Predicting Invasive Predator Impact via the Comparative Functional Response Approach: Linking Application to Ecological Theory

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Predicting Invasive Predator 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 prey 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 predator-prey 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 predator and prey dynamics. The CFRA assertion that predators with a higher functional response will have larger impacts on prey 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.

Keywords

Predator-prey dynamics; Rosenzweig-MacArthur model; Lotka-Volterra; conversion efficiency; eradication; numerical response; invasive species management

Introduction

Biological invasions are a pervasive aspect of global change (National Research Council 2000; Hassan et al. 2005), challenging the conservation of biodiversity and natural resources (Simberloff et al. 2013) and costing billions each year in control efforts and environmental damages and losses (Pimentel et al. 2005). 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 predators can vary significantly across predator and native prey 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” or CFRA). The functional response describes the short-term impacts of a predator on prey by characterizing how a predators’ feeding rate varies with prey abundance. Holling (1959a,b; 1965) proposed the three most commonly modelled forms of predator functional response: linear with a ceiling (Type I), saturating (Type II), and sigmoidal (Type III). The specific shape of the functional response is determined by a predator's foraging style and can be described by parameters for the predator’s attack rate, which specifies the rate at which predators encounter and successfully capture prey, and handling time, which includes the time spent pursuing, consuming, and digesting prey (Holling 1959a,b; Jeschke et al. 2002). Empirically, the form of the functional response can be characterized, and functional response parameters can be estimated, through relatively short-term predation trials across a range of prey abundances (e.g., Hassell 1978; Juliano and Williams 1987; Soluk 1993; Vonesh and Bolker 2005; McCoy et al. 2011; Alexander et al. 2014).

The functional response describes instantaneous mortality rates, but when paired with other processes, short-term mortality can be linked to longer-term predator and prey population dynamics (Murdoch and Oaten 1975; Oaten and Murdoch 1975; Murdoch et al. 2003). In basic Lotka-Volterra predator-prey models (Lotka 1910; Volterra 1926; Berryman 1992), the functional response, the numerical response (the change in predator abundance as a function of change in prey abundance), the prey rate of increase, and predator background mortality rate provide the framework for predicting changes in predator and prey 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 prey and may act to destabilize predator-prey dynamics, as compared with a density independent Type I functional response (Murdoch et al. 2003). Thus, it has been proposed that understanding the functional responses of predators can allow predictions of predator impacts on food webs and ecosystem processes. For instance, 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 predators functional responses scale-up to influence longer term dynamics, we must consider them within the context of the predators numerical response and background mortality rate because these processes also influence long term predator-prey dynamics, and thus the impact of an invasive predator.

The basic CFRA (e.g., Alexander et al. 2014; Dick et al. 2014) begins by identifying the focal taxa; typically, a non-native predator of concern, a native “comparator” predator, and the focal native prey. The selection of these taxa has important implications for the inferences that a CFR study can support (Vonesh et al. 2017). 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 predators on the focal prey. Typically these studies are conducted over short time-scales (often < 24 hrs) in small simple experimental venues in the laboratory (e.g., Cuthbert et al. 2019, 2021) or field mesocosms (Alexander et al. 2014; Wasserman et al. 2016). The functional responses of the

invader and native predator consuming the native prey are then compared. Because the functional response quantifies the strength of predator-prey 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). A “higher” functional response indicates that the invader kills more prey than the native comparator predator, at least at some prey densities. In this case the curve of the invader's functional response lies above that of the native predator (e.g., as the top dotted curve in Fig. 1a falls above the bottom solid curve). Further, referencing Murdoch and Oaten (1975), the general form of the invader's functional response (Type I-III) is examined to support inferences about the long term impact of the invader on predator-prey stability (Dick et al. 2014). “Ecologically damaging” invaders are those that have greater impacts on native prey, reducing the long-term abundance and stability of the focal prey, potentially impacting the native consumer through effects on the shared resource. Thus, advocates propose that this comparison of invader and native comparator functional responses on a native prey 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 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 predator-prey dynamics may be shaped by the predator'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 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 been cited nearly 2,000 times (see Appendix A). 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).

