

Toward a modular theory of trophic interactions

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Abstract

Species traits and environmental conditions determine the existence and strength of trophic interactions, but how they do so is poorly understood. To enable the informed inclusion of such driving factors in dynamic trophic-interaction models, we revisit and expand the functional and numerical response functions using a modular approach which is readily integrated into existing models. We divide the trophic interaction between predator and prey into eight steps: (1) search, (2) prey detection, (3) attack decision, (4) pursuit, (5) subjugation, (6) ingestion, (7) digestion, and (8) nutrient allocation. Formulating this as a modular functional-response function, we build a general dynamical model where trophic interactions can be explicitly parameterized for multiple traits and environmental factors. We then concretize this approach by outlining how a specific community can be modeled by selecting key modules (steps) and parameterizing them for relevant factors. This we exemplify for a community of terrestrial arthropods using empirical data on body size and temperature responses. With species interactions at the core of community dynamics, our modular approach allows for quantification and comparisons of the importance of different steps, traits, and abiotic factors across ecosystems and trophic interaction types, and provides a powerful tool for trait-based prediction of food-web structure and dynamics.

Toward a modular theory of trophic interactions

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TR and KW conceived the project,
KW led the writing of the manuscript,
TJ led the development of the mathematical framework and writing of the supplementary material,
TJ, KW, and AC developed the mathematical framework,
All authors contributed to the development of ideas, writing and editing of the manuscript

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Abstract

Species traits and environmental conditions determine the existence and strength of trophic interactions, but *how* they do so is poorly understood. To enable the informed inclusion of such driving factors in dynamic trophic-interaction models, we revisit and expand the functional and numerical response functions using a modular approach which is readily integrated into existing models. We divide the trophic interaction between predator and prey into eight steps: (1) search, (2) prey detection, (3) attack decision, (4) pursuit, (5) subjugation, (6) ingestion, (7) digestion, and (8) nutrient allocation. Formulating this as a modular functional-response function, we build a general dynamical model where trophic interactions can be explicitly parameterized for multiple traits and environmental factors. We then concretize this approach by outlining how a specific community can be modeled by selecting key modules (steps) and parameterizing them for relevant factors. This we exemplify for a community of terrestrial arthropods using empirical data on body size and temperature responses. With species interactions at the core of community dynamics, our modular approach allows for quantification and comparisons of the importance of different steps, traits, and abiotic factors across ecosystems and trophic interaction types, and provides a powerful tool for trait-based prediction of food-web structure and dynamics.

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1. Introduction

Ecological communities are composed of multiple interacting species. A fundamental interaction type is the trophic, or feeding, interaction, and trophic interactions are affected by many factors. Traits of both the predator and the prey, such as their body sizes (Brose et al., 2006; Laigle et al., 2018), dictate whether a trophic interaction can take place. The nutritional needs of a consumer will also affect which resources it prioritizes (Couture et al., 2010; Ibanez et al., 2017; Razeng and Watson, 2015). Moreover, environmental conditions, such as temperature, can alter metabolic requirements (Brown et al., 2004; Gillooly et al., 2001), behaviour (Roitberg and Myers, 1979), or mobility (Grigaltchik et al., 2012; Sentis et al., 2012). Together, factors like these dictate which trophic interactions can occur, how strong the interactions are, and ultimately the structure and dynamics of ecological communities (e.g. Gravel et al., 2016; Laigle et al., 2018; Rall et al., 2012; Sentis et al., 2014).

