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Food web functional responses

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This article reviews the nature of functional responses that have commonly been used to represent feeding relationships in the ecological literature. It compares these with the range of functional response forms that are likely to characterize species in natural communities. The latter set of responses involves many more variables. The article reviews the history of functional response models, and examines previous work that has allowed the functional response of a predator to a single type of prey to depend on additional variables beyond the abundance of that prey type. While a number of more complex functional responses have been discussed over the years, many variables affecting feeding rates are still typically omitted from models of food webs. The influences on functional responses from trophic levels above that of the predator or below that of the prey are particularly likely to be ignored, although models and data have suggested that they can have large effects on the functional response. The influences of adaptive behavior and of the time-scale of response measurement are also too often ignored. Some of the known and unknown consequences of these omissions are discussed.

KEYWORDS

adaptive behavior, consumer-resource interaction, feeding, food web, functional response, predation, switching

-An adequate study of any complex phenomenon ultimately requires an integrated analysis of major systems and not just fragments of them. –C. S. Holling (1965, p. 1).

Introduction; early functional response theory

The above quotation is the opening sentence in one of the foundational articles about functional responses. The functional response of a predator species to a particular prey species is a quantitative description of the amount eaten by an average predator individual over a relatively short time period in terms of the variables affecting that amount. The one variable that always affects that amount is the abundance of the focal prey. Holling (1959) introduced his original set of three functional response shapes as potential relationships between the abundance of a single prey species and the amount eaten by a single average predator individual from a particular predator population. This work inspired many empirical studies that examined the amount eaten of a single prey type by isolated predator individuals under conditions that were identical except for having a range of different prey abundances. The results of most, although not all, such experiments could be characterized as linear, concave or sigmoid; i.e., Holling's type I, II, and III responses. These were all strictly increasing relationships. The reviews by Jeschke et al. (2002, 2004) showed that all three types occurred, as did dome-shaped responses, which decreased with prey abundance above some threshold value. This last response

(type IV) had also been predicted and observed by [Holling \(1965, 1966\)](#). [Holling and Buckingham \(1976\)](#) showed that decreasing segments in a functional response could also occur as the result of adaptive behavior in a detailed simulation model of mantids consuming flies. For unknown reasons, the possibility of this fourth type had been dropped from most functional response articles and from textbooks by the late 1970s.

[Jeschke and Tollrian \(2005\)](#) proposed what they labeled a “new type” of functional response, which they called “roller coaster shaped”. This response included a decreasing segment at moderately high prey densities, followed by an increasing segment at very high densities. The shape was a result of adding what they termed a “confusion effect”. Confusion caused the attack success rate to decrease with increasing prey density, and this was sufficient to overcome the positive effect of increased encounter rate over an intermediate range of densities. Such non-monotonic responses had been illustrated before ([Abrams, 1989](#), Figure 1, p. 97). In that study, the predator’s foraging strategy was determined by an optimal “foraging effort”, which increased both the intake rate and the foraging cost. This model assumed that fitness was a difference between the benefit function (food intake) and the cost function (disease, injury or other adverse effects from consumption). In models having different concave functions for the intake and cost relationships, such non-monotonic responses were common. Increasing relationships with more complex shapes had earlier been predicted based on optimal foraging ([Abrams, 1982](#)). It was clear that a simple three- or four-way classification was insufficient.

Holling’s type II response is the most commonly observed form of single-prey functional response ([Jeschke et al., 2002](#); [Uiterwaal et al., 2022](#)). It was originally defined as one that had a negative second derivative. However, it is now often equated with Holling’s “disk equation” formula, which is identical to the Michaelis-Menten function. Holling’s derivation was based on the idea that food required “handling” after capture, and that no new captures were possible during the handling period. Negative second derivatives can be produced by other mechanisms, including behavioral adjustment of foraging time or effort ([Abrams, 1982](#)). These other mechanisms, and cases where “handling” time can be adjusted adaptively ([Abrams, 1982](#); [Anholt et al., 1987](#)) usually produce shapes different from the disk equation. However, for systems in which predator individuals differ from each other in their exact responses, the disk equation often produces a reasonable fit to the mean response. The approximate fit and the mathematical simplicity of the disk equation formula, make it by far the most common representation of type II responses. There has been at least one measured response that was flat over the range of prey densities that was characteristic of the natural environment ([Abrams et al., 1990](#)); this presumably would have been classified as type II if sufficiently (but unrealistically) low prey densities had been explored.

Holling’s work represented a major advance over the linear (“mass action”) responses incorporated into the Lotka-Volterra models and early food web models ([May, 1973](#); [Pimm, 1982](#)). Nevertheless, the set of responses proposed by Holling are unlikely to represent more than a small fraction of the predator-prey interactions in nature. They are not sufficient because the ultimate goal of describing predation quantitatively is to understand the dynamics of predators and prey that are found in natural ecological systems. These almost always have multiple predator and prey species, and also have additional trophic levels. The abundances of lower levels usually affect prey foraging, and thus prey availability to the predator. The abundances of higher-level predators will often alter the foraging activity by the focal predator species; if so, they will obviously affect the focal predator’s consumption rates. The abundances of species on both higher and lower adjacent trophic levels should therefore enter into a functional response that is designed to understand the dynamics of any predator and prey species pair in a natural system ([Abrams, 2010b](#)). (Note that the term “predator” will be used here in a broad sense that includes all consumers, while “prey” will usually be used to include both plants and non-living resources.)

