.

Effect sizes of attack rate were not significantly positive across consumer taxonomic groups (Fig. 4A; Table 2). Regarding consumer functional feeding group, non-native carnivores had a significantly higher attack rate compared to native analogues (Table 2, Fig. 4B); however, effect sizes did not differ significantly among functional feeding groups (test of moderators: $F_{(2,45)} = 1.79$, $P = 0.17$). Effect sizes of attack rate of freshwater taxa were significantly positive (Table 2, Fig. 4C), but did not significantly differ among 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, Fig. 4D).

Molluscs, insects and crustaceans had significantly positive effect sizes of MCR (Table 2, Fig. 5A); however, taxonomic groups did not differ significantly ($F_{(4,47)} = 1.74$, $P = 0.16$). Contrary to the trend observed for attack rate, non-native carnivores did not have a significantly higher MCR compared to natives, but a positive effect size was observed for non-native omnivores and herbivores (Table 2, Fig. 5B). Nevertheless, we found no significant differences among functional feeding group effect sizes ($F_{(2,49)} = 2.35$, $P = 0.11$). As observed for attack rates, MCR was significantly positive only for freshwater taxa (Table 2, Fig. 5C), 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, Fig. 5D) and

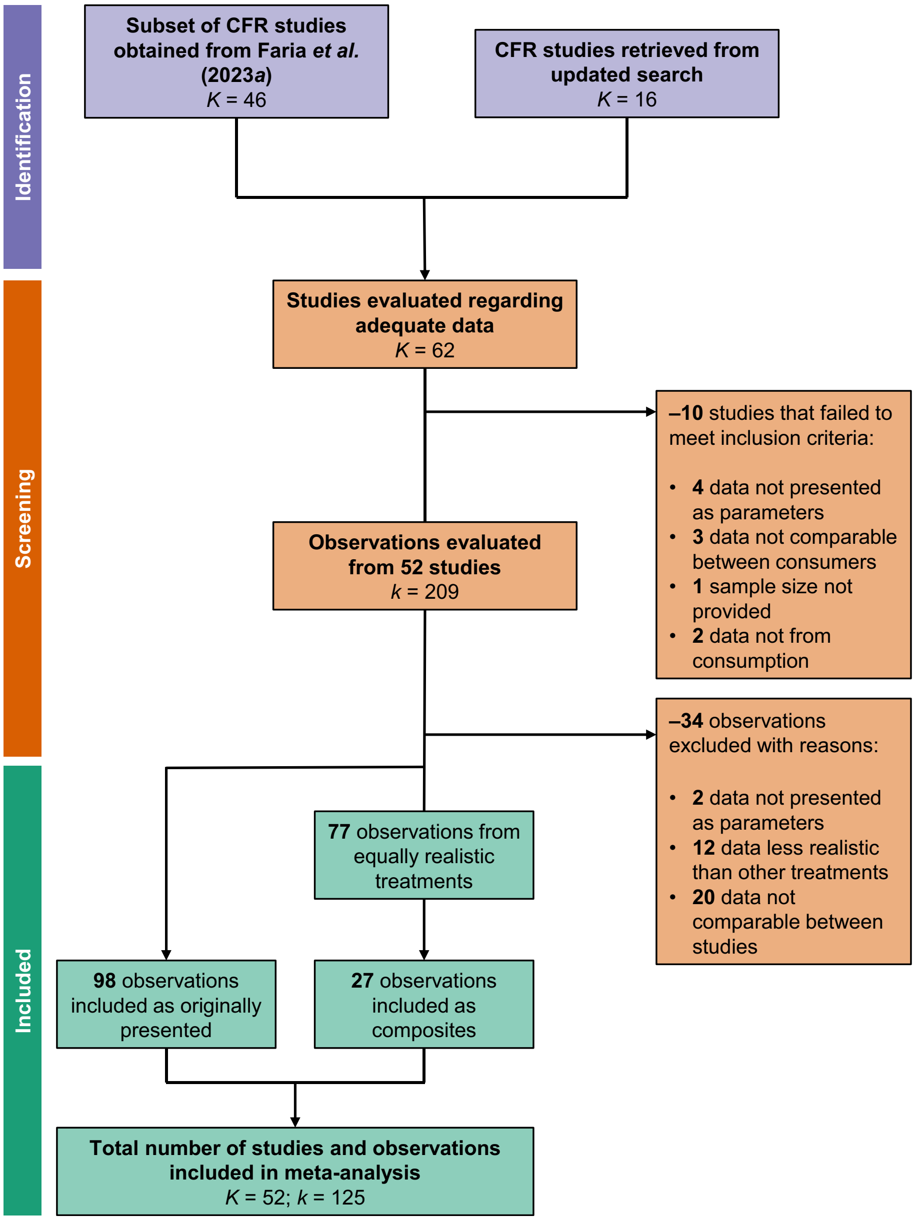

**Fig. 2.** PRISMA flowchart showing the number of studies ($K$) that used the comparative functional response (CFR) approach and observations ($k$) as pairs of non-native and native species consuming the same resource that were retrieved, screened and included in our final data set.

also significantly different from observations of temperate regions ($F_{(1,50)} = 5.08$, $P = 0.03$).