Because of their fundamental importance for community dynamics, there is extensive research on the occurrence and strength of trophic interactions and how these interactions are affected by species traits such as body size (e.g. Brose, 2010; Brose et al., 2019; Jonsson et al., 2018; Spitz et al., 2014) and environmental factors such as temperature (e.g. Grigaltchik et al., 2012; Rall et al., 2012; Sentis et al., 2012). Trophic interactions can be mathematically encapsulated by the functional response, which describes a consumer's intake rate relative to prey density, and the numerical response, which describes the consumer's reproductive rate relative to consumption (Holling, 1959; Solomon, 1949; Stouffer and Novak, 2021). The functional and numerical responses form the backbone of dynamic trophic-interaction and food-web models. It is possible to parameterize both functional and numerical responses based on species traits and environmental factors (e.g. Jeschke et al., 2002; Laubmeier et al., 2018; Sentis et al., 2012; Vucic-Pestic et al., 2011). This allows the prediction of, for example, food-web dynamics from species' traits or the effect of changing environmental conditions. In particular, parameterizing the functional response based on metabolic theory, where metabolic rates are scaled relative to body size (Brown et al., 2004), has proven powerful for predicting food-web structure and dynamics (e.g. Curtsdotter et al., 2019; Gravel et al., 2013; Jonsson et al., 2018; Schneider et al., 2012, 2014; Vucic-Pestic et al., 2010).

Although significant progress has been made in predicting community dynamic outcomes from allometric (body-size based) food-web models, the tests of these models against empirical data also show that body size does not fully explain empirically observed food-web dynamics (Curtsdotter et al., 2019; Jonsson et al., 2018; Schneider et al., 2012, 2014). We know that many factors other than body size influence the occurrence and strength of feeding interactions (e.g. Kalinoski and DeLong, 2016; Preisser et al., 2007; Schmitz and

Suttle, 2001). For example, behaviours and traits such as prey defenses and predator hunting mode alter the predator-prey body-size relationship (Binz et al., 2014; Kalinoski and DeLong, 2016; Schmitz, 2007; Schneider et al., 2012, 2014), but are not covered by the existing allometric functions, and environmental factors such as temperature or habitat complexity can interact with body size to alter interaction strengths (e.g. Sentis et al., 2014; Vucic-Pestic et al., 2011; Vucic-Pestic et al., 2010). It is currently unclear how to add such additional traits and factors to the functional or numerical responses; current formulations of the functional and numerical response functions collapse distinct parts of the predation process - such as subjugation and ingestion - into aggregated terms such as overall "attack rate" and "handling time" (e.g. Schneider et al., 2012, 2014), obfuscating how best to add traits or factors that have diverse effects on different parts of the predation process.

We propose that the best way to understand the effect of diverse species traits, and of other factors, on trophic interactions is to break a trophic interaction into distinct steps, determine which steps are affected by which factors, and then explicitly focus on the most affected steps. This approach is based on the realisation that a trophic interaction consists of multiple steps, each of which represents a key part of the predation process, and that each of these steps may be affected by traits and environmental factors in different ways, often combining to non-intuitive dynamic outcomes for the community (e.g. Dell et al., 2014; Gilbert et al., 2014; Grigaltchik et al., 2012; Rall et al., 2010).

For clarity, we define "step" as one of the eight distinct parts of the predation process: search, detection, decision, pursuit, subjugation, ingestion, digestion, and allocation of nutrients. These are further defined in section 2. All eight steps occur in every trophic interaction, although some become trivial in some interactions which means we can simplify by omitting those steps. For example, *pursuit* is usually not an important step in the case of herbivory and the steps of *detect-subdue* happen simultaneously with *ingestion* for filter feeders. We define "modules" as those steps that are selected as most important for a given interaction. For a given interaction then, one would usually select less than eight modules to focus on. Depending on the question, availability of data, factors of interest, or desired level of complexity, the same interaction could be modeled with different combinations of modules. A trophic interaction can then be described as a whole by putting modules together, either conceptually, or explicitly as a mathematical model which we demonstrate later.

The advantages of this modular approach are, firstly, that it allows for direct comparisons of factors, in terms of which step(s) they affect and how, and of interactions and ecosystems, in terms of relevant steps and factors. Secondly, selecting the most relevant steps as modules simplifies and focuses research on the most important elements of the interaction, while remaining clear about which steps are affected. Finally,

we can disaggregate the functional and numerical response by unpacking it into a modular structure, as we demonstrate later. Modules can be parameterized explicitly by the traits or factors affecting the step, as observed and estimated in any particular community. This enables the explicit inclusion of behaviours and traits that strongly affect a particular feeding interaction, but are not currently included in generalized trophic-interaction models. The proposed approach simultaneously allows for the inclusion of environmental factors, such as temperature. Importantly, we perform this unpacking in a way such that the functional response remains analytically intact. This means that our disaggregated functional response can directly be employed in current dynamic trophic-interaction models.

