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Predicting invasive consumer impact via the comparative functional response approach: linking application to ecological theory

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Abstract The Comparative Functional Response Approach (CFRA) was developed to provide a practical methodology by which short-term experiments can be used to forecast the longer-term impacts of a potential invading consumer. The CFRA makes inferences about potential invader impact based on comparisons of the functional responses of invader and native consumers on native resources in a common experimental venue. Application of the CFRA and derivative approaches have proliferated since it was introduced in 2014. Here we examine the conceptual foundations of the CFRA within the context of basic Lotka–Volterra consumer-resource theory. Our goals are to assess whether core predictions of the CFRA hold within this framework, to consider the relative importance of background mortality and consumer assimilation efficiency in determining predator impact, and to leverage this conceptual framework to expand the discussion regarding stability and long term consumer and resource dynamics. The CFRA assertion that consumers with a higher functional response will have larger impacts on resources only holds as long as all other parameters are equal, but basic theory indicates that predator impacts on prey abundance and stability will depend more on variation in conversion efficiency and background mortality. While examination of the CFRA within this framework highlights limitations about its current application, it also points to potential strengths that are only revealed when a theoretical context is identified, in this case the implications for stability and conceptual links to competition theory.

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Introduction

Invasive predators are among the most damaging group of invasive species for global biodiversity, causing dramatic reductions and even extinctions in

native prey populations (Salo et al. 2007; Doherty et al. 2016). However, the impacts of introduced consumers can vary significantly across taxa and systems (Doherty et al. 2016). The development of a quantitative framework to rapidly assess potential impacts of invaders has remained elusive (Lodge et al. 1998; Kolar and Lodge 2001; Simberloff et al. 2013; Dick et al. 2014). To address the need for tools to identify high-impact invasive alien consumers, Dick et al. (2013, 2014) proposed the comparative analyses of invader and native functional responses (hereafter "comparative functional response approach", CFRA).

The functional response describes instantaneous mortality rates (Holling 1959a, b, 1965; Soluk 1993; Vonesh and Bolker 2005; McCoy et al. 2011), but when paired with other processes, short-term mortality can be linked to longer-term consumer and resource population dynamics (Murdoch and Oaten 1975; Oaten and Murdoch 1975; Hassell 1978; Murdoch et al. 2003). In basic Lotka–Volterra consumer-resource models (Lotka 1910; Volterra 1926; Berryman 1992), the functional response, consumer background mortality, consumer conversion efficiency (i.e., via the numerical response, the change in consumer abundance as a function of change in resource abundance), and the resource rate of increase and carrying capacity provide the framework for predicting changes in consumer and resource abundance through time. Within this theoretical context, changes in functional response parameters (e.g., values of attack rate, or handling time) or type (e.g., Type II vs. III) may result in changes in the predicted population dynamics (i.e., abundance and stability; Murdoch and Oaten 1975). For example, a Type II functional response generates positive density dependence for the resource and may act to destabilize consumer-resource dynamics, as compared with a density independent Type I functional response (Hassell 1978; Murdoch et al. 2003). Thus, it has been proposed that understanding the functional responses of consumers can allow predictions of their impacts on food webs and ecosystem processes. Dick et al. (2014) argue that understanding the functional response of invasive consumers can be used to predict longer-term impacts of invaders on native ecosystems. However, to predict how understanding the shape of native and invasive consumers' functional responses scale-up to influence longer term dynamics, we

must consider them within the context of the other key processes of the Lotka–Volterra framework that shape long term consumer-resource dynamics.

Consumer–resource dynamics as embodied in classic theory (e.g., Murdoch and Oaten 1975; Oaten and Murdoch 1975; Murdoch et al. 2003) rely on not only the functional response but also on other rates and functional relationships like numerical responses via conversion efficiency and background mortality that the CFRA and derivatives rely on but do not fully address. These parameters could have rivalling or even neutralizing effects that arise from differences in the functional responses of two consumers. Given that invasive species are often released from their natural enemies which can alter background mortality (e.g., Colautti et al. 2004; Liu and Stiling 2006; Heger and Jeschke 2014) and that conversion efficiency can vary even among closely related taxa (e.g., Fenton et al. 2010; Montagnes and Fenton 2012; Li and Montagnes 2015), looking at these other parameters may provide insights into alternative explanations for observed patterns or explanations for the cases where predictions of CFRA have not been supported (Guo et al. 2017).