We did not find evidence that non-natives from a distinct genus relative to those in the native community have higher FR parameters (Table 3, Fig. 6). By contrast, non-natives that share their genus with the native community had significantly positive effect sizes for MCR (Table 3, Fig. 6B), with results differing in strength from consumers that do not share the same genus ($F_{(1,42)} = 4.99$, $P = 0.03$).

Only two effect sizes ($a$ and MCR 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). 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 $= -0.591$, $P = 0.22$; MCR: mean intercept $= 0.128$, $P = 0.75$), thus we did not find evidence of a publication bias using this method. Additionally, we

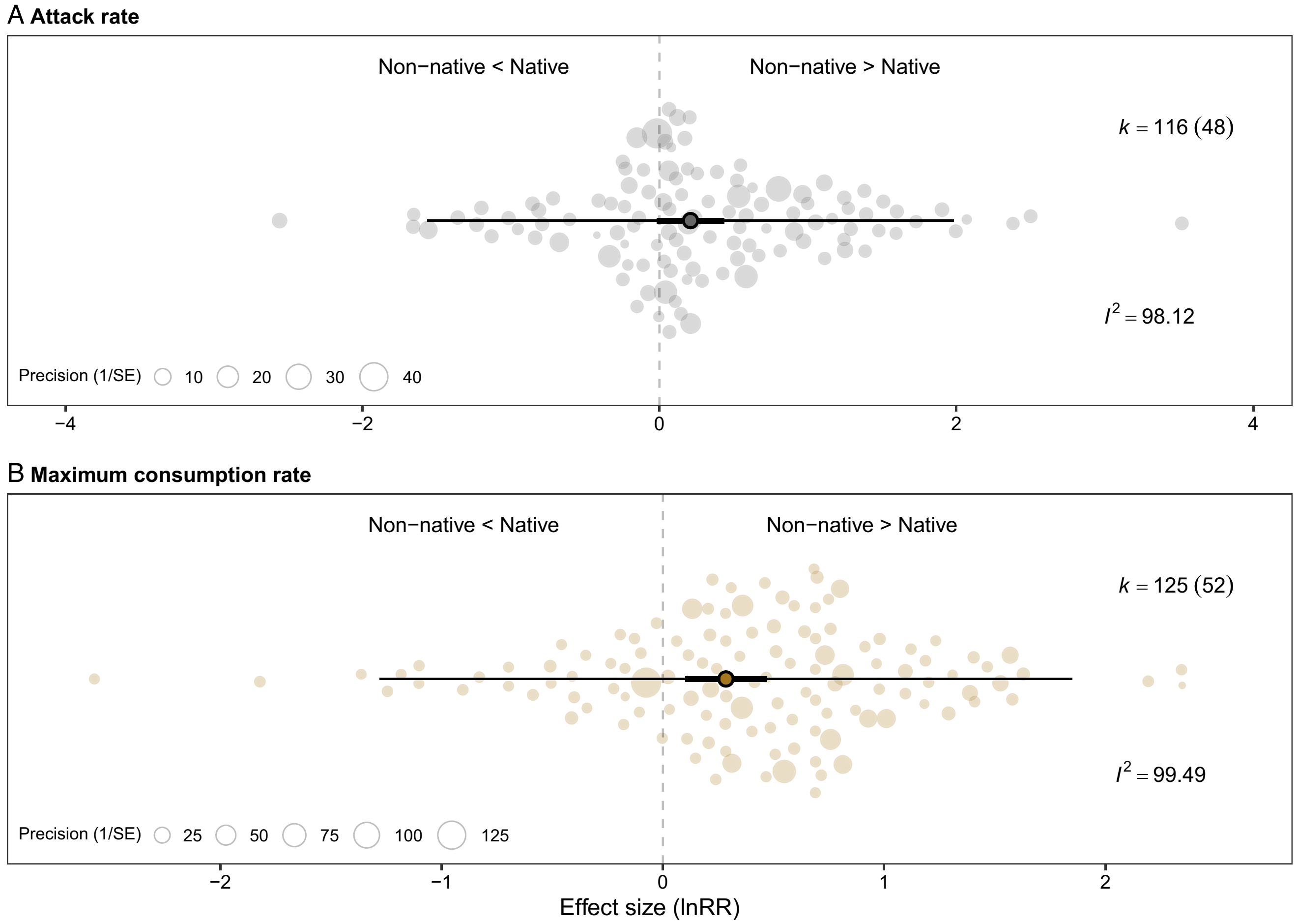

**Fig. 3.** Orchard plots of the overall effect size (lnRR) obtained by our null multilevel meta-analysis model for both response variables: (A) attack rate and (B) maximum consumption rate. Positive effect sizes indicate that non-native species have higher functional response parameters than natives. 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 at 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.

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 MCR there was a subtle change from 0.285 to 0.295 (Table S1).

## V. DISCUSSION

Many hypotheses in invasion science aim to explain the subset of non-native species that are both successful invaders and cause significant negative impacts in invaded ecosystems (Catford, Jansson & Nilsson, 2009; Ricciardi *et al.*, 2013; Enders *et al.*, 2020; Daly *et al.*, 2023). Non-native species are often deemed more damaging than native species to resource populations (Salo *et al.*, 2007; Paolucci, MacIsaac & Ricciardi, 2013; McKnight *et al.*, 2016). Thus, the Resource Consumption Hypothesis posits that successful and impactful non-native species are able to use key resources more efficiently than trophically analogous native species (Ricciardi *et al.*, 2013; Dick *et al.*, 2014; Faria *et al.*, 2023a). Here, we provide the largest quantitative test of this hypothesis to date using data from CFR studies. We found that, in general, non-native species have higher maximum consumption rates and a tendency for higher attack rates compared to analogous native species, corroborating the hypothesis. Nevertheless, the consumptive *per-capita* effects of non-native species vary depending on other factors, such as their taxonomic group and functional feeding group, as well as with the ecosystem or habitat where the interaction takes place.

### (1) Resource consumption hypothesis

Attack rates were significantly higher only for non-native carnivores and freshwater taxa, although tendencies were mostly positive in favour of non-native species. These results