For illustrating the modular approach, we here focus on two-species trophic interaction models, but the general approach is actually best-suited to modeling groups of interacting species or even entire food webs. When applied across multiple species, relevant modules can be expressed as functions of traits (Violle et al., 2007) which those species differ in, meaning that the single model can parameterize the entire community. This extends the utility of similar models, for example, the allometric trophic network (ATN) model, to traits beyond body size. In addition to modeling trophic-interaction strength, the modular approach can predict which interactions are likely to exist at all (i.e. food-web structure) by recognizing that "no interaction" is one end of the trophic-interaction strength continuum. In this way, we can use the modular approach to model both strength and existence of trophic interactions for an entire community based on a few easily measurable traits, giving rise to a powerful way to predict food-web structure and dynamics (Bartomeus et al., 2016; Morales-Castilla et al., 2015; Violle et al., 2007). Furthermore, the modular approach readily incorporates the effects of multiple predator and prey species, allowing the integration of predator interference or facilitation (Losey and Denno, 1998; Schmitz, 2007), trophic interaction modifications (Terry et al., 2017), and prey-switching (Elliott, 2004; Morozov and Petrovskii, 2013), among other community effects generally omitted from two-species trophic-interaction models.

We propose that the modular approach to trophic interactions can provide the structure needed to advance trophic interaction research and eventually provide a general theory of trophic interactions. In what follows, we begin by defining the division of the predation process into the eight steps, where each step represents a module for a particular trophic interaction, and then outline how to use the modules to build the functional response for a dynamic trophic-interaction model. We then illustrate our framework with an explicit example based on empirical data, advanced as a worked-through demonstration of how to apply this framework. In doing so, we have no intent of a full empirical evaluation, since such evaluation can only eventually be realized by applying this framework across many different trophic interactions. While we here

present the modular approach primarily in terms of predator-prey interactions, we intend it to be applicable to trophic interactions of any kind. We end by outlining applications of the modular approach and the steps needed to test and validate it in order to advance it into a modular theory of trophic interactions.

2. The eight steps composing a trophic interaction

We propose that a general theory for understanding trophic interactions can be achieved by breaking the predation process down into its component steps. We formalize an approach that unpacks the functional and numerical responses into distinct steps, describes the selection of the most important steps as modules, and how the effect of various traits and environmental factors on each module may be included in a coherent way. This approach thus forms the foundation for a modular theory of trophic interactions.

Trophic interactions have regularly been broken into steps before (e.g. Boukal, 2014; Griffiths, 1980; Holling, 1959; Jeschke et al., 2002; Lafferty et al., 2015; O'Brien et al., 1990). One complication inherent in previous divisions of the predation process is that each division uses different steps, lumps adjacent parts of the predation process together, and is often not explicit about the boundaries between the steps they use. For example, it is often unclear whether 'attack' refers to pursuit, subjugation, or both. These fuzzy boundaries obscure the importance of each step (because they are not directly comparable) and the possible insights which might be gained in terms of how traits and other factors actually affect trophic interactions. We here, therefore, explicitly define eight steps (which are compatible with all other divisions) and encourage clear declaration in future in terms of which of these steps are most relevant for presented research, so that we may create a common framework and dialogue with which to compare the effect of traits and other factors on trophic interactions. We present these steps sequentially, but recognize that a predation event will not always occur linearly; a predator may cycle between searching and pursuing as the prey flees for example, or between pursuit and subjugation, or other steps. However, these steps are still distinct in terms of the effect of traits or environmental factors or the importance of the step for a given interaction.