The basic CFRA (e.g., Alexander et al. 2014; Dick et al. 2014) begins by identifying the focal taxa; typically, a non-native consumer/predator of concern, a native "comparator" consumer, and the focal native prey/resource. The selection of these taxa has important implications for the inferences that a CFR study can support (Vonesh et al. 2017a). The investigators then conduct experiments with these taxa to estimate the general form and specific parameter values for the functional response of the native and non-native consumers on the focal prey/resource (e.g., Juliano and Williams 1987). Typically these studies are conducted over short time-scales (often < 24 h) in small simple experimental venues in the laboratory (e.g., Cuthbert et al. 2019a, 2021) or field mesocosms (Alexander et al. 2014; Wasserman et al. 2016). The functional responses of the invader and native consumers on the same native resource are then compared. Because the functional response quantifies the strength of consumer-resource interactions, the difference in magnitude of invader/native functional responses is thought to explain and predict invader impacts. Specifically, the CFRA hypothesizes that "ecologically damaging invasive species have higher functional responses than comparator native species" (Dick et al. 2014).
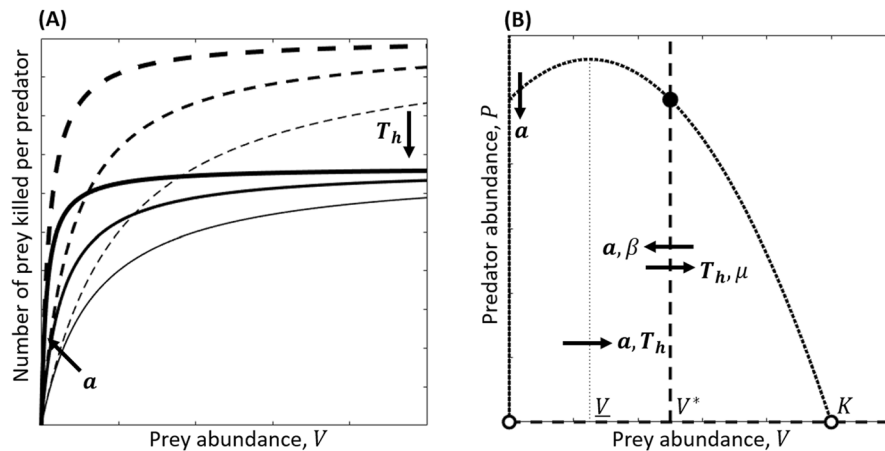
Fig. 1 A Holling type-II functional response $\frac{aV}{1+aT_hV}$, with attack rate a representing the slope at low prey abundance V, and handling time T_h representing the inverse of the asymptotic values at high V. Dashed vs normal lines represent 2 different values of handling time, while each of the 3 lines represent different values of attack rate, with thickness proportional to attack rate. **B** Effect of parameters on prey-predator nullclines and equilibria. Dashed lines represent predator nullclines (where solutions cross horizontally), while dotted lines represent prey nullclines (where solutions cross vertically). The vertical predator nullcline represent the equilibrium prey abundance $V^* = \frac{\mu}{a(\beta - \mu T_h)}$, while the thin vertical dotted line represents the maximum $\underline{V} = \frac{1}{2}\left(K - \frac{1}{aT_h}\right)$ of the nonlinear prey nullcline. Empty dots at $V = 0$ and $V = K$ represent saddle equilibria (unstable), while the full dot represents the stable coexistence equilibrium. The slope of the nonlinear prey nullcline at this coexistence equilibrium approximates its stability and resilience: negative slope ($V^* > \underline{V}$) means stable, and the larger the absolute value of this negative slope the higher the resilience; otherwise a positive slope ($V^* < \underline{V}$) means unstable coexistence that diverges from the equilibrium and converges to a limit cycle with periodic coexistence. In both panels the effect of parameters is indicated by the arrows, pointing in the direction of an increase in the specified parameters. Functional response parameters (in bold) directly affect both the equilibrium prey abundance and the stability and resilience of prey-predator coexistence. Other predator parameters (conversion efficiency β and mortality μ) only directly affect the equilibrium prey abundance, and through it indirectly affect stability and resilience. Prey carrying capacity K only directly affects stability and resilience

A "higher" functional response indicates that the invader consumes more of the resource than the native comparator, at least at some resource densities. In this case the curve of the invader's functional response lies above that of the native consumer. Two processes control the "height" of the Holling type-II functional response, the attack rate and the handling time. As attack rates increase from low to higher values the height of the functional response increases. Similarly, as we decrease the handling time from higher values to lower values the height of the functional response also increases (Fig. 1A). Further, referencing Murdoch and Oaten (1975), the general form of the invader's functional response (Type I, II, or III) is examined to support inferences about the long term impact of the invader on consumer-resource stability (Dick et al. 2014). Ecologically damaging invaders are those that have greater impacts on native resources/prey, reducing their long-term abundance and stability and potentially impacting native consumers through effects on the shared resource. Thus, advocates propose that this comparison of invader and native comparator functional responses on a native resource species in a common experimental venue offers a practical methodology by which short-term experiments can be used to forecast the longer-term impacts of present and future invaders.

Since the CFRA framework was proposed (Dick et al. 2013; Dick et al. 2014) there has been a proliferation of related indices. Rather than considering the shape of the functional response in its entirety, Cuthbert et al. (2019b) propose the Functional Response Ratio (FRR) index, which is the ratio of the estimated functional response attack rate and handling time parameters. Recognizing that consumer-resource dynamics may be shaped by the consumer's numerical response in addition to the functional responses, the Relative Impact Potential (RIP) index was proposed as another modification of the CFRA (Dick et al. 2017b; Dickey et al. 2020). The RIP index

combines some information related to the functional response with proxies for the numerical response as a measure of invasive species ecological impact. The RIP index itself has subsequently given rise to additional daughter indices. For instance, when applied in the context of biological control, the RIP has been relabelled as the Relative Control Potential (RCP) of a particular biocontrol agent (Cuthbert et al. 2018). When applied in the context of invasive plant species, Dickey et al. 2020 proposed the Relative Interspecific Competitive Potential (RICP) and Dickey et al. 2018 combined the RIP metric multiplied by a proxy for propagule pressure to calculate Relative Invasion Risk (RIR). Thus, between 2014 and 2021 we've seen the rise of six conceptually similar indices (i.e., CFRA, FRR, RIP, RCP, RIR and RICP) being promoted in the literature. This family of indices was recently reviewed by Dickey et al. (2020). The CFRA is more strongly linked to empirical data than many of the derivative approaches because key parameters are estimated from experimental data, albeit often in simplified experimental venues. However, acquiring empirical data on other core processes vital to understanding the functional response, the numerical response and propagule pressure is more challenging and consequently the derivative indices increasingly rely on proxy variables. The sensitivity to variation in these other parameters and proxies for predator impacts needs to be considered within the same conceptual framework.