Those critical 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. 2017). 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 prey populations over longer time scales is consistent with the theoretical framework the CFRA is founded on. As discussed above, 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 for the cases where predictions of CFRA have not been supported (Guo et al. 2017). Here we examine the conceptual foundations of the CFRA within the context of basic Lotka-Volterra predator-prey 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 predator functional responses to identify ecologically damaging invaders.

Methods

To link the CFRA to ecological theory, we use the classic Rosenzweig-MacArthur prey-predator model (RM model; Rosenzweig and MacArthur 1963; Murdoch et al. 2003). The RM model is the simplest form of the LV model that still incorporates the biologically realistic elements of density-dependent prey growth and predation relevant to the CFRA. In the RM model, prey abundance, V , grows logistically in the absence of predators, with an intrinsic growth rate r and carrying capacity K (Table 1). Thus, without predation, prey abundance V would increase to carrying capacity K . Predation occurs through a Holling-type II functional response describing the number of prey attacked by a single predator in a unit time as a saturating function of prey abundance V (Fig. 1A). Predators, P , only feed on the focal prey, and die with mortality μ in the absence of prey. The model thus reads

$$\begin{aligned}\dot{V} &= rV \left(1 - \frac{V}{K}\right) - \frac{aVP}{1 + aT_h V} \\ \dot{P} &= \frac{\beta aVP}{1 + aT_h V} - \mu P\end{aligned}\tag{Equation 1}$$

The dot notation describes the instantaneous rate of change of prey and predator 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 prey abundance V is low, and the handling time T_h describes the time spent by a single predator individual to attack, handle, and digest a single prey individual, and its inverse $1/T_h$ characterizes the maximum consumption rate by a single predator when prey abundance V is large. Finally, β describes the conversion efficiency of the predator, the proportion of prey consumed (thus bounded between 0 and 1) that is effectively transformed into predator abundance. To stress the effect of parameters on consumption, when prey abundance V is low, the functional response increases approximately linearly with rate a , but when prey abundance increases the handling time contributes to saturation to the asymptotic value of $\frac{1}{T_h}$ for large prey 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.

Although we use the RM model as our baseline, our approach can be generalised to a wide range of formulations. To ensure that predators can grow when prey 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 prey $\dot{V}$ or predator $\dot{P}$ is 0. The prey nullclines ($\dot{V} = 0$) are thus given by $V = 0$ and

$$P = \frac{r}{a} \left(1 - \frac{V}{K} \right) (1 + aT_h V) \quad (\text{Equation 2})$$

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

$$V = \frac{\mu}{a(\beta - \mu T_h)} \quad (\text{Equation 3})$$

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 predator extinction equilibrium with prey at their carrying capacity K . When this carrying capacity is larger than the predator vertical nullcline (Eq. 3), this equilibrium is also unstable and there is a coexistence equilibrium (V^*, P^*) with abundances

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

for the prey and

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

(Equation 5)

for the predator, at the intersection of the predator vertical nullcline (Eq. 3) and the prey parabolic nullcline (Eq. 2). When this intersection happens at the right of the parabola's maximum ($V^* > \bar{V}$), prey-predator coexistence is stable, while if $V^* < \bar{V}$ coexistence is unstable and prey-predator coexist periodically (stable limit cycle). Prey-predator coexistence (in)stability is quantified by

$$\lambda = K - \frac{1}{aT_h} \left(\frac{\beta + \mu T_h}{\beta - \mu T_h} \right)$$

(Equation 6)

that is, the slope of the prey parabolic nullcline (2) at the equilibrium (V^*, P^*) . If negative ($\lambda < 0$) prey-predator 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 predator-prey theory provides an ideal conceptual framework to examine the links between the functional response, key demographic processes, and long term prey abundance and stability (see Appendix B for additional analytical details).