The abundances of prey/resources occupying other trophic levels are not the only “other” abundances that influence the consumption rates of one prey type by one predator type. Alternative prey/food types that can be utilized by the predator are almost certain to affect the consumption rate of a focal prey type. This is inevitable in the multi-species versions of Holling’s non-linear responses because they all imply some form of handling or processing, which temporarily prevents foraging. When predator density affects the functional responses in a system with one predator species (or type), it is quite likely that the abundance of a second predator species would also have some effect on the intake rate of the first predator. In fact, many other species in the food web containing a particular predator and particular prey have the potential to affect the consumption of that prey by that predator. Different ages, sizes, and/or genotypes within any of the species in the food web may also alter the functional response of a given predator type to a given prey type ([DeLong et al., 2021](#); [Uiterwaal et al., 2022](#)).

Because it ignores both other trophic levels and alternative prey, the simplified framework for studying functional responses that arose from Holling’s early work is now largely at odds with the philosophy he expressed in the opening quotation from his early article. The present article will examine some potential effects of other species on the functional response of a particular predator to a particular prey. It will also document that the contemporary literature using or dealing with functional responses has continued to ignore many of these effects.

Current usage of the term “functional response” frequently assumes that the response is a characteristic of a given pair of predator and prey species. This assumption underlies the many attempts to determine the “best” expression for describing such

a response (Jeschke et al., 2002, 2004; DeLong, 2021; Novak and Stouffer, 2021b). However, several recent experiments have shown that functional response shapes in the simplest case of an isolated predator individual consuming different abundances of a single prey type can be greatly altered by the spatial and physical properties of the experimental environment (Uiterwaal and DeLong, 2018; Juliano et al., 2022). Adaptive behavior and other types of phenotypic plasticity are also likely to produce different functional response shapes in different environments (Werner and Peacor, 2003).

Another problem with current usage of the term “functional response” is the implicit idea that functional responses are independent of the time frame over which they are measured. The use of functional responses in the ordinary differential equation models that characterize most theory in community ecology is implicitly independent of time; the response at one point in time only depends on current abundances. However, a change in the rate of predation (or even just nutrient uptake) following some change in food/prey abundance is often not instantaneous. The change in abundance must often be detected. Consumption itself requires time. Consumption also often leads to growth, which causes a change in future foraging and consumption behaviors. Organisms have finite lifespans and it is rare for optimal traits to be independent of the point in that lifespan and the individual’s condition at that point (de Roos and Persson, 2013). A functional response that is linear when measured over a short time span will usually become non-linear when measured over a longer time span (Abrams, 1991b); non-linear responses will change shape when measured over different time-spans. The issue of the duration of the measurement is particularly important when reproduction only occurs after a significant period of resource intake. Clearly, if a differential equation model is being used to describe population dynamics, the interval should not be overly long. However, there is no single “best” interval, and different intervals may be optimal for answering different questions about system dynamics. This may require that responses be measured over a number of time intervals.

The four major omissions from much of the functional response literature identified above are: (1) lack of alternative prey/foods; (2) lack of effects from abundances of species occupying other trophic levels, and frequent lack of predator abundance effects on its own response; (3) lack of consideration of adaptive processes affecting functional response shape, and the fact that these differ depending on the environment and other members of the biological community; (4) lack of attention to the effects of the time interval being described on the shape of a functional response. All of these issues share an underlying need to consider the wide diversity of food webs and of processes affecting the form of functional responses. These will be considered in more detail in subsequent sections. My own work and that of others (e.g., Kratina et al., 2007; DeLong, 2021) has raised this need for multispecies responses,

but much of the recent literature has concentrated on the two-species case, as mentioned above. DeLong’s (2021) book on functional responses, while calling for more work on multispecies responses, notably does not refer to most of the existing theoretical literature on such responses.

Two-trophic level functional responses that incorporate two or more variables

Including non-living resources as a “trophic level” and plants as consumers means that functional responses are required to describe all of the consumer-resource interactions in a biological community. In most real-world systems, the response of a consumer to any single resource will incorporate two or more population sizes. The two simplest cases of functional responses requiring two population sizes are those involving two prey/resource types and those in which the number of predators/consumers affects the short-term intake rate of an individual predator/consumer to a single prey/resource. Both of these cases have a relatively long history of inclusion in some models, even though they are only considered in the minority of the literature of empirical functional response measurements.