Perhaps because of the importance of understanding the impacts of invasive consumers and the ease of conducting short-term functional response experiments, studies using the CFRA and its derivatives have become common in recent years, particularly in aquatic systems. We are aware of at least 127 related studies since 2013 which have collectively been cited nearly 2000 times (see Supplementary Information). The CFRA and related approaches have been used to try and predict the impacts of a broad range of consumer types, ranging from freshwater and marine fish (Alexander et al. 2014; Laverty et al. 2017; South et al. 2017), bivalves (Kemp and Aldridge 2018; Joyce et al. 2020), snails (Xu et al. 2016), amphipods (Bollache et al. 2007; Laverty et al. 2014), shrimp (Barrios-O'Neill 2014b), crayfish (Madzivanzira et al. 2021), sea squirts (Hoxha et al. 2018), aquatic insects (Cuthbert et al. 2019b), ladybird beetles (Crookes et al. 2018) and geckos (Haubrock et al. 2020). The

approach has even been suggested as a useful tool to better understand competitive interactions between native and non-native plants (Dickey et al. 2020). Advocates highlight that across this diverse range of trophic and taxonomic groups, the high-impact invaders deemed high-impact by CFRA comparisons were significantly associated with higher FRs compared to native trophic analogues and that the RIP metric substantially improves this association, with 100% predictive power of high-impact invaders (Dick et al. 2017b). Indeed, advocates argue for the use of the CFRA as a conceptual foundation to unify the field of invasion ecology (Dick et al. 2017a).

Some critics of the CFRA have highlighted that making general inferences based on patterns observed from post hoc comparisons of non-randomly selected species pairs can be problematic (Vonesh et al. 2017a; b). For example, data on the CFRA for failed invaders or for a range of potential comparator consumers are often unavailable. Other authors express concern about scaling from small experimental venues to natural systems (Griffen et al. 2020; Griffen 2021). Here we examine whether the assertion that species with higher functional responses have greater impacts on resource populations over longer time scales is consistent with the theoretical framework the CFRA is founded on. Here we examine the conceptual foundations of the CFRA within the context of basic Lotka–Volterra consumer-resource theory. Our goal is to assess whether core predictions of the CFRA hold and to consider the relative importance of other factors shaping long term dynamics. By connecting the CFRA more explicitly to this ecological theory, we hope to provide an example of a more comprehensive logical framework for considering the utility of using consumer functional responses to identify ecologically damaging invaders.

Methods

Conceptual framework

To link the CFRA to ecological theory, we use the classic Rosenzweig–MacArthur consumer-resource model (RM model; Rosenzweig and MacArthur 1963; Murdoch et al. 2003). The RM model is the simplest form of Lotka–Volterra consumer-resource theory (LV model) that still incorporates the biologically

realistic elements of density-dependent resource growth and predation relevant to the CFRA. In the RM model, prey/resource abundance, V, grows logistically in the absence of consumers, with an intrinsic growth rate r and carrying capacity K (Table 1). Thus, in the absence of a consumer, resource abundance V would increase to carrying capacity K. Consumption occurs through a Holling-type II functional response describing the number of resource attacked by a single predator in a unit time as a saturating function of resource abundance V (Fig. 1A). Consumers, P, only feed on the focal resource, and die with mortality μ in the absence of resources. The model thus reads

$$\dot{V} = rV\left(1 - \frac{V}{K}\right) - \frac{aVP}{1 + aT_hV}$$
$$\dot{P} = \frac{\beta aVP}{1 + aT_hV} - \mu P \tag{1}$$

The dot notation describes the instantaneous rate of change of resource and consumer abundances, V and P, while the attack rate a and the handling time T_h characterize the Holling type-II functional response. The attack rate a describes the initial slope of this functional response, when resource abundance V is low, and the handling time T_h describes the time spent by a single consumer individual to attack, handle, and digest a single resource individual, and its inverse $1/T_h$ characterizes the maximum consumption rate by a single consumer when resource abundance V is large (Fig. 1A). To stress the effect of parameters on consumption, when resource abundance V is low, the functional response increases approximately linearly with rate a, but when resource abundance increases the handling time contributes to saturation to the asymptotic value of $\frac{1}{T_h}$ for large resource abundances. An increase in attack rate increases the initial slope of the functional response, while an increase in handling time decreases the asymptotic value of the functional response (Fig. 1A). Finally, β describes the conversion efficiency of the predator, the proportion of resource consumed (thus bounded between 0 and 1) that is effectively transformed into predator abundance.

Although we use the RM model as our baseline, our approach can be generalised to a wide range of formulations. To ensure that consumers can grow when resources are abundant, conversion efficiency β must be larger than the product of mortality μ and handling time T_h, thus we always assume $\beta > \mu T_h$. The behaviour of the model can be understood by looking at the nullclines, i.e., the curves along which either of the rate of change of resource $\dot{V}$ or predator $\dot{P}$ is 0. The resource nullclines, obtained by setting the right-hand side of the first equation in Eq. (1) equal to 0 ($\dot{V} = 0$), are thus given by $V = 0$ and

$$P = \frac{r}{a}\left(1 - \frac{V}{K}\right)\left(1 + aT_hV\right) \tag{2}$$

The latter nullcline is a downward facing parabola in the (V, P) positive plane (Fig. 1B), with maximum at $\underline{V} = \frac{1}{2}\left(K - \frac{1}{aT_h}\right)$. Consumer nullclines, obtained by setting the right-hand side of the second equation in Eq. (1) equal to 0 ($\dot{P} = 0$), are given by $P = 0$ and

$$V = \frac{\mu}{a(\beta - \mu T_h)} \tag{3}$$

Table 1 Description of the parameters of the Rosenzweig–MacArthur (1963) formulation of the Lotka–Volterra prey-predator model

Variables	Description	Units
V	Prey abundance	Prey individuals
P	Predator abundance	Predator individuals
Prey parameters		
r	Intrinsic growth rate	1/time
K	Carrying capacity	Prey individuals
Predator functional response parameters		
a	Attack rate	1/(time*predator individual)
T_h	Handling time	Time/prey individual
Other predator parameters		
β	Conversion efficiency	Predator individuals/Prey individuals
μ	Natural mortality rate	1/time