Previous suggestions of how to break a trophic interaction into parts generally recognize three stages: a consumer must first Locate, then Attack, and finally Consume its prey (e.g. Boukal, 2014; Griffiths, 1980; Holling, 1959; O'Brien et al., 1990). We additionally recognize the stage of Decision (Fig. 1). After locating its potential prey, a predator must decide that it is worth proceeding to attack it. We further break down each of the broad stages of Locate, Decide, Attack, and Consume into 1-3 more specific steps. This breakdown gives a total of eight steps that collectively describe the "predation cycle" (see Bateman et al. 2014 and Jeschke et al. 2002 for similar divisions, but which lack or omit *decision* and do not break consumption

into all its component steps). All the steps we use have been at least mentioned by previous work, but we are unaware of any work that uses all eight. Frequently two or more steps are aggregated or steps are mentioned but omitted from the mathematical framework. Each previous division may therefore be arrived at by applying our framework, by selecting only relevant modules.

Here, we group the eight steps into four stages to simplify and aid conceptualization, as well as to enable comparison with previous divisions that aggregate the finer steps into broader stages. We define these four stages (underlined, roman numerals) and their *steps* (in italics, numbered according to Fig. 1) as follows:

Stage I: Location is the stage where a predator and prey go from being in the same location but unaware of each other, to the predator identifying the presence of the prey and pin-pointing its position. This begins with the predator *searching* (step 1) for the prey either actively or passively. Once encountered (i.e., the prey comes within the predator’s sensory range but is not yet detected), the predator then *detects* (step 2) and identifies the prey.

Stage II: Decision is the stage where a predator *decides* (step 3) whether to attack a detected prey individual based on the likelihood of a successful attack, the risk and cost of attack, and the perceived benefit of consumption.

Stage III: Attack occurs when the predator has decided to exploit the prey. It begins with the *pursuit* (step 4) followed by *subjugation* (step 5) of the prey, and ends when the prey is immobilized (often the death of the prey, depending on the type of interaction).

Stage IV: Consumption involves the predator *ingesting* (step 6) and *digesting* (step 7) the prey and assimilating the nutrients, and then finally *allocating* (step 8) the energy and nutrients into maintenance, growth, or reproduction.

Finally, the proportion of time a predator devotes to foraging plays a very important role in terms of the effect of foraging on both predator and prey populations. This proportion can also be affected by traits and the environment (Jeschke et al., 2002) and therefore forms an additional term that can be included as a module in our framework. We expand on this in section 4.2.

To summarize, the division of a trophic interaction into steps is conceptually useful to move from a fuzzy, low-resolution image of a trophic interaction as formalised in the original functional-response function, to a higher-resolution image allowing us to discern the role of traits and other factors. This modular approach allows us to make more sense of how species traits and environmental context relevant for each respective step convert into cumulative interaction probability and strength across steps (Fig. 1) and from there to quantitative interaction dynamics (Fig. 2). While added complexity in a model rapidly becomes intractable (Evans et al., 2013), the modular approach aids in finding and adjusting the optimal trade-off between

simplicity and complexity based on the needs of the model and availability of data or information with which to build it.

3. The benefits of a modular approach

As described above, trophic interactions are composed of a sequence of steps, each of which can be affected by diverse traits and environmental factors. When considering a specific trophic interaction or factor, the complexity of the interaction can be reduced to a feasible and sufficiently accurate summary by omitting less influential steps. The solution we are advocating here is to define each step in an unequivocal way, then perform the removal of unimportant steps with clear intent. This will challenge us to identify what factors affecting each step we need to consider. The proposed approach also makes it possible to 'upgrade' the relationship with effects of additional traits and environmental factors as new information is obtained.

Some steps will be very important for a certain interaction, but essentially irrelevant in another. For example, the *pursuit* step, where a consumer pursues its resource, is important for many predator-prey interactions but few plant-herbivore interactions because plants do not run. The importance of traits or environmental factors can be studied and understood in terms of which step(s) they affect. The trait of camouflage, for example, is important to the *detection* step, where a consumer detects its resource (Ruxton, 2009), but camouflage is unlikely to affect the *ingestion* step. A model incorporating traits or environmental factors can be built by selecting as modules the steps most affected by the selected traits or factors. For each of the selected modules, the relationship between the trait or environmental factor(s) and the likelihood of the step successfully occurring can be estimated to the desired level of accuracy. The selected modules can then be combined to form the functional and numerical response functions of a dynamic trophic model (Fig. 2).