Results

The CFR approach is framed around identifying consumers with a “higher” functional response relative to a similar native consumer on a particular prey. Within the classic Rosenzweig-MacArthur (1963) prey-predator model with a Holling type-II functional response, two processes control the “height” of the consumer functional response, either increasing the attack rate or decreasing the handling time can result in a higher functional response. Figure 1a shows a Holling type-II functional response 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 . Figure 1a illustrates that as attack rates increase from low (bottom solid and dashed lines) to higher values the height of the functional response increases. Similarly, as we decrease the handling time from higher values (solid lines) to lower values (dashed lines) the height of the functional response also increases. Thus, to explore the dynamical consequence of having a “higher”

functional response to long term prey abundance and stability we explore the consequence of increasing attack rates and decreasing handling times relative to other parameters (Fig. 1b).

Figure 1b shows the effect of model parameters on the long term equilibrium abundance of prey and predators through prey-predator nullclines. Thus, we can ask if this theory supports the CFRA hypothesis that having a higher functional response (e.g., either higher attack rates or lower handling times) results in a greater impact on prey (i.e., lower long term equilibrium abundance). We can also examine the sensitivity of prey abundance to changes in functional response parameters relative to other key parameters like predator conversion efficiency, β , or predator background mortality, μ . Dashed lines represent predator nullclines (where solutions cross horizontally), while dotted lines represent prey nullclines (where solutions cross vertically). The vertical predator nullcline represents the equilibrium prey abundance $V^* = \frac{\mu}{a(\beta - \mu T_h)}$, while the thin vertical dotted line represents the maximum of the nonlinear prey nullcline $\bar{V} = \frac{1}{2} \left(K - \frac{1}{a T_h} \right)$. Empty dots at 0 and 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 represents its stability and resilience: negative slope ($V^* > \bar{V}$) means stable, and the larger the absolute value of this negative slope the higher the resilience; otherwise a positive slope ($V^* < \bar{V}$) indicates an unstable coexistence that diverges from the equilibrium and converges to a limit cycle with periodic coexistence. 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, but indirectly affect stability and resilience. Only prey carrying capacity K directly affects stability and resilience.

The effect of changes in predator parameters on the predator impacts on prey changed the long term equilibrium prey abundance V^* (Fig. 2). Increasing either the predator attack rate a or conversion efficiency β increases predator impact on prey in a nonlinear way, resulting in a lower long term prey equilibrium abundance. In contrast, increasing handling time T_h and background mortality μ positively effects prey equilibrium abundance. Thus, predators with lower handling times will have larger impacts

on prey over longer 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 prey dynamics.

However, the functional response parameters have a smaller impact on prey equilibrium abundance compared to other predator parameters. For instance, relative prey equilibrium abundance decreases much more steeply as we increase conversion efficiency (moving left to right in Fig. 2) than it does for attack rate. Similarly, prey abundance increases much more rapidly as we increase background mortality than it does for handling time (Fig. 2). Thus, while theory supports the CFRA assertion that the height of the FR contributes to long term predator impacts, it also reveals that other factors not explicitly addressed within the CFRA are relatively more important.

To illustrate, compare several hypothetical pairs of predators. The invader predator has parameter values: $a = 1.5$, $T_h = 0.5$, $\beta = 0.5$, and $\mu = 0.25$. In Figure 2b, the native has a lower attack rate and larger handling time ($a = 1$, $T_h = 1$; i.e., the invader has a higher FR) but the native has a lower background mortality ($\mu = 0.125$) and equivalent conversion efficiency and thus has stronger impacts on prey over the long term. In Fig. 2c, the invader has a higher functional response, as in Fig. 2b, but the native has a higher conversion efficiency ($\beta = 0.82$) and equivalent background mortality ($\mu = 0.25$) leading to larger impacts by the native than the invasive. In both examples, despite an initially faster growth of the invading predator with respect to the native due to a higher functional response for the invasive, a lower mortality rate μ (Fig. 2b) or larger conversion efficiency β (Fig. 2c) in the native consumer can allow long-term resistance to invasion. Thus, in neither case does the invasive predator 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 conversation efficiency and background mortality.