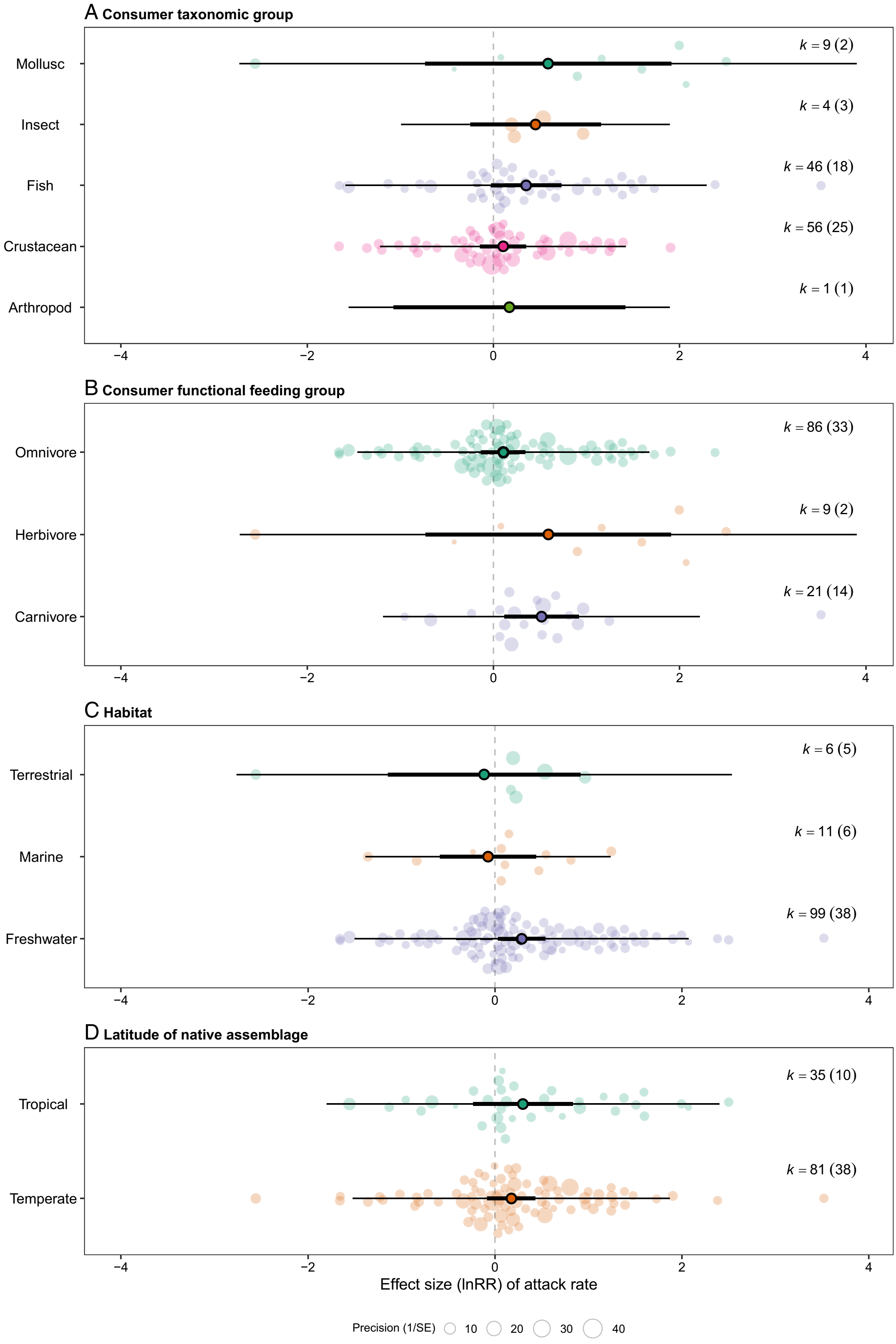

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Table 2. Mean estimated effect sizes for both response variables ($\ln RR_a$: attack rate and $\ln RR_{MCR}$: maximum consumption rate) and their corresponding 95% confidence intervals (95% CI), obtained for each group from univariate meta-regression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

| | $\ln RR_a$ | 95% CI | $\ln RR_{MCR}$ | 95% CI |
|---|---|---|---|---|
| Consumer taxonomic group | | | | |
| Arthropod | 0.171 | [−1.074 to 1.416] | 0.216 | [−0.592 to 1.024] |
| Crustacean | 0.105 | [−0.143 to 0.354] | 0.302 | [0.089 to 0.515] |
| Fish | 0.351 | [−0.027 to 0.729] | 0.194 | [−0.097 to 0.485] |
| Insect | 0.452 | [−0.250 to 1.154] | 0.414 | [0.068 to 0.760] |
| Mollusc | 0.587 | [−0.735 to 1.909] | 1.042 | [0.441 to 1.643] |
| Consumer functional feeding group | | | | |
| Carnivore | 0.517 | [0.115 to 0.919] | 0.177 | [−0.238 to 0.591] |
| Herbivore | 0.590 | [−0.728 to 1.908] | 1.004 | [0.328 to 1.680] |
| Omnivore | 0.106 | [−0.131 to 0.344] | 0.289 | [0.099 to 0.479] |
| Habitat | | | | |
| Freshwater | 0.287 | [0.032 to 0.541] | 0.341 | [0.148 to 0.533] |
| Marine | −0.074 | [−0.589 to 0.442] | −0.120 | [−0.657 to 0.417] |
| Terrestrial | −0.116 | [−1.147 to 0.915] | 0.333 | [−0.045 to 0.711] |
| Latitude of the native assemblage | | | | |
| Temperate | 0.176 | [−0.081 to 0.433] | 0.191 | [−0.025 to 0.406] |
| Tropical | 0.299 | [−0.235 to 0.832] | 0.607 | [0.305 to 0.909] |

reveal that, in general, non-native species do not differ from native species 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 on reproduction, and likewise successfully invade when resources are highly available (Blumenthal, 2006). Both hypotheses are rooted in the idea of spatiotemporal fluctuations in resources favouring non-native species over natives (Davis, Grime & Thompson, 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 these conditions; however, when resource availability increases, for example in response to human disturbance, non-native species will likely outperform native species (Daehler, 2003). Although most of the studies providing evidence for these hypotheses were performed with plants (Liu & van Kleunen, 2017; Knauf *et al.*, 2021), the postulated mechanisms may also apply to animal consumers. Experimental design characteristics may also explain this pattern, since FR studies typically employ non-replacement protocols, whereby resources are not replenished following consumption. This could dampen the detection of differences at low resource densities between natives and non-natives as they rapidly consume all available resources (Alexander *et al.*, 2012). However, since our study compares non-natives with natives, and the absolute parameters/FR shapes are thus not of as much interest as the comparisons, the above explanations are considered robust.