Since $\beta > \mu T_h$, this is a vertical straight line in the (V, P) positive plane (Fig. 1B). Intersections of nullclines of different species represent equilibria. There is always an unstable extinction equilibrium at the origin of the (V, P) positive plane, representing extinction of both species, and the consumer extinction equilibrium with resource at their carrying capacity K. When this carrying capacity is larger than the consumer vertical nullcline (Eq. 3), this equilibrium is also unstable and there is a coexistence equilibrium (V^*, P^*) with abundances

$$V^* = \frac{\mu}{a(\beta - \mu T_h)} \tag{4}$$

for the resource and

$$
\begin{aligned}
P^* &= \frac{r}{a}\left(1 - \frac{V^*}{K}\right)\left(1 + aT_h V^*\right) \\
&= \frac{r}{a}\left(1 - \frac{\mu}{aK(\beta - \mu T_h)}\right)\frac{\beta}{\beta - \mu T_h} \\
&= r\beta \frac{aK(\beta - \mu T_h) - \mu}{a^2 K(\beta - \mu T_h)^2}
\end{aligned}
\tag{5}
$$

for the consumer. The coexistence equilibrium thus occurs at the intersection of the consumer vertical nullcline (Eq. 3) and the resource parabolic nullcline (Eq. 2). When this intersection happens at the right of the parabola's maximum $(V^* > \underline{V})$, consumer-resource coexistence is stable, while if $V^* < \underline{V}$ coexistence is unstable and consumer and resource coexist periodically (stable limit cycle). Consumer-resource coexistence (in)stability is approximated by

$$\lambda = -\frac{r}{aK}(2aT_h V^* - aT_h K + 1) = -\frac{r}{aK}\left(\frac{\beta + \mu T_h}{\beta - \mu T_h}\right) + rT_h \tag{6}$$

that is, the slope of the resource parabolic nullcline (Eq. 2) at the equilibrium (V^*, P^*). If negative $(\lambda < 0)$ consumer-resource coexistence is stationary, otherwise periodic. The magnitude of λ quantifies the degree of (in)stability, the larger the absolute value the more (un)stable. An increase in stability means a shorter return time to equilibrium after a small perturbation (increased resilience), while an increase in instability means a faster divergence from the equilibrium after a small perturbation. Thus, this formulation for classic consumer-resource theory provides an ideal conceptual framework to examine the links between the functional response, key demographic processes, and long term resource abundance and stability (see Supplementary Information for additional analytical details).

Analysis

Within the context of this conceptual framework we examine the assertions of the CFRA. The CFRA proposes that invaders with a higher functional response than a native comparator as measured in short-term experiments will have larger longer-term impacts on native resource abundance and will thus be a concern for management. Is the assertion that a "higher" functional response results in larger long-term impacts on resources consistent with classic LV consumer-resource theory? Within the classic RM consumer-resource model two processes control the "height" of the consumer functional response, the attack rate and handling time (Fig. 1A). As attack rates increase from low to higher values the initial steepness of the functional response increases. As we decrease the handling time from higher values to lower values the height (asymptotic value) of the functional response increases (Fig. 1A). Thus, to explore the dynamical consequences of having a higher functional response for impacts of consumers on resources we examine the sensitivity of resource abundance to changes in functional response parameters relative to other key parameters–consumer conversion efficiency, β, and background mortality, μ.

First we qualitatively examined the impact of resource and consumer parameters on the long term equilibrium abundance of a resource and consumer through consumer-resource nullclines (Fig. 1B). Dashed lines represent consumer nullclines (where solutions cross horizontally), while dotted lines represent resource nullclines (where solutions cross vertically). The vertical consumer nullcline represents the equilibrium resource abundance V^* (Eq. 4), while the thin vertical dotted line represents the maximum of the nonlinear resource nullcline $\underline{V}$. Open symbols at 0 and K on the resource abundance axis in Fig. 1B represent saddle equilibria (unstable), while the full symbol represents the stable coexistence equilibrium.

When considering the impacts of an invading consumer on system stability, the CFRA generally invokes theory that indicates that different

functional response forms (e.g., Holling type-II versus III) result in categorically different consequences for stability. The RM consumer-resource modelling framework provides an explicit framework to explore how differences in the functional responses between consumers that share the same functional form (i.e., both type-II) affect consumer-resource coexistence equilibrium stability (λ). An increase in stability means a shorter return time to equilibrium after a small perturbation, while an increase in instability means a faster divergence from the equilibrium after a small perturbation. In fact, the slope of the nonlinear resource nullcline at this coexistence equilibrium approximates its stability and resilience: negative slope ($V^* > \underline{V}$) means stable, and the larger the absolute value of this negative slope the higher the resilience; otherwise a positive slope ($V^* < \underline{V}$) indicates an unstable coexistence that diverges from the equilibrium and converges to a limit cycle with periodic coexistence.