Choice between two or more prey/resources

One of the earliest modifications of Holling’s framework was to consider the impact of having more than a single prey type (although this was implicit in the logic behind the type III response). Studies in the 1970s employed an extension of the type II response in which “handling” any of the resource types made it impossible to capture any of the other resource types (Murdoch and Oaten, 1975; Oaten and Murdoch, 1975). Under this response, handling any resource prevented capture of either that or any other resource. Thus, the “passive” saturation effect was based on the combined effects of “handling” all resources. This was an advance over single-species responses, but it did not consider adaptive behavior.

This multi-species type II model formed the basis of early theory on optimal diet choice (Schoener, 1971; Pyke et al., 1977), which predicted a sudden dropping of lower quality foods from the diet when the abundance of higher quality food(s) exceeded a threshold abundance. However, the actual functional form of predation rate functions (i.e., functional responses) implied by optimal diet theory failed to be incorporated into models in population or community ecology until much later (Fryxell and Lundberg, 1994; Ma et al., 2003). These were theoretical works, and there has been little subsequent experimental exploration of functional responses in two or more prey systems involving diet choice based on handling/processing time. As a result, major

reviews of empirical works have concentrated on studies of functional responses in single resource systems: this includes [Jeschke et al. \(2002, 2004\)](#), [DeLong \(2021\)](#), and [Novak and Stouffer \(2021b\)](#). The last of these ([DeLong, 2021](#)) has a chapter (Chapter 5) on “multispecies functional responses” and one (Chapter 7) on “optimal foraging”. However, neither chapter presents a mathematical expression for a response incorporating adaptive diet choice.

“Switching” ([Murdoch, 1969](#)) is the only other type of adaptive diet choice that has been included in a significant number of community models. This describes the increase in relative consumption rate of a single resource with increases in its relative abundance. This is adaptive when resources are nutritionally substitutable and there is a tradeoff in relative consumption rates. [Matsuda \(1985\)](#) used a simple instantaneous switching function in an analysis of the evolution of switching behavior. One potential problem with this approach is the lack of a time lag required to estimate abundances and shift preferences, a feature that is capable of changing dynamics significantly ([Abrams and Matsuda, 2004](#)). Even if there is no time lag, the likely inability to estimate the relative abundances of two rare resources can cause significant differences in the dynamics of systems that do not come to a stable equilibrium ([Abrams and Matsuda, 2003](#)). The small number of empirical studies of switching has prevented adoption of a “standard approach” to modeling this phenomenon.

Switching in multiple-prey systems depends on the nature of the tradeoffs involved; i.e., the similarity of different prey in terms of their spatial location and required capture techniques ([Matsuda and Namba, 1991](#)). The behavioral dynamics approach of [Abrams and Matsuda \(2004\)](#) can be applied to multiple resources. [van Leeuwen et al. \(2013\)](#) proposed a framework for modeling switching in multiple-prey systems, but there are likely to be a variety of different representations depending on the nature of the similarities and differences between prey in the foraging strategy required to capture them.

Most models of consumption in multi-prey (food) systems have assumed nutritional substitutability of the foods. This is true of the work described above, and it leads to increased relative consumption of foods when their relative abundance increases. The presence of nutritional interactions between food types in conjunction with adaptive foraging has a variety of potential effects on functional responses to each food ([Abrams, 1987](#)). Several mechanisms produce the opposite of switching. One of these operates in the case of two nutritionally essential resources that involve a consumer foraging/intake tradeoff. [Abrams \(1987\)](#) showed that increasing the abundance of one essential resource favors an increase in the relative foraging effort directed at another essential resource, as this would then be the one limiting population growth. A second mechanism involves resources of different qualities under time- and capacity-limited foraging ([Abrams, 1990a,b](#)); here, increasing the abundance of a low quality resource favors increasing foraging time or

effort on the higher quality resource(s). [Hossie et al. \(2021\)](#) have recently reported a case in which the relative amounts of palatable and unpalatable prey determine the level of predator-dependence in the functional response. Increasing palatable prey also increased predation on unpalatable prey in their system, the opposite of what was predicted by [Abrams \(1990a,b\)](#). However, it is consistent with the increased foraging time predicted with a tradeoff between foraging (for either resource) and predation risk.

It is known that some predators may have difficulty distinguishing some non-prey items from their prey. [Kratina et al. \(2007\)](#) showed that increased abundance of a non-prey species reduced the consumption rate of prey by a predatory flatworm. This type of effect may be common, but there appear to have been very few experimental studies designed to examine this possibility. It is also not known how frequently these non-prey items occupy the same trophic level as the prey whose risk of predation is reduced. Another possibility left out of formal functional response models of two- or more-prey systems is direct interactions between prey species that change the vulnerability/availability of one or more of them to the predator.

The factors that produce decreasing sections of a predator’s response to a single prey can have similar effects in systems having two or more prey. Two of the major factors producing such a response are related to potential negative effects of prey consumption on the predator. These include risk of injury during the capture process and the potential presence of parasites and/or toxic substances in the prey ([Abrams, 1989](#)). These features can have a number of effects in multiple-prey systems, depending on the nature and consequences of interactions between the negative effects. These consequences have yet to be explored in detail in models or empirical systems.