When considering the impacts of an invading predator on system stability, the CFRA generally invokes theory that indicates that different functional response forms (e.g., Hollings type-II versus III) result in categorically different consequences for stability. The Rosenzweig-MacArthur (1963) prey-predator modelling framework provides an explicit framework to explore how differences in the functional responses between predators that share the same functional form (i.e., both type-II) affect

prey-predator 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 Fig. 3a we show that increasing the attack rate a and conversion efficiency β have a negative impact on relative prey-predator coexistence equilibrium stability. Increase mortality μ has a positive effect and handling time T_h has a non-monotonic effect, increasing stability when either very large or very small. From the CFRA perspective, a predator 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 predator 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 relative prey-predator coexistence equilibrium stability, compared to changes in handling time and background mortality.

Furthermore, the effect of stability on transient dynamics to prey-predator coexistence equilibrium depends upon prey 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. 3b) versus $K = 2$ (Fig. 3c). Despite reaching the same prey equilibrium abundance V^* , a higher value of prey carrying capacity K in (Fig. 3c) is responsible for a larger predator equilibrium abundance, reached after longer and more pronounced oscillations in prey-predator transient abundances.

Discussion

Invasive predators have had 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 predators and leans on classic ecological theory in which the functional response is a key process linking predator and prey longer-term dynamics. The CFRA argues that potential invaders with higher functional responses than typical native predators 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. 2017). Here we examine the conceptual foundations of the CFRA within the context of Lotka-Volterra predator-prey theory to examine whether core predictions of the CFRA hold within this foundational framework for understanding predator-prey interactions and to consider the relative importance of other factors shaping long term dynamics.

A core argument of the CFRA is that a predator with a “higher functional response” than comparator native predators will have damaging impacts if it were to invade. This central assertion motivates the use of short duration functional response experiments to predict predators 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 predator-prey modelling framework, the assertions of the CFRA are justified but only under a limited set of conditions. Specifically, predator 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 prey equilibrium abundance (Fig. 2A). However, this outcome only holds true when all other relevant parameters are held equal and constant for all predators being compared.

The impact of predators on prey populations are not determined solely by the values of a and T_h , and we show that other predator parameters can have even larger effects on prey abundance than indicated by the functional response alone. Within the RM framework, prey abundance is more sensitive to changes in predator 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 prey- and predator- dependencies within the functional response (e.g., Barrios-

O'Neill 2014a), fewer have focused on the importance of assimilation efficiency and the predators 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 predator-prey systems. For example, Fenton et al. 2010 reviewed 15 protozoan predator-prey systems for which parameters of both the functional and numerical response have been estimated. Biologically plausible assimilation efficiency estimates ranged from 5 to 75% (Fenton et al. 2010; Table 2). Further, the studies reviewed included four comparisons of different predators consuming the same prey under similar conditions. Absolute differences in conversion efficiency for protist predators on shared prey ranged from 0.02 to 0.41 with an average of 0.25. Similarly, Krenkel 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. 2c shows that differences in conversion efficiency of this magnitude can overwhelm differences in functional response parameters, such that a predator with a higher functional response does not have the larger impact on prey long term abundance. Thus, the logic of the CFRA is oversimplified. Predators with higher functional responses may have larger impacts, but it depends on their conversion efficiencies, which may not even be constant through time. Even when prey quality (e.g., species, condition, size, traits) is fixed (as in two predators feeding on the same prey type), conversion efficiency may vary with predator identity or traits (e.g., size, stage), environmental conditions (e.g., temperature; e.g., Krenkel et al 2013), and prey abundance (Fenton et al 2010) in a manner that can alter the long term outcome of predator-prey dynamics.

Recognizing that predator-prey dynamics may be shaped by predator conversion efficiency and numerical responses in addition to the shape of the functional response, Dick et al. (2017, 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., 2019)) or another proxy is sometimes used. The proxy for the numerical

response is typically an estimate of predator abundance, as Dickey et al., (2020) argue estimates of predator 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 predator with higher functional responses as well as higher numerical responses than a comparative native consumer are likely to have problematic impacts. However, this simplification contradicts basic ecological theory because it treats predator abundance and the predator 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 predators eat more prey than less abundant and less prodigious predators, which simplifies the ecology to a degree that severs the conceptual connection between the functional and numerical responses of predators to prey dynamics. We suggest the assertion that these indices are phenomenologically 100% accurate begs closer examination, because theory does not support such accuracy given what is measured by these indices (e.g., Fig. 2b, c).