To have a more quantitative understanding of consumer parameters impacts, we analytically computed (normalized) sensitivity indices of resource equilibrium abundance V^* (Eq. 4) and consumer-resource coexistence stability λ (Eq. 6) with respect to all consumer parameters, i.e., those affecting the functional response (attack rate a and handling time T_h) and those not (conversion efficiency β and mortality μ; Supplementary Information). To support these analytical results, we also computed numerically and plotted relative change of resource equilibrium abundance V^* and consumer-resource coexistence stability λ driven by a relative change of each of the four consumer parameters (Fig. 2). Each parameter is varied for the largest interval allowing for stable consumer-resource coexistence (defined by $\underline{V} < V^* < K$). In Supplementary Information, we also plot the relative change in consumer equilibrium abundance P^* (Eq. 5) for each of the four consumer parameters (Figure SI 1), and showcase examples where we simultaneously vary two parameters to determine their interaction, plotting a surface of relative change of resource equilibrium abundance V^* and consumer-resource coexistence stability λ (Figure SI 2). Furthermore, as an illustration of the risks of only considering functional response parameters, we simulate two case studies of consumer-resource dynamics (Eq. 1), one in which a higher functional response of the invader species fails to predict the long-term outcome of invasion,
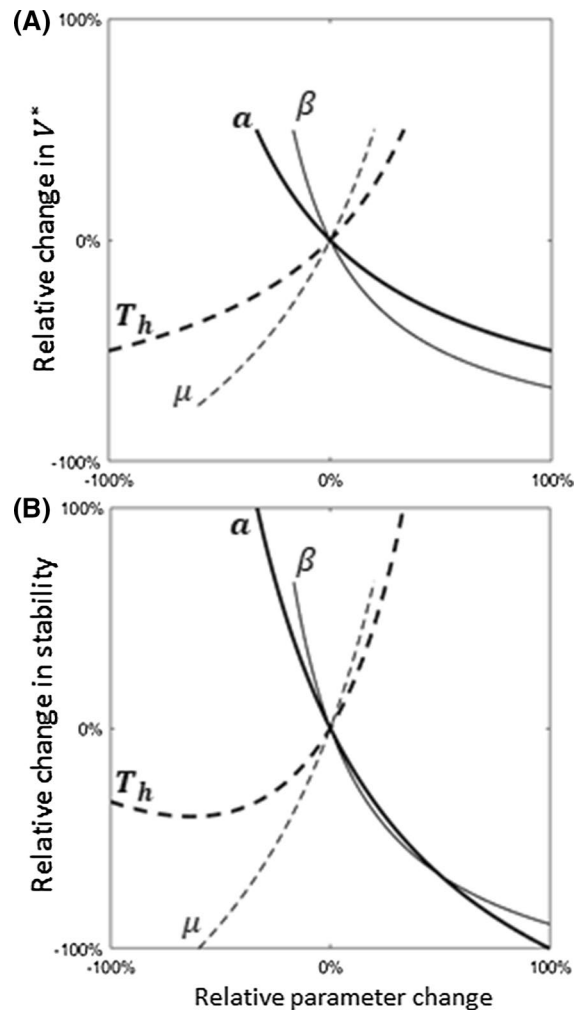

Fig. 2 A Effect of predator parameter change on the equilibrium prey abundance V^* and **B** on the prey-predator coexistence equilibrium stability. Thick lines represent functional response parameters, while normal lines represent other predator parameters. Increasing attack rate a and conversion efficiency β in (**A**) have a negative impact on prey equilibrium abundance, while increasing handling time T_h and mortality μ has a positive effect. Functional response parameters a and T_h have in fact a smaller impact on prey equilibrium abundance compared to other predator parameters. Increasing attack rate a and conversion efficiency β in (**B**) have a negative impact on equilibrium stability, increasing mortality μ has a positive effect, while increasing handling time T_h has a non-monotonic effect, increasing stability when sufficiently large but reducing stability when small. Parameter values: $a = 1.5$, $T_h = 1$, $\beta = 0.5$, and $\mu = 0.25$. Parameter ranges are chosen so that coexistence equilibrium is stable ($\underline{V} < V^* < K$)

and another in which a resource parameter (carrying capacity K), typically not considered in the CFR approach, affects consumer-resource coexistence stability and long-term consumer abundance.

Results

Changes in consumer parameters altered the long term impacts of consumers on a resources' long term equilibrium abundance V^* (Fig. 2A). Increasing either the consumer attack rate a or conversion efficiency β increases consumer impact on resources, resulting in a lower long term resource equilibrium abundance. In contrast, increasing handling time T_h and background mortality μ results in higher resource equilibrium abundance. Thus, consumers with lower handling times will have larger impacts on resource over long time scales. This is consistent with the CFRA argument that consumers with higher functional responses (i.e., larger a or smaller T_h) have larger long-term impacts on resource dynamics. However, the functional response parameters have a smaller impact on resource equilibrium abundance compared to other consumer parameters (mathematically proved in Supplementary Information and numerically illustrated in Fig. 2A). For instance, relative resource equilibrium abundance decreases more steeply as we increase conversion efficiency (moving left to right in Fig. 2A) then it does as we increase the attack rate. Similarly, resource abundance increases much more rapidly as we increase background mortality than it does for handling time (Fig. 2A). Thus, while theory supports the CFRA assertion that the height of the FR contributes to long term consumer impacts, it also reveals that other factors not explicitly addressed within the CFRA are relatively more important. In Supplementary Information we show analytically that this is a general result not dependent on specific parameter values, i.e., normalized sensitivities of non-functional response parameters conversion efficiency β and consumer mortality μ are always larger (in absolute value) than those of functional response parameters attack rate a and handling time T_h, implying a larger impact on resource equilibrium abundance. We also illustrate one example of how this framework can be leveraged to explore interactions between functional response and other parameters on resource abundance, by simultaneously varying consumer attack

rate and background mortality (Fig. SI 2A). Impacts of parameters on consumer abundance are also provided in Supplementary Information (Fig. SI 1).

To better illustrate these general results, consider two hypothetical scenarios where the consumer with the higher functional response does not have the larger long term impact. In both examples the invader consumer has a higher functional response (parameter values: $a = 1.5$, $T_h = 0.5$, $\beta = 0.5$, and $\mu = 0.25$). In the first example (Fig. 3A), the native consumer has a lower attack rate and larger handling time ($a = 1$, $T_h = 1$) but the native also has a lower background mortality ($\mu = 0.125$). In the second example (Fig. 3B), the native has a higher conversion efficiency ($\beta = 0.82$) and equivalent background mortality ($\mu = 0.25$). In both examples, despite an initially faster growth of the invading consumer with respect to the native due to a higher functional response for the invasive, a lower mortality rate μ (Fig. 3A) or larger conversion efficiency β (Fig. 3B) in the native consumer can allow long-term resistance to invasion. Thus, in neither case does the invasive consumer persist or have a larger long term impact than the native, despite having a higher functional response. The impact of the differences in the functional response are outweighed by differences in conversion efficiency and background mortality.