A final feature of functional responses to two or more foods/resources is the presence of between-individual variation in response parameters. Nearly 40 years ago, [Chesson \(1984\)](#) used models in which two types of predators within a single species each had standard multi-species type II responses with different parameter values. He pointed out that the presence of such variation could cause either positive or negative switching when functional responses are measured at the level of the entire consumer/predator population. [Berkhout and Morozov \(2022\)](#) examined the individual and population-wide responses of a snail species in which individuals are specialized, but the population contains many different specialists. The population-wide functional response in this system clearly varies with the composition of the predator population, but the relative consumption rates of different prey types is relatively insensitive to their relative abundances.

The set of multiple-resource models reviewed above have largely been limited to the case of just two resources. Adaptive diet choice involving three or more prey/resources is potentially more complicated because of the much greater variety of tradeoff relationships that may occur. If, for example, tradeoffs arise from

different spatial distributions of the prey, the degree of spatial overlap of all of the possible pairs of species and their movement rates should affect the shape of the multi-species responses. In cases with several prey that have different spatial distributions, it is possible for increased abundance of a particular prey with a spatial distribution similar to that of the focal prey to increase the predation rate on that focal prey. Empirical studies of functional responses with three or more prey are uncommon; Smout et al. (2010) and Beardsell et al. (2022) are exceptions to this generalization. However, Smout et al. (2010) do not incorporate any aspects of diet choice or optimal foraging.

Predator-dependent single-prey models

A second exception to single-variable functional responses is the class of models of a single prey (food) type that include an effect of the predator's abundance on its own functional response, an effect that is usually assumed to be negative. Beddington (1975) and DeAngelis et al. (1975) independently extended the type II response by adding a term proportional to predator density to the denominator of the function. This could reflect interference of predator individuals with each other's foraging. It could also arise from the prey exhibiting behaviors that reduce their own activity levels when predators are abundant, thereby reducing both food intake and predation risk. Both of these early models [and the related model of Crowley and Martin (1989)] assumed a simple homogeneous environment. Even without active habitat selection by prey, spatially heterogeneous environments produce results that could be interpreted as predator dependence if the functional response were measured at the level of the metacommunity as a whole (Abrams and Wilson, 2004).

When they are considered, the effects of predator density on the predator's functional response are usually assumed to be negative (Arditi and Ginzburg, 2012; DeLong, 2021; Ginzburg and Damuth, 2022). However, positive effects may occur when predators hunt cooperatively (Cosner et al., 1999), or simply when prey escape behavior in response to one predator individual makes the prey more easily detected by other predator individuals. We do not have any reviews estimating how often such positive effects occur, or what range of functional forms is needed to describe them. Both positive and negative effects may occur in the same predator-prey pair. Two different mechanisms producing negative effects are predator individuals attacking other predators (or other direct interference effects) and predators causing prey to change their behavior (e.g., remain in refugia), reducing their availability to other predator individuals. These two mechanisms require quite different functional representations.

Predator-prey models that have considered adaptive predator-avoidance by prey have all implied predator-dependence of the predator's functional response to the prey.

In these cases, the functional form of the predator-dependence depends on the nature and functional form of the prey's tradeoff between predator avoidance and some other fitness-enhancing activity. As a result, different models have not suggested a single functional response formula. Those that have expressed predator-avoidance effects in terms of the general shape of the tradeoff (e.g., Abrams, 1991a,b; Abrams and Vos, 2003) are particularly likely to be ignored in the functional response literature because they do not propose a specific functional form. In these cases, the functional response shapes have been expressed in terms of the derivatives of the component functions of the expression for predator per capita growth rate. These functions are seldom studied. In many animals, social or reproductive behaviors vary with abundance, and can reduce the time available for foraging; this provides additional potential influences of predator abundance on their own functional responses.

A large literature on predator-dependent functional responses has been devoted to discussing the extreme simplification of predator effects in which the functional response is represented as an increasing function of the ratio of prey abundance to predator abundance (Arditi and Ginzburg, 1989, 2012; Ginzburg and Damuth, 2022). This obviously restricts the formula to cases of negative predator density effects on the predator's functional response. Ginzburg and Damuth (2022) have recently argued for an expanded ratio dependence in which the denominator (predator abundance) can be raised to a positive power other than 1. Various reviews have shown significant differences between the results of empirical measurements of predator effects and the original ratio-dependent models (Skalski and Gilliam, 2001; Novak and Stouffer, 2021b). An early critique of ratio dependence pointed out that there were many causes of predator-dependence, virtually none of which led to ratio dependence (Abrams, 1994). Some of these mechanisms led to more extreme predator dependence, and most of the mechanisms required functional forms different from either pure or expanded ratio dependence. The simple 1-predator-1-prey version of either the original or expanded ratio-dependent response predicts that a rare predator population can increase on arbitrarily low prey abundance, provided the predator abundance is sufficiently low. This property, which can produce unusual outcomes, has never been demonstrated experimentally, and is impossible with reasonable constraints on predator movement rates and energy stores. In spite of continuing defenses of ratio dependence (e.g., Tyutyunov and Titova, 2021; Ginzburg and Damuth, 2022), the problem of extending this form to incorporate multispecies effects is another one of its major limitations (Abrams, 1997, 2015). The issue here is that different mechanisms producing strong predator dependence require qualitatively different modifications when two or more prey are considered. Barraquand (2014) provides other arguments against general use of ratio-dependent response.