Conversely, maximum consumption rates were significantly higher overall, specifically for invertebrates (except arthropods), omnivores and herbivores, freshwater taxa and non-native species that shared their genus with the native community. Non-native invertebrates (except arthropods) showed higher MCR than natives, which is consistent with findings of a comparison of native *versus* non-native consumer effect sizes in the field (Paolucci *et al.*, 2013), but this pattern was not observed for fishes. Among invertebrates, molluscs presented the highest differential MCR, 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

*(Figure legend continued from previous page.)*
**Fig. 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 functional feeding group, (C) habitat and (D) latitude of the native assemblage. Positive effect sizes indicate that non-native species have higher functional response parameters than native species 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 at 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 an individual effect size, scaled according to its precision.

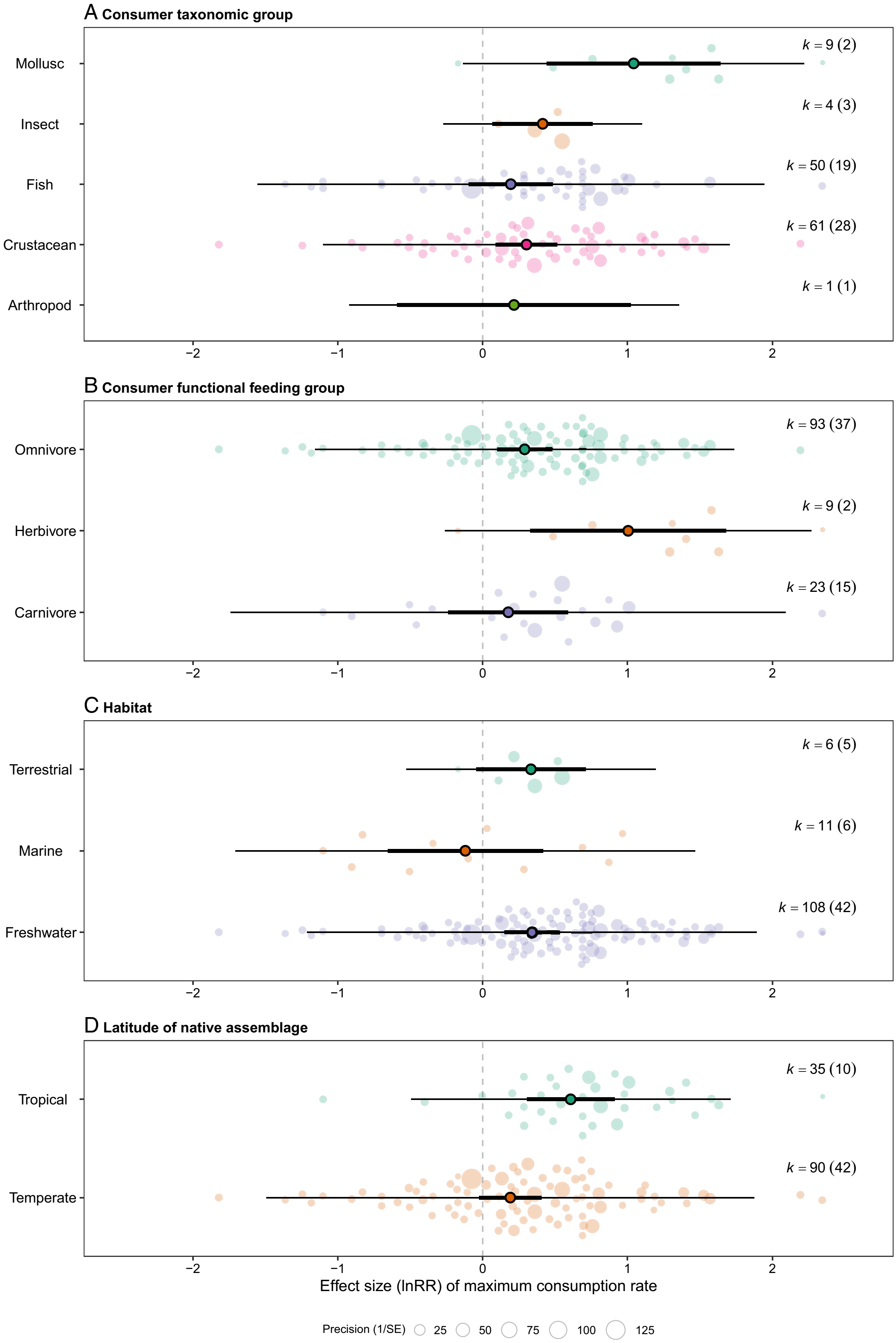

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Table 3. Mean estimated effect sizes for both response variables ($\ln RR_a$: attack rate and $\ln RR_{MCR}$: maximum consumption rate) and their corresponding 95% confidence intervals (95% CI), considering taxonomic distinctiveness of the non-native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