Our results also show that non-functional response parameters have larger impacts on consumer-resource stability. In Fig. 2B we show that increasing the attack rate a and conversion efficiency β have a negative impact on relative consumer-resource coexistence equilibrium stability. Increasing mortality μ has a positive effect and handling time T_h has a non-monotonic effect, increasing stability when sufficiently large but reducing stability when small. From the CFRA perspective, a consumer with a higher Holling type-II functional response due to an increased attack rate would then have a destabilizing effect, while having a higher functional response due to reduced handling time could either increase or decrease stability. Notably, one consumer might have a "higher" functional response but have a and T_h values that are pushing stability in different directions. While the parameter values in these simulations are hypothetical the magnitude of differences in parameter values are comparable to those observed in empirical systems. Overall, functional response parameters tend to have smaller impacts on
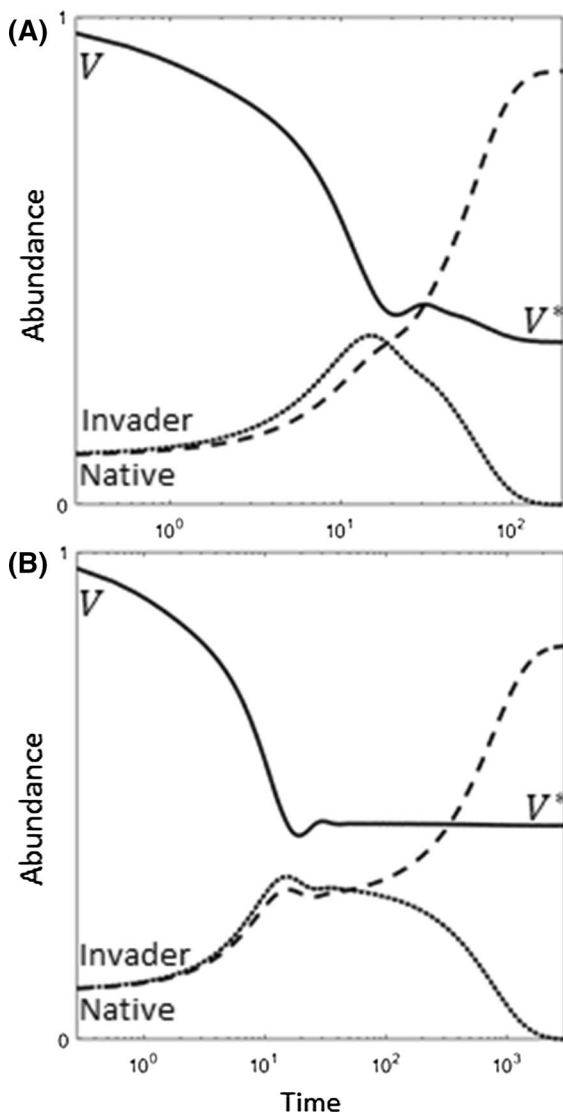
Fig. 3 The effect of a higher invasive functional response (both higher attack rate a and lower handling time T_h) does not predict the outcome of invasion. The normal line represents prey abundance, the dotted line represents invader predator abundance, and the dashed line represents native predator abundance. Despite an initially faster growth of the invader with respect to the native due to a higher invader functional response, a **A** lower mortality rate μ, and **B** a larger conversion efficiency β of the native species can allow long-term resistance to invasion. Invader parameter values: $a = 1.5$, $T_h = 0.5$, $\beta = 0.5$, and $\mu = 0.25$. Native predator parameters: $a = 1$, $T_h = 1$, $\beta = 0.5$, and $\mu = 0.125$ in (**A**) and $a = 1$, $T_h = 1$, $\beta = 0.82$, and $\mu = 0.25$ in (**B**)

relative consumer-resource coexistence equilibrium stability, compared to changes in conversion efficiency and background mortality (demonstrated in

Supplementary Information if handling time is sufficiently large and illustrated in Fig. 2B).

Furthermore, the effect of stability on transient dynamics to consumer-resource coexistence equilibrium depends upon resource carrying capacity K (i.e., paradox of enrichment; Rosenzweig 1971; Gilpin and Rosenzweig 1972). Consider the example where $a = 1.5$, $T_h = 0.5$, $\beta = 0.5$, $\mu = 0.25$, and $K = 1$ (Fig. 4A) versus $K = 2$ (Fig. 4B). Despite reaching the same resource equilibrium abundance V^*, a higher value of resource carrying capacity K in Fig. 4B is responsible for a larger consumer equilibrium abundance, reached after longer and more pronounced oscillations in consumer-resource transient abundances.

Discussion

Invasive consumers can have dramatic negative impacts on native biodiversity and developing tools to better identify which potential invaders will be relatively more damaging could help guide management strategies (Lodge et al. 1998; Dick et al. 2017a). The CFRA was developed to try and fill this need. It leverages short-duration experiments designed to characterize the functional responses of native and potential invading consumers and leans on classic ecological theory in which the functional response is a key process linking consumer and resource longer-term population dynamics. The CFRA argues that potential invaders with higher functional responses than typical native consumers are likely to be most damaging and therefore should be the focus of containment and management. While advocates have used post hoc analysis of selected empirical case studies to argue the effectiveness of the approach, critics have advised caution (Vonesh et al. 2017a, b). Here we examine the conceptual foundations of the CFRA within the context of Lotka–Volterra consumer-resource theory to examine whether core predictions of the CFRA hold within this foundational framework for understanding consumer-resource interactions and to consider the relative importance of other factors shaping long term dynamics.

A core argument of the CFRA is that a consumer with a "higher functional response" than comparator native consumers will have damaging impacts if it were to invade. This central assertion motivates

the use of short duration functional response experiments to predict consumers that will have damaging effects over the long run. However it is unclear whether this assertion is supported by or consistent with basic ecological theory. In this study we show that within the context of the RM consumer-resource modelling framework, the assertions of the CFRA are justified but only under a limited set of conditions. Specifically, consumer functional responses can be higher either by increasing the attack rate or reducing the handling time (Fig. 1A), and we show that either pathway to a higher FR always results in lower long term resource equilibrium abundance (Fig. 2A). However, this outcome only holds true when all other relevant parameters are held equal and constant for all consumers being compared (Fig. 3).