Ecological systems and functional responses are both extremely diverse. No predator species is characterized by an exactly ratio dependent response; this was one of many points of agreement in [Abrams and Ginzburg \(2000\)](#). There are some experimental studies where generalized ratio dependence with a predator exponent of 1 fits the data better than other exponents ([Novak and Stouffer, 2021b](#)), but there are likely many models that are more consistent with the underlying mechanisms of predator dependence that would provide a better fit in these cases. The goal of ecological theory is to understand natural systems; how they change with environmental shifts and how they evolve over time. Predator dependence can arise from many causes, two of the main ones being anti-predator behavior by prey and antagonism between predators. [Abrams and Ginzburg \(2000, p. 339\)](#) list three additional mechanisms and point out the existence of more. All of these mechanisms lead to different models. Making a model without consideration of which mechanism applies makes it impossible to predict responses to environmental change or the nature of evolutionary change in predatory or anti-predatory traits. Knowing the basic mechanism for predator-dependence of the response is needed to address these questions. For example, does defending against one type of predator increase or decrease vulnerability to the second predator type? Ecological theory requires a diversity of more complex models, rather than simpler ones, if it is to describe natural rather than simplified laboratory systems. The simplest versions of such models should have functional response forms that are tailored to the known or suspected mechanism of predator- (and other species-) dependence.

Other trophic levels and additional predators; the missing components of functional response formulas

The main theme of this article is the excessive focus on 1-predator-1-prey interactions in studying trophic functions (i.e., functional responses). The functional response literature has very little consideration of species/resources occupying trophic levels above and below that of the focal predator-prey pair. It has long been known that one or both of these may influence the predator's functional response in a focal predator-prey pair by affecting the predator's foraging behavior ([Sih, 1980](#); [Abrams, 1982, 1984](#); [Lima and Dill, 1990](#)). The evidence for such effects has increased steadily over the years ([Lima, 1998](#); [Werner and Peacor, 2003](#); [Preisser et al., 2005](#); [Creel and Christianson, 2008](#); [Peckarsky et al., 2008](#); [Loeuille, 2010](#); [Allen et al., 2022](#)). Nevertheless, even relatively comprehensive reviews of functional responses have largely ignored the effects of abundances at trophic levels above or below the predator-prey pair (e.g., [DeLong, 2021](#); [Novak and Stouffer, 2021a,b](#); [Stouffer and Novak, 2021](#); [Uiterwaal et al., 2022](#)). Having adaptive behavior of the two intermediate species in a four-species food

chain in theory allows effects of species that are three levels removed from the focal species ([Abrams, 1992a](#)). This scenario also can produce reversal in the sign of the immediate effect of increased density of one species on its predator or its prey ([Abrams, 1992a](#)).

Even without considering additional trophic levels, the presence of a second predator species or type on the same trophic level as the first one will usually alter a prey's functional response to its own resource(s) as well as altering the functional response of the first predator. The existence and nature of these effects again depends on the nature of the prey's correlation between food/resource intakes and exposure to the different predator types. There are many possibilities here ([Matsuda et al., 1994, 1996](#)), so they do not lead to a single functional response formula. As a result, the analyses of such systems have usually addressed other issues, such as the stability of the dynamics produced by the adaptive foraging, and have not called attention to the implications for functional response theory.

Adaptive foraging under predation risk is not the only way that other trophic levels can influence a functional response. [Holt and Barfield \(2013\)](#) pointed out that, in many systems with plant, herbivore, and carnivore trophic levels, the abundance of the plant influences the ability of the carnivore to detect herbivores. This often involves a decreased ability of the herbivore to detect the predator in the presence of abundant vegetation. In other cases, the plant may produce chemicals that attract predators when it is itself under attack by the herbivores. Both of these mechanisms make the predator's functional response to herbivores an increasing function of plant abundance. [Holt and Barfield's \(2013\)](#) used simple models to show that such interactions can destabilize simple food chains or lead to alternative equilibria.

Given the long history of work documenting the effects of predators on prey activity and feeding, it seems strange that there has not been more effort devoted to exploring the effect of predators on the prey species' functional response(s) to their own foods. One possibility for this continuing neglect is the assumption that the effects of higher-level predators are independent of the effects of prey density on the mid-level predator's functional responses to its foods. In this case, higher-level predators would reduce the lower-level predator's food intake by the same proportion, regardless of food abundance. However, this is not what models of adaptive behavior suggest ([Abrams, 1984, 1992a, 1995](#); [Liu et al., 2014](#)). The model discussed in the following paragraphs is another, even simpler example of the impacts of adaptive foraging under predation risk on the prey's functional response.