Our analyses connecting the CFRA to RM predator-prey theory also highlights the sensitivity of longer term prey abundance to background mortality, μ . Increasing predator background mortality increases prey 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 predators 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 predator could have a lower functional response and still be more impactful because of a lower background 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 (Dahlsten and Garcia 1989; Myers et al. 2000; Baxter et al. 2008; Green and Grosholz 2021). As with conversion efficiency, predator 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.

Framing the CFRA within LV theory also provides a more 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 prey resource. Currently, the CFR approach loosely invokes LV theory to frame the discussion about an invaders impact on predator-prey 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 FR type alone has important implications for stability. Increasing the attack rate has a negative impact on prey stability, while increasing handling time has a non-monotonic effect that enhances stability when either very large or very small. However, once again we see that, as in the case of prey 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 prey resource availability for generating hypotheses about predator effects on stability (i.e., the paradox of enrichment; Rosenzweig 1971). Fig. 3b,c illustrate that the impact of an invading predator on system stability could depend on factors like system productivity (e.g., eutrophic versus oligotrophic lakes).

Finally, strengthening links to theory provides a baseline for thinking about invasive consumer effects on native consumers that share the same prey. In cases where predator-prey systems are simple and predators are largely limited by the shared prey (a fundamental assumption of basic LV theory) and predators interact primarily through the shared prey, long term equilibrium prey abundance for each predator 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 predator that has the lower V^* (Fig. 1b) has both larger impacts on prey abundance but is also more likely to negatively impact native “comparator” taxa.

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. We examined the arguments of the CFRA within the classic RM predator-prey model. While the assertion that predators 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 to have larger effects on a predators long-term impacts on both prey and system stability. In the absence of explicit consideration of background mortality and conversion efficiency it is impossible to disentangle whether the predictive power of the CFRA in examinations of *post hoc* selection of successful invasions is due to non-random sampling of invading consumers (Vonesh et al. 2017), the purported differences in the functional responses of consumers, or these other more influential parameters. While 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. These generalizations will necessarily depend upon the theoretical framework invoked, and our point is not to overly dwell on these specific outcomes. 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.

Statements and Declarations

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Competing Interests

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

Authors Contributions

J.R.V, P.L., and M.W.M. conceived the ideas for the paper concept. P.L. implemented the modelling. All authors contributed to the writing of the manuscript.

Data Accessibility

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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

Figure Captions

Figure 1. (A) Holling type-II functional response $FR = \frac{aV}{1+aT_hV}$, 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. (B) Effect of parameters on prey-predator nullclines. 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 of the nonlinear prey nullcline $\bar{V} = \frac{1}{2} \left(K - \frac{1}{aT_h} \right)$. Empty dots at 0 and 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 represents its stability and resilience: negative slope ($V^* > \bar{V}$) means stable, and the larger the absolute value of this negative slope the higher the resilience; otherwise a positive slope ($V^* < \bar{V}$) 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, but indirectly also stability and resilience. Prey carrying capacity K only directly affect stability and resilience.

Figure 2. (A) Effect of predator parameter change on the equilibrium prey abundance V^* . Thick lines represent functional response parameters, while normal lines represent other predator parameters. Attack rate a and conversion efficiency β have a negative impact on prey equilibrium abundance, while 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. (B) and (C) The effect of a higher invasive functional response (both higher attack rate a and lower handling

time T_h) do 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 (B) lower mortality rate μ , and (C) 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 (B) and $a = 1$, $T_h = 1$, $\beta = 0.82$, and $\mu = 0.25$ in (C).