The impact of consumers on resource populations are not determined solely by the values of a and T_h, and we show that other consumer parameters have larger effects on resource abundance than indicated by the functional response alone. Within the RM framework, resource abundance is more sensitive to changes in consumer conversion or assimilation efficiency, β, than to changes in either functional response parameter. While many studies have quantified predation rates, characterized the form of the functional response (e.g., Jeschke et al. 2002), and examined the importance of incorporating various resource- and consumer- dependencies within the functional response (e.g., Barrios-O'Neill 2014a), fewer have focused on the importance of assimilation efficiency and the consumers numerical response (Fenton et al. 2010; Montagnes and Fenton 2012; Li and Montagnes 2015). However, studies have revealed that, like functional response parameters, conversion efficiency can vary considerably across consumer-resource systems. For example, Fenton et al. 2010 reviewed 15 protozoan consumer-resource systems for which parameters of both the functional and numerical response have been estimated. Biologically plausible assimilation efficiency estimates (constrained between 0 and 1) ranged from 0.05 to 0.75 predators prey^{-1} (mean = 0.34 ± 1SD 0.21; Fenton et al. 2010; "e" in Table 2). Predators consuming the same species of prey often differed substantially in their conversion efficiency. The studies reviewed by Fenton et al. 2010 included four pairs of different consumers preying on the same resource species under similar conditions. The absolute differences in
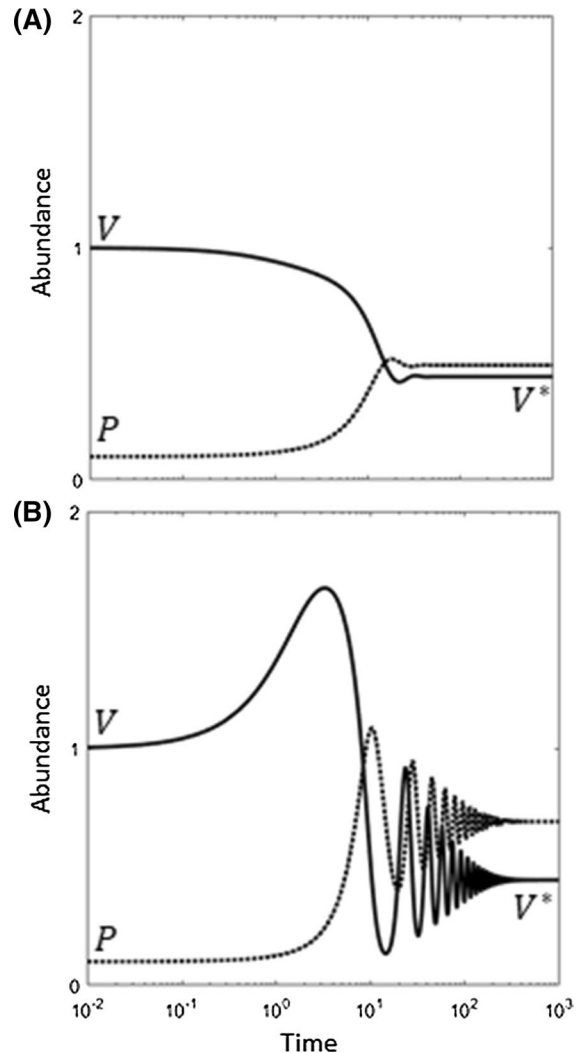

Fig. 4 The effect of stability on the transient dynamics to prey-predator coexistence equilibrium driven by different prey carrying capacity K. The normal line represents prey abundance and the dotted line represents predator abundance. Despite reaching the same prey equilibrium abundance V^*, a higher value of prey carrying capacity K in (**B**) with respect to (**A**) is responsible for a larger predator equilibrium abundance, reached after longer and more pronounced oscillations in prey-predator transient abundances. Parameter values: $a = 1.5$, $T_h = 0.5$, $\beta = 0.5$, $\mu = 0.25$, and $K = 1$ in (**A**) while $K = 2$ in (**B**)

conversion efficiency for protist consumers on shared resources in the four pairings ranged from 0.02 to 0.41 and average of 0.25 predators prey^{-1} (Table 2). Similarly, Krengel et al. (2013) found conversion efficiencies varied nearly two-fold for different species of ladybird beetles depredating the same aphid pests.

Our example in Fig. 3 shows that differences in conversion efficiency of this magnitude can overwhelm differences in functional response parameters, such that a consumer with a higher functional response does not have the larger impact on resource long term abundance. Thus, the logic of the CFRA is oversimplified. consumers with higher functional responses may have larger impacts, but it depends on their conversion efficiencies, which may not even be constant through time or across resource densities (Ginzburg 1998). Even when resource quality (e.g., species, condition, size, traits) is fixed (as in two consumers feeding on the same resource type), conversion efficiency may vary with consumer identity or traits (e.g., size, stage), environmental conditions (e.g., temperature; Krengel et al 2013), and resource abundance (Fenton et al 2010) in a manner that can alter the long term outcome of consumer-resource dynamics.

Our analyses connecting the CFRA to RM consumer-resource theory also highlights the sensitivity of longer term resource abundance to background mortality, μ. Increasing consumer background mortality increases resource equilibrium abundance and these effects are more sensitive to changes in background mortality than the parameters of the functional response. Like conversion efficiencies, there are biological reasons to expect that there may be considerable and systematic variation in background mortality between native and introduced consumers. For example, "enemy release" is a foundational hypothesis for explaining biological invasions. Enemy release proposes that a decrease in regulation by consumers and other natural enemies experienced by an invading species in the invading range facilitates invasion establishment (Colautti et al. 2004; Liu and Stiling 2006; Heger and Jeschke 2014). Thus, if invading consumers systematically tend to have lower background mortality rates, this would have a relatively bigger effect on their impact than a higher functional response. Moreover, an invading consumer could have a lower functional response and still be more impactful because of a lower background mortality rate. Explicit consideration of background mortality provides a direct link to management strategies currently absent from the CFRA discussion. While it is less clear how mitigation strategies can impact attack rate and handling time, the link to intervention and invader mortality is intuitive and already a common management approach. Indeed, there are numerous examples of mitigation strategies that attempt to eradicate invaders by increasing mortality (Dahlsten and Garcia 1989; Myers et al. 2000; Baxter et al. 2008; Green and Grosholz 2021). As with conversion efficiency, consumer impacts may be more sensitive to variation in background mortality than to the functional response parameters, thus manipulating background mortality provides a more natural target for management efforts. In cases where data on background mortality is a logistically less tractable endpoint to quantify empirically, data from CFRA could be contextualized based on theoretical constructs such as from metabolic theory (e.g. McCoy et al. 2008).