If the abundance of higher-level predators led to a relatively uniform decrease in foraging by their prey, this would not change the shape of the prey's functional response to resources. However, even the simplest possible model of adaptive prey foraging under predation risk (i.e., one with linear functional and numerical responses for a fixed prey behavior) predicts

that different predator abundances will alter the shape of the prey's functional response to its resource, when prey foraging implies increased predation risk. Assume that the prey and predator species have underlying linear functional responses in the absence of adaptive prey behavior. The prey's intake of food is assumed to increase linearly with foraging time (t), while predation risk increases faster than linearly. The latter is inevitable if some times of day entail more foraging risk than others. The abundance of predator, prey and resource are denoted P , N , and R . The prey's functional response to its resource is given by cRt , where c is a capture rate per unit resource abundance while a prey individual is foraging, and t is the fraction of available time spent foraging. Intake may include some resource capture independent of active foraging (at a rate, c_0R) and intake while foraging (c_1tR). There may be other sources of increased mortality with foraging and these may also increase non-linearly (here assumed to increase quadratically, $d_1t + d_2t^2$). The per capita capture rate by a predator individual increases with the prey foraging time, with a per capita attack rate given by, $s_0 + s_1t + s_2t^2$. A simple expression for the per capita growth rate of the prey is thus,

$$b(c_0 + c_1t)R - d_0 - (d_1t + d_2t^2) - (s_0 + s_1t + s_2t^2)P \quad (1)$$

Solving for the foraging time t that maximizes fitness yields,

$$t_0 = \frac{bc_1R - d_1 - s_1P}{2(d_2 + s_2P)} \quad (2)$$

I assume this optimum is reached very rapidly relative to population changes. I also assume that P is not large enough to make the optimum zero, although this is a potential aspect of the functional response. Substituting this optimal foraging time into the expressions for the prey's functional response and the predator's functional response yields the following expression for the prey's functional response to its resource:

$$\left(c_0 + \frac{c_1(bc_1R - s_1P)}{2(d_2 + s_2P)} \right) R \quad (3)$$

Note that this is no longer linear in R , and that it is a decreasing function of P . Substituting the optimal time into the expression for the predator's functional response, $(s_0 + s_1t + s_2t^2)N$, yields,

$$N \left[s_0 + \frac{(bc_1R - d_1 - s_1P)(bc_1s_2R + s_1s_2P + 2d_2s_1 - d_1s_2)}{4(d_2 + s_2P)^2} \right] \quad (4)$$

This expression is still linear in N , but it is affected non-linearly by both R and P . [Abrams \(1984\)](#) presents another

simple example in which increases in resource abundance can reduce prey foraging, changing the sign of the effect of resource abundance on the top-predator's functional response. Neither that model nor the one presented above is meant to be a realistic model of any particular system. However, the dependence of functional responses on the abundances of multiple trophic levels is a general feature of situations with a tradeoff between food intake and predation risk ([Abrams, 1992a, 1995; Abrams and Vos, 2003](#)).

Theory such as this suggests that behavioral responses to foraging reward and risk lead to effects of species on non-adjacent trophic levels on each other's functional responses. The obvious question is why these higher and low levels have not appeared in the functional responses of most community and food web models. The most likely explanation is the lack of experiments that have measured responses in more than a single pair of species. On a practical level, predators usually have greater space requirements than their prey. As a result, sufficient replication of treatments with a range of different, but realistic predator abundances is not consistent with the space and time limitations of most laboratory environments. This is discussed further in the final section Reshaping functional response theory. Another practical issue is the likely dependence of anti-predator responses to the duration of the functional response measurement, an issue discussed in the next section.

The non-instantaneous nature of functional responses

[Barraquand \(2014, p. 3\)](#) ends the abstract of his article on functional responses with this statement: "The loose connection of ODE models with empirical data and spatial/temporal scaling up of empirical measurements constitute more serious challenges to our understanding of trophic interactions and their consequences on ecosystem functioning." Even in the absence of adaptive behavioral change based on the abundances of other species, functional responses are often imperfectly represented by ordinary differential equations (ODEs) based solely on current population densities. Modeling of anti-predator behavior has long incorporated dynamics for learned anti-predator behaviors ([Dill, 1973](#)). This study used a simulation model, and most subsequent work has been analytical. Incorporating dynamic behaviors in the context of the ODE models that are typically used in population/community ecology requires that behaviors themselves be represented by specific dynamical equations, as in [Abrams \(2000, 2010a\)](#) and [Abrams et al. \(2007\)](#). The presence of behavioral dynamics raises the possibility that those traits do not reach a stable equilibrium, particularly in multi-species systems ([Abrams et al., 2007](#)). This would mean that the functional response in those cases may not even be approximated by an expression that only involves current abundances. Individual-based simulation models could

incorporate more detailed schemes for the dynamics of behavior, such as the “Sarsa” model of learning (Sutton and Barto, 2018; McNamara and Leimar, 2020). Nevertheless, in some simple types of predation based on rapid changes in satiation or hunger, functional responses based solely on current abundances are likely to be a good approximation.