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

resources compared to the native snail *Bellamya aeruginosa* (Xu *et al.*, 2016). Likewise, non-native omnivores and herbivores exhibited higher MCR compared to their native counterparts. This result, however, should be interpreted in line with the usual experimental setting applied in FR studies. In general, experiments are performed by 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, Thuillier & Spataro, 2018). Nevertheless, their capacity for consuming significantly more food than native omnivores when resources are abundant reveals their opportunistic habits, an important trait in successful invasive species (Vatland & Budy, 2007; Romanuk *et al.*, 2009). Herbivores, typically represented by molluscs in our data set, had the highest MCR mean effect size, contributing to the body of evidence that non-native snails are highly efficient consumers when resources are abundant (Morrison & Hay, 2011; Liu *et al.*, 2021).

### (2) **Predictions**

We found that, in accordance with our prediction, differences between non-native and native species in attack rate and MCR were significantly greater than zero only for freshwater taxa and not for marine and terrestrial taxa. This finding should be interpreted with caution, owing to the relatively small number of terrestrial and marine studies for comparison. Nevertheless, the pattern is consistent with the view that a greater degree of insularity in lakes and river basins creates evolutionary isolation and thus greater potential naiveté 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 (see Anton *et al.*, 2020). 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 taxa on islands to compare the effect of insularity in this realm.

Regarding the latitude of the native assemblage, our results were contrary to expectations, with significant differences in the MCR of non-native species that are introduced to tropical and sub-tropical latitudes. The stronger predation pressure in the tropics due to greater diversity does not seem to provide protection against novel consumers as anticipated (Freestone *et al.*, 2021). In fact, as there are more specialised interactions in the tropics (Dobzhansky, 1950), 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 (Pyšek *et al.*, 2008; Chong *et al.*, 2021), and one that impedes a balanced interpretation of these results.

We expected that non-natives from a distinct genus would be more impactful to resources due to the lack of shared evolutionary history that makes prey more vulnerable to them (Ricciardi & Atkinson, 2004; Anton *et al.*, 2020). However, we found that MCRs 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 available food resources (Ricciardi & Mottiar, 2006). Indeed, non-native species are more likely to establish and impact native communities when they are closely related to natives, consistent with the latter hypothesis (Ma *et al.*, 2016; Xu *et al.*, 2024). Taxonomic distinctiveness, driven by prey naiveté and lack of resident enemies, might be most pronounced when the invasive non-native species is a top predator (therefore lacking a native trophic analogue) or some other uncontrolled consumer (e.g. zebra mussels *Dreissena polymorpha*) (Ricciardi *et al.*, 2013). From a methodological

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**Fig. 5.** Orchard plots showing effect size (lnRR) estimates of maximum consumption rate from univariate meta-regressions with potentially influential moderators: (A) consumer taxonomic group, (B) consumer functional feeding group, (C) habitat and (D) latitude of the native assemblage. Positive effect sizes indicate that non-native species have higher functional response parameters than natives 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 at 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 an individual effect size, scaled according to its precision.