If knowledge is lacking about a particular step, research can be focused on that step (for direction as to how, see Box 1). Once obtained, the new knowledge can easily be integrated into the model by updating the corresponding module. Research from similar ecosystems can provide a reference or baseline for a module and how it is affected by traits or environment when studying a new community. Equivalent modules can be compared across different ecosystems in terms of the importance of that module or what factors influence the module, increasing our fundamental understanding of what governs trophic interactions and community dynamics across ecosystems. The field of trophic interactions is key to our understanding of ecological communities, but currently lacks sufficient structure to maximize the information gained from each research project. A modular approach can provide that structure.

4. Using the modular approach to build the functional and numerical response functions

The modular approach is valuable as a conceptual tool for pinpointing which parts of the predation process shape a trophic interaction, and especially for comparing different interactions or the effect of diverse traits or environmental factors. When it comes to building models of trophic interactions, however, the modular approach truly shines by facilitating explicit and flexible inclusion of any traits or factors to create a model with the desired level of simplicity or complexity. Importantly, this approach is compatible with existing trait-based trophic-interaction models, such as the Allometric Trophic Network (ATN) model (see section 2.1 in appendix S1). In this section, we first describe the development of trait-based models, upon which our framework builds, and then describe how to use the modular approach to build modular functional and numerical response functions which can then be used as the core of a dynamic trophic-interaction model, where traits, environmental variables, or other factors can be explicitly and flexibly incorporated as parameters in the model.

4.1 Trait-based models

Our framework builds on attempts at using traits to predict trophic interactions and thereby food-web structure and dynamics. Traits (primarily body size) were first used to phenomenologically predict food-web structure (e.g. Cohen and Newman, 1985; Neubert et al., 2000; Williams and Martinez, 2000). Although some of these structural models reference the potential importance of different stages (e.g. Neubert et al., 2000, reference the importance of the stages Capture and Consume as responsible for a lower energetic limit preventing large predators from eating very small prey), they do not use steps explicitly.

Early trait-based *dynamic* models were the beginning of linking traits to different parts of the predation process, but at a very coarse-grained level. Most of these models use traits to parameterize the functional and numerical responses, a precedent which we expand on here. For example, body size was linked to the attack rate and handling time parameters of Holling's Type II functional response (Eq. 6) to create allometric functions (i.e. where parameter values scale with body size) (Berlow et al., 2009; Otto et al., 2007; Yodzis and Innes, 1992). Attack rate aggregates steps 1-5 and handling time aggregates steps 1-7. Later models (e.g. Schneider et al., 2012, 2014; Vucic-Pestic et al., 2011) developed these allometric functional responses further by recognizing that, within attack rate, body size has a different effect on Location (steps 1 and 2) than on the likelihood of attack success (an aggregate of steps 3-5). They propose that Location increases

allometrically with body size because larger predators have a larger visual range, while likelihood of attack success follows a hump-shaped relationship with the predator-prey body-size ratio, because predators are more successful at attacking prey smaller than themselves, but have little motivation to attack small prey with limited energy content. Even the proportion of time spent foraging has been linked to body size, due to its effect on gut size and therefore hunger and motivation to forage (Jeschke et al., 2002).