Many of the influences on consumption rates discussed in this article are not instantaneous, and can have large stochastic components. In addition, the full effect is likely to be delayed. Holling’s suggested learning mechanism in his type III functional response implies that, if a given prey density drops to a value lower than it had previously, the initial consumption rate will be greater than its quasi-equilibrium value for that lower prey density. On the other hand, if the prey density is increased very rapidly, the capture rate will initially be lower than its quasi-equilibrium, because the predator has had relatively little recent practice capturing this prey. These lags were not part of Holling’s original formulas, which implied instantaneous change in predator consumption with prey density. It is also possible that rapid behavioral dynamics produces population cycles; this is the case when an effectively type II response is produced from a linear one by behavioral or rapid evolutionary change, as in Abrams (1992b).

In spite of these possibilities, there are likely to be many cases in which the behavioral change is rapid enough to assume a quasi-equilibrium with respect to current abundances. However, it is desirable to consider the possibility of significant lags, particularly when the abundances influencing the benefits or costs of foraging cannot be quickly and accurately estimated by the consumer.

The next section will propose some steps that could be taken to change the direction of current theory regarding trophic functions so that it is more in keeping with the opening quotation from Holling (1965). An alternative representation of functional responses is to break them down into dynamic components that define the foraging and anti-predator strategies of all the species involved. Even when this approach is not adopted, the “species involved” should include many others in addition to the focal predator and prey. Such a model may also need dynamic variables describing different nutrient stores in the predator or nutrient contents in the different prey/food types. There have been other recent calls for breaking trophic interactions into components for modeling (e.g., Wootton et al., 2021). However most of these (including Wootton et al., 2021) do not consider adaptively changing components of species other than the focal predator-prey pair.

Reshaping functional response theory

At the current time we have very few if any models that have predicted the dynamics of ecological systems in the field over

many generations. It will obviously be quite a while before such models are both developed and tested. In the meantime, theory can contribute to this ultimate goal by identifying the types of effects and processes that might be important in determining the form of such models. These processes will need to include a more flexible concept of functional responses than the current focus on pairwise interactions influenced only by immediate predator and prey densities. As suggested in the previous section, this may require that the parameters of current functional responses, such as attack rates or handling times, be expressed as dynamic variables. Below is a list of six more specific changes or additions to current functional response theory.

1. It is necessary to have a better understanding of the relationship between functional and numerical responses, as the latter determines how the former affects an organism’s fitness.

Our understanding of numerical responses is much more limited than our understanding of functional responses. It is commonly assumed in differential equation models of interacting species that mortality is independent of food consumption, and that reproduction is a simple increasing function of food consumption rate (or consumption rate of the limiting nutrient). However, mortality is in fact affected by food consumption in many systems (Montagnes et al., 2019), and there are few studies in animals quantifying how intake rates of different resources affect the different components of fitness.

Most ecologists would agree that the vast majority of consumers require more than a single resource, and that there are limits to consumption rates. Even animals that are highly specialized on a single food are likely to have other requirements (water sources for terrestrial animals; areas with cover from predation; nesting sites), and it is common for such “other factors” to be limited in abundance. Many of these categories constitute “essential” or nearly essential resources, and “consuming” some of these categories interferes with consuming other categories. However, an additional resource from a different nutritional category is generally expected to have a different effect on a consumer’s functional response to a particular resource than is a second resource from the same nutritional category. If a simplified representation is being used, some of the “different category” resources may be approximated by a direct negative effect of predator abundance on its per capita growth rate.

2. The taxonomic and ecological range of functional response studies should be broadened.

The limited range of species used in functional response studies is illustrated by the comprehensive database by Uiterwaal et al. (2022). Functional response theory should not be restricted to “predators” in the narrow sense of animals that eat other animals. Holling did not require that the food items be living entities, as was clear from his famous experiment with

blindfolded humans searching for paper disks on a table top. However, the consumption of nutrients by plants or fungi as well as non-living material by detritivores have been largely ignored in the functional response literature. [Tilman's \(1982\)](#) book on resource competition (based on plants) did not mention functional responses by name. The models used in that book assumed that the uptake rate of a single resource by a consumer was proportional to the consumer per capita population growth plus the consumer per capita death or loss rate. In practice this was equivalent to assuming a type II functional response to the single limiting resource, a linear numerical response to that limiting resource, with a mortality rate independent of nutrient intake. Theory involving plants and other consumers of non-living resources has used a very narrow range of functional forms for functional responses, usually following [Tilman's \(1982\)](#) effective assumption of a single-resource type II functional response to whichever resource type was limiting, and consumption of the other resources at a rate just sufficient to make them co-limiting. [Tilman \(1982\)](#) and later authors (e.g., [Huisman and Weissing, 2001](#)) followed [León and Tumpson \(1975\)](#), who first proposed this set of assumptions, but did not provide empirical support. The reduced uptake rates of other resources are assumed to have no effect on the uptake rate of the limiting resource. This assumption also appears not to have been tested in most systems.