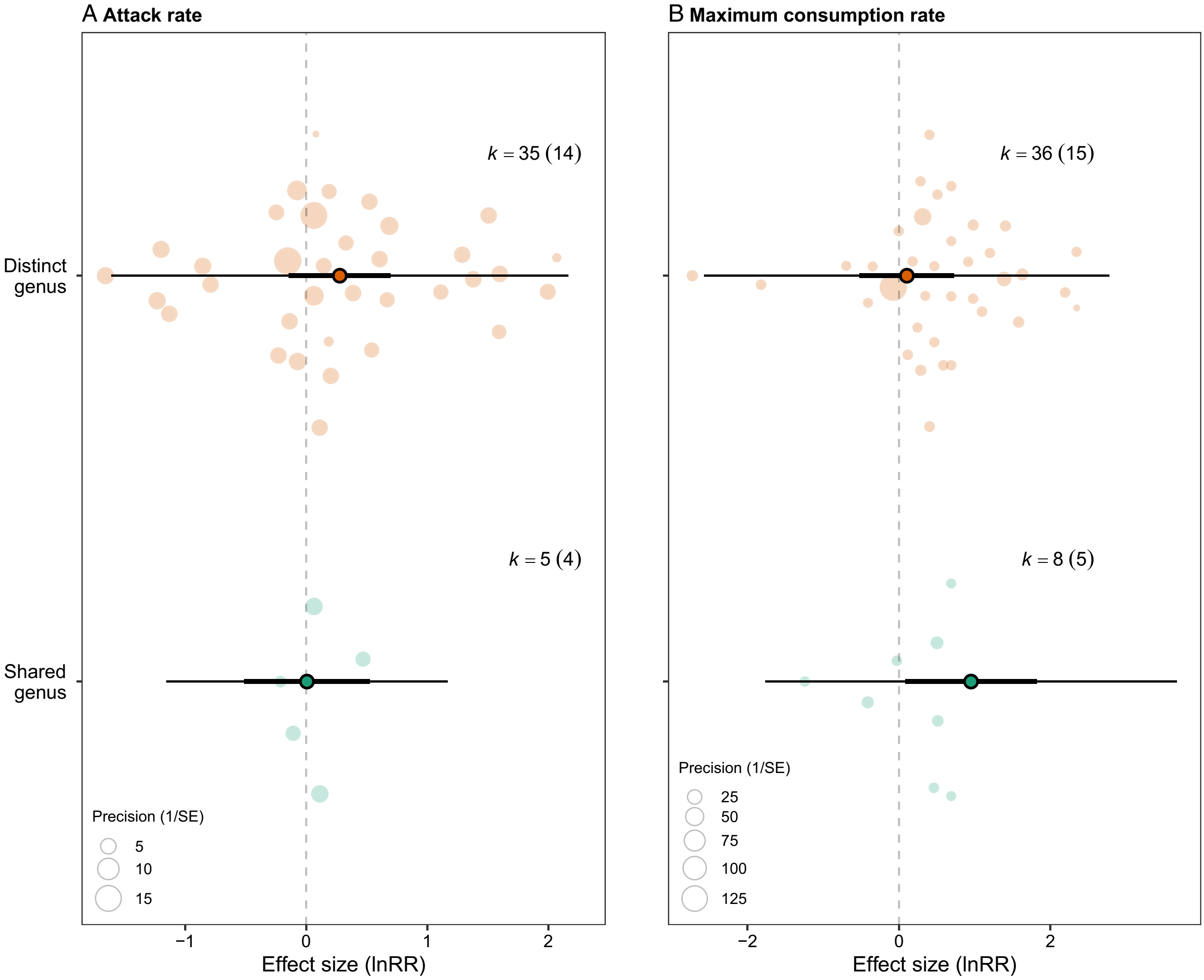

**Fig. 6.** Orchard plots showing effect size (lnRR) estimates from univariate meta-regression considering taxonomic distinctiveness of the non-native species as an influential moderator, for both response variables: (A) attack rate and (B) maximum consumption rate. Positive effect sizes indicate that non-native species have higher functional response parameters than natives 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 an individual effect size, scaled according to its precision.

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 are not a strong refutation of this hypothesis.

### (3) Study limitations, future directions and concluding remarks

The CFR approach was originally designed as a tool to understand known impacts of non-native species and to predict the consumptive impact of newly introduced species with no history of invasion elsewhere (Dick *et al.*, 2014, 2017a). Here, we used studies that compared non-native *versus* native species without explicit consideration of non-native negative impacts in the field. Therefore, a subset of invasive non-native species with demonstrable empirical impacts would likely show stronger effect sizes. We recognise that the selection of most established non-native species assessed in the studies was likely motivated by a prior impact, 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 (e.g. a novel taxonomic order). Additionally, the results of our meta-analysis are based on the subset of non-native species investigated by the studies found in the literature search. These are not necessarily representative of other non-native species, as not all non-native species have been studied in this perspective. Despite not finding evidence for publication bias, we should keep in mind that author or publication biases might be a concern (Jeschke *et al.*, 2019), since it is likely that impactful non-native species are studied more frequently than non-native species with low impact.