Figure 3. (A) Effect of predator parameter change on the prey-predator coexistence equilibrium stability. Thick lines represent functional response parameters, while normal lines represent other predator parameters. Attack rate a and conversion efficiency β have a negative impact on prey equilibrium abundance, mortality μ has a positive effect, while handling time T_h has a non-monotonic effect, increasing stability when either very large or very small. Panels B and C show 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 (C) with respect to (B) 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 (B) while $K = 2$ in (C).

FIGURE 1.

FIGURE 2.

FIGURE 3.

Supplementary Material Appendix B

Prey equilibrium abundance sensitivity to parameters

$$\frac{\partial V^*}{\partial a} = -\frac{\mu}{a^2(\beta - \mu T_h)} < 0$$

$$\frac{\partial V^*}{\partial T_h} = \frac{\mu^2}{a(\beta - \mu T_h)^2} > 0$$

$$\frac{\partial V^*}{\partial \beta} = -\frac{\mu}{a(\beta - \mu T_h)^2} < 0$$

$$\frac{\partial V^*}{\partial \mu} = \frac{\beta}{a(\beta - \mu T_h)^2} > 0$$

Normalized sensitivity indexes

$$\frac{\partial V^*}{\partial a} \frac{a}{V^*} = -1 < 0$$

$$\frac{\partial V^*}{\partial T_h} \frac{T_h}{V^*} = \frac{\mu T_h}{\beta - \mu T_h} > 0$$

$$\frac{\partial V^*}{\partial \beta} \frac{\beta}{V^*} = -\frac{\beta}{\beta - \mu T_h} < 0 \text{ } (< -1, \text{stronger than } a)$$

$$\frac{\partial V^*}{\partial \mu} \frac{\mu}{V^*} = \frac{\beta}{\beta - \mu T_h} > 0 \text{ } (\text{stronger than } T_h)$$

Coexistence stability sensitivity to parameters

$$-\frac{\partial \lambda}{\partial a} = -\frac{1}{a^2 T_h} \left(\frac{\beta + \mu T_h}{\beta - \mu T_h} \right) < 0$$

$$-\frac{\partial \lambda}{\partial T_h} = -\frac{1}{a T_h^2} \left(\frac{\beta + \mu T_h}{\beta - \mu T_h} \right) + \frac{1}{a T_h} \left(\frac{2\beta\mu}{(\beta - \mu T_h)^2} \right) = -\frac{\beta^2 - \mu^2 T_h^2 - 2\beta\mu T_h}{a T_h^2 (\beta - \mu T_h)^2} > 0 \text{ if } T_h > \frac{\beta}{\mu} (\sqrt{2} - 1)$$

$$-\frac{\partial \lambda}{\partial \beta} = -\frac{2\mu}{a(\beta - \mu T_h)^2} < 0$$

$$-\frac{\partial \lambda}{\partial \mu} = \frac{2\beta}{a(\beta - \mu T_h)^2} > 0$$

Normalized sensitivity indexes

$$-\frac{\partial \lambda}{\partial a} \frac{a}{|\lambda|} = -\frac{\beta + \mu T_h}{|a K T_h (\beta - \mu T_h) - \beta - \mu T_h|} < 0$$

$$-\frac{\partial \lambda}{\partial T_h} \frac{T_h}{|\lambda|} = -\frac{\beta^2 - \mu^2 T_h^2 - 2\beta\mu T_h}{(\beta - \mu T_h) |a K T_h (\beta - \mu T_h) - \beta - \mu T_h|} > 0 \text{ if } T_h > \frac{\beta}{\mu} (\sqrt{2} - 1)$$

$$-\frac{\partial \lambda}{\partial \beta} \frac{\beta}{|\lambda|} = -\frac{2\beta\mu T_h}{(\beta - \mu T_h)|aKT_h(\beta - \mu T_h) - \beta - \mu T_h|} < 0$$

$$-\frac{\partial \lambda}{\partial \mu} \frac{\mu}{|\lambda|} = \frac{2\beta\mu T_h}{(\beta - \mu T_h)|aKT_h(\beta - \mu T_h) - \beta - \mu T_h|} > 0$$

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