In both plants and animals, there has been very little systematic exploration of the shapes of the relationships between other (non-resource) species abundances and foraging/uptake by a focal consumer species on a focal resource. [Holt and Barfield's \(2013\)](#) treatment of plant effects on predator-herbivore encounter rates also calls for more study of such cases. However, effects of species that are two-or-more trophic levels removed from the focal species have seldom if ever been examined with experiments having the same multiple-density treatments as in traditional functional response studies.

3. Functional response experiments with different durations should be carried out and compared.

Experimental duration is likely to have a larger impact on the functional response when the abundance being varied is that of a higher-level predator, rather than a prey species. The initial detection of a predator by a prey individual will typically not allow accurate estimation of predation risk. In such a case, the optimal strategy is usually for the prey individual to reduce its activity until a better estimate or risk can be obtained. Even without more information, the prey will eventually exhaust its energy (nutrient) reserves, and this will tend to increase the advantage of foraging, even if the risk is still unknown. This process will usually occur on a more rapid time scale than major changes in species abundances. Variation in the food available to the prey individual experiencing risk should also contribute to time-dependent responses in their own behavior. Because periods of high food abundance are

not likely to persist indefinitely, an organism should initially have higher consumption rates than would be optimal if that food abundance were known to persist for a long time in the future. The consequence of these behavioral considerations is that experiments with a fixed, very short time interval (the usual basis of functional response measurements) may be misleading when using a time scale that is more relevant to population dynamics. One study examining the impact of the measurement duration for functional response shape is [Li et al. \(2018\)](#).

4. The effects of additional species on different trophic levels should be explored both theoretically and experimentally.

Most of the literature on predator functional responses that considers multiple species only addresses additional prey species. The difficulty of carrying out a sufficient number of experimental treatments to determine the shape of multi-variable functional responses has deterred studies with two or more predator types or different/multiple prey. However, even comparing two different abundances of two variables would give some insight into the qualitative nature of the interaction between these variables in determining the consumption rate. [Abrams and Schmitz \(1999\)](#) showed that the combination of high and low quality foods in habitats involving different predation risks produced several novel features in a time- and capacity- limited forager's functional response. Many other scenarios combining diet choice and predation risk have yet to be explored.

5. Adaptively flexible functional responses in models with three or more trophic levels and two or more species per level should be investigated.

Paradoxically, models of food webs containing many species are more likely to use the simplest possible (type I) functional responses than are models with only a few (five or fewer) species ([Al-Khudhairy and Rossberg, 2022](#)). Early food web models (e.g., [May, 1973](#); [Pimm, 1982](#)) almost always assumed linear functional responses. A system with two adaptively flexible species on each of three trophic levels is likely to exhibit qualitatively different functional response forms than any of those discussed above. A relatively full investigation of such a model should offset the tendency of models of larger foodwebs to assume linear functional responses. Recent empirical work has suggested that a variety of different interference effects occur between different mammalian top predators ([Engebretsen et al., 2021](#)). [Gobin et al. \(2022\)](#) discuss several modifications of type II responses in the context of models of a relatively well-studied boreal system in which five vertebrate species were represented. They analyze food web properties of best-fit models with different functional response forms, and conclude that type II responses produce relative poor fits to observed population and food web data. This was at least in part due to the inability of

this functional response formula to represent known aspects of consumption, including predator interference, switching, caching, and surplus killing.

6. More *in-situ* studies of functional responses are required.

There is little doubt that the difficulty of carrying out multi-species functional response studies on an appropriate spatial scale has contributed to their scarcity. This is particularly true of potential studies involving the effects of higher-level predators. The space and labor required for monitoring multiple species in an experimental setup is often prohibitive, and it is often impossible even come close to replicating field conditions, which usually include spatial heterogeneity. *In situ* experiments are likely to provide the best chance of studying the types of multi-species responses discussed here. These include experimental use of predator cues, such as scent or sound (e.g., Allen et al., 2022), or implanted sensors that can detect predation events (Wilmers et al., 2015; Cruz-Font et al., 2019).

The functional response literature has grown significantly in the past decade. This suggests that the time may be ripe for a broadening of the set of assumptions made about those responses. I am not alone in calling for a broadened scope for functional response studies. For example, Kratina et al. (2009, p. 425) opened their article with the following two sentences “Realistic functional responses are required for accurate model predictions at the community level. However, controversy remains regarding which type of dependencies need to be included in functional response models.” I would disagree with the idea that there was or is much controversy; the majority of studies still ignore dependency of functional responses on species other than the focal prey without presenting any justification for doing so.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

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Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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