We also note that impact can change over time (e.g. because novelty and naivety diminish temporally; Saul & Jeschke, 2015). However, 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 (Strayer *et al.*, 2006; Crystal-Ornelas & Lockwood, 2020). Indeed, it was observed for invasive plants that their negative effects on the native community decline over longer time periods (Iacarella, Mankiewicz & Ricciardi, 2015b). Effects can also vary along spatial gradients. A study assessing the *per-capita* effects of a known invasive predator *Hemimysis anomala* (bloody red mysid shrimp) from two distinct sites with different times since introduction found that feeding rates were higher at the invasion front (i.e. the recently invaded site) (Iacarella, Dick & Ricciardi, 2015a). It also highlights more broadly that ecological impacts can differ among distinct populations of non-native species due to eco-evolutionary processes and local contexts (Howard *et al.*, 2018; Haubrock *et al.*, 2024). Thus, future studies should consider time since introduction and spatial factors, and should clearly state if they are evaluating a novel or established non-native population.

Our finding that non-native species have a higher consumption rate than native counterparts, particularly when resource availability is high, 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 the predation pressure on native biota (Dick *et al.*, 2017b), which may result in boom–bust dynamics that complicate our ability to control non-native populations (Strayer *et al.*, 2006; Haubrock *et al.*, 2022). 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 (Simberloff & Holle, 1999; Pope *et al.*, 2008). What remains to be tested is if increased resource availability coupled with multiple non-native species will always result in more impact, or if other mechanisms, such as indirect effects or interference competition, can prevent impact (e.g. Bunke *et al.*, 2019; Faria, Vitule & Olden, 2023b). In other words, are highly resource-abundant communities more susceptible to impacts than previously anticipated? Or does higher resource availability actually negate the impact, because the species will have enough to consume (even though non-natives will consume at higher rates)? In this case, we encourage more research by applying CFR to reveal such feedback processes, thereby informing best management practices.

Invasion science has relied on invasion history and qualitative or quantitative assessment protocols to identify and prioritise non-native species that should be managed (Faria *et al.*, 2023a); nonetheless, as the number of new introductions worldwide continues to rise, a lack of historical data will impede applications of 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 dominated by a subset of total species diversity (McKinney & Lockwood, 1999), our focus should be on prevention rather than remediation (Leung *et al.*, 2002). As many invasive non-native species have negative impacts that ultimately stem from resource consumption, quantifying such impacts using rapid experiments in terms of resource use is a practical way of predicting and therefore proactively targeting those most likely to cause harm (Dick *et al.*, 2017a). Our meta-analysis corroborates this, showing that non-native species indeed display higher consumption rates, and in some cases greater attack rates. We also highlight high-risk contexts for consumptive effects, including freshwater environments. Overall, these results support the use of the CFR approach as a rapid risk assessment tool for existing and emerging non-native species to cause negative impacts worldwide.

## VI. CONCLUSIONS

(1) Maximum consumption rates of non-native species are higher than their native counterparts, supporting the Resource Consumption Hypothesis, which can partly explain how successful non-native species can reduce native resource populations and restructure food webs.
(2) Particular taxa and trophic interactions were associated with the greatest differential functional responses between non-natives and natives, specifically molluscs, insects and crustaceans as well as herbivores and omnivores in terms of maximum consumption rates.
(3) Consumption rate differences between non-native and native species were greatest for freshwater taxa, which could indicate greater sensitivity of insular freshwater food webs to novel consumers, lending weight to inland waters as a priority for management. These differences need to be further explored using a larger, more comprehensive data set of terrestrial (mainland and island) and marine systems as these become available.
(4) There is a current lack of data from CFR studies across space and time to allow us to investigate if consumptive impact depends on these factors. Therefore, future studies employing the CFR approach should consider these context dependencies to consolidate it further as an impact assessment tool and a guide for invasive non-native species management.

## VII. ACKNOWLEDGEMENTS

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## VIII. AUTHOR CONTRIBUTIONS

L.F.: Formal analysis, Investigation, Writing – Original Draft, Visualisation, Supervision. R.N.C.: Validation. J.W.E.D.: Validation. J.R.S.V.: Supervision. All authors contributed to Conceptualisation, Writing – Review & Editing.

## IX. DATA AVAILABILITY STATEMENT

Data and code can be accessed at https://doi.org/10.6084/m9.figshare.26042386.

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Studies identified with an asterisk (*) were included in the meta-analysis; studies identified with a dagger symbol (†) are cited only within the online supporting information.

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## XI. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** PRISMA-EcoEvo checklist.

**Table S1.** Results from sensitivity analysis: mean effect size (lnRR) estimates and their corresponding 95% confidence interval (95% CI) for both response variables ($\mathrm{lnRR}_a$: attack rate and $\mathrm{lnRR}_{\mathrm{MCR}}$: maximum consumption rate).

**Dataset S1.** Papers identified, screened and included, as well as extracted data to perform the meta-analysis of comparative functional response studies.

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