Framing the CFRA within LV theory provides an explicit conceptual framework for generating hypotheses about how invaders are likely to impact system stability and competitive impacts on native consumers mediated through a shared resource. Currently, the CFR approach loosely invokes LV theory to frame the discussion about an invader's impact on consumer-resource stability around differences in functional response type (e.g., Type I, II, III). However, when considered within the RM framework, we see that differences within a Type II functional response type alone has important implications for stability. Increasing the attack rate has a negative impact on stability, while increasing handling time has a non-monotonic effect that enhances stability when large but hinders stability when very small. However, once again we see that, as in the case of resource long term abundance, system stability is often more sensitive to changes in conversion efficiency and background mortality than to functional response parameters. The RM also highlights the potential value in considering resource availability for generating hypotheses about consumer effects on stability (i.e., the paradox of enrichment; Rosenzweig 1971). Figure 4 illustrates that the impact of an invading consumer on system stability could depend on factors like system productivity (e.g., eutrophic versus oligotrophic lakes).

Recognizing that consumer-resource dynamics may be shaped by consumer conversion efficiency and numerical responses in addition to the shape of the functional response, Dick et al. (2017a, b, 2020) modified the CFRA to propose the Relative Impact Potential (RIP) index. The RIP index combines some information related to the functional response with proxies for the numerical response as a measure of invasive species ecological impact. Proxies for the

functional response in the RIP are typically quantified as the ratio of the attack rate and handling time (i.e., their Functional Response Ratio (FRR; Cuthbert et al. 2019c)) or another proxy is sometimes used. The proxy for the numerical response is typically an estimate of consumer abundance, as Dickey et al. (2020) argue estimates of consumer conversion efficiencies are difficult to measure. Thus, the RIP often reduces to the ratio of the invader maximum feeding rate multiplied by its estimated abundance over the native-comparator feeding rate multiplied by its estimated abundance. Proponents of the RIP index suggest that an invading consumer with higher functional responses as well as higher abundances than a comparative native consumer are likely to have problematic impacts. However, this simplification contradicts basic ecological theory because it treats consumer abundance and the consumer feeding rate as independent uncoupled phenomena (e.g., see independent axes in Fig. 2 Dickey et al. 2020). In practice, the RIP asserts that abundant, voracious consumers eat more resources than less abundant and less voracious consumers, which simplifies the ecology to a degree that severs the conceptual connection between the functional and numerical responses of consumers to resource dynamics. Moreover, using relative abundance as a proxy for the numerical response limits applications of the RIP to already well established invasions (i.e. assumes native and invasive consumer populations are at or close to equilibrium) and invasive consumers have already reached their impact potential. The RIP is not expected to be informative for assessing the impact of new or potential invaders. We suggest the assertion that these indices are phenomenologically 100% accurate (sensu Dickey et al. 2020) begs closer examination and may stem from study system/publication bias (see Vonesh et al. 2017a, b), because theory does not support such accuracy given what is measured by these indices (e.g., Fig. 3). Perhaps the predictions of the CFRA could be improved by pairing short term functional response experiments with consumer growth response experiments. For instance, measuring changes in consumer biomass across resource densities could provide insight into the assimilation efficiencies of different consumers. While changes in consumer biomass do not necessarily map directly to numerical responses, they provide a more direct link to ecological theory,

like the RM model, that we use to predict consumer-resource dynamics (Fenton et al 2010).

More explicit connection between the CFRA and the ecological theory it implicitly leans on can yield important insights into its limitations, but also guide its application and development. For example, strengthening links to theory provides a baseline for thinking about invasive consumer effects on native consumers that share the same resource. In cases where consumer-resource systems are simple and consumers are largely limited by the shared resource (a fundamental assumption of basic LV theory) and consumers interact primarily through the shared resource, long term equilibrium resource abundance for each consumer is analogous to Tilman's resource-ratio hypothesis, R* (Tilman 1982). The resource-ratio hypothesis predicts that when consumers compete for a shared limiting resource the species that can survive at the lowest equilibrium resource level (i.e., R*) will outcompete others. Thus, under these assumptions, the consumer that has the lower $V*$ (Fig. 1b) has both larger impacts on resource abundance but is also more likely to negatively impact native "comparator" taxa.

Here we examined the arguments of the CFRA within the classic RM consumer-resource model. While the assertion that consumers with a higher functional response will have larger impacts holds while all other parameters are equal, RM theory indicates that variation in conversion efficiency and background mortality are likely among consumers and are likely to have larger effects on a consumer's long-term impacts on both resource and system stability. Thus, at this point, it is impossible to disentangle whether the putative predictive power of the CFRA in examinations of post hoc selection of successful invasions is due to differences in the functional responses of the focal consumers, as suggested, or sampling bias of invading consumers (Vonesh et al. 2017a), or differences in the other processes examined here, conversion efficiency, background mortality, or resource carrying capacity, or a combination of these factors. While our examination of the CFRA within this framework highlights limitations, it also points to potential strengths that are only revealed when a theoretical context is identified, in this case the implications for stability and conceptual links to competition theory. Regardless, generalizations will necessarily depend upon the theoretical framework

invoked, and our point is not to overly dwell on these specific outcomes from our analysis. Rather, we want to urge caution when inferring the impacts of invasive consumers based solely on their functional responses, to highlight the value explicitly linking the CFRA to theory to strengthen its logical foundation, and to guide research through more mechanistic hypotheses that better contextualize the generality of insights gained.

Data accessibility Not applicable for this study.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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