The models discussed above have provided a general and powerful way to predict broad patterns of food-web structure and dynamics (e.g. Jonsson et al., 2018; Schneider et al., 2012, 2014; Vucic-Pestic et al., 2010), but their success is still limited (e.g. Jonsson et al., 2018). This is because, while body size may drive gross trends of predator-prey interactions, its importance can be significantly modified by other traits (e.g. Kalinoski and DeLong, 2016; Klecka and Boukal, 2013). In describing the models above, many of authors discuss the importance of other traits and the environment, and their different effects on different steps, but omit them from their models in favour of a simpler, generalizable, and broadly successful model. For example, Vucic-Pestic et al 2010 experimentally obtained a scaling exponent for handling time of -0.94, rather than -0.75 as predicted by allometric arguments. They hypothesize that this is because the *digestive* part of handling time is affected by metabolism and should therefore follow allometric scaling, while the *ingestive* part of handling time (which was the short-term response they measured) is limited by morphological factors which scale more linearly with body size. Similarly, they note a type II functional response when predators are of similar size to their prey, but a type III response when prey are much smaller. They find this is caused by habitat complexity limiting the *encounter* rate (i.e. *searching*), because smaller prey are able to find refuge in the habitat where their predators cannot follow them, but when predators are of similar size as their prey then the prey loses its refuge. While omitting these factors for the sake of simplicity and generalizability has created effective and powerful models for broad patterns, the time has come for a mechanistic model which accounts for these omitted details. We believe that the modular approach to trophic interaction, as outlined here, can tackle this problem.

4.2 Arriving at a general model

Each step defined in section 2 “The eight steps composing a trophic interaction” can be described by a mathematical function relating the probability of that step successfully occurring (in the case of steps within Location, Decision and Attack) or efficiency of energy conversion (in the case of steps within Consumption) to the factors affecting it (Fig. 1). Here, we take a step back and revisit the derivation of the functional and numerical responses of predators with all eight steps of a trophic interaction clearly in mind. We arrive at

a more explicit formulation of the functional and numerical responses relative to existing formulations (e.g. Holling’s type II functional response (Holling, 1959), the ATN model (Otto et al., 2007; Schneider et al., 2012, 2014), and others (e.g. Jeschke et al., 2002; Koen-Alonso, 2007)), with parameters that specifically relate to each step. We do so by considering each step of a foraging interaction as one in a sequence of probabilities (or proportions). Together, the steps describe the cumulative probability of the step occurring: i.e., the probability that a predator successfully Locates, Decides to attack, and Attacks a prey individual. They further describe the cumulative proportion of Consumption, i.e., subdued (killed) prey, eventually allocated to reproduction (Fig. 1). The probability that the trophic interaction occurs, or proportion of the prey population which is subdued, is then the cumulative probability of the steps describing Location, Decision and Attack, while the strength of the interaction, from the predator point of view, also includes the stage of Consume. We here include the step of ingestion as part of the numerical response, reasoning that a subdued prey is usually killed and that therefore quantifies the effect of the interaction on the prey population regardless of the proportion of killed prey that is ingested by the predator. There are cases, however, where it may make more sense to include ingestion in the functional response. For example, in herbivorous interactions it is usually the proportion of the resource *ingested* by the consumer which is relevant to the resource population. We also emphasize that we here include the time taken for ingestion as part of handling time (Eq. 4), which does affect the functional response. By understanding which step(s) a given factor affects and how, we can mechanistically relate that factor to the relevant parameter(s) of the dynamic model.

We explicitly lay out all eight steps here (Fig. 1), but suggest that in most cases a satisfactory model can be built by selecting only the few most important steps as modules. For example, differences in interaction strengths within a given community may be primarily driven by the prey traits ”mobility” and ”camouflage” and predator traits that help them *detect* camouflaged prey or *pursue* speedy prey. In such a case, a satisfactory model may be built from only two modules: detection and pursuit. This allows for the flexible inclusion and emphasis of whichever traits or factors and whichever modules are deemed most important, resulting in a model as simple or complex as required.

The modular functional and numerical response functions we develop here can replace the functional and numerical response functions in any dynamic trophic-interaction model, such as a Lotka-Volterra predator-prey model (Lotka, 1920; Volterra, 1926) or the ATN model (Berlow, 1999; Otto et al., 2007; Schneider et al., 2012, 2014). Incorporating these functions into dynamic models thereby mathematically relates the effect of traits or the environment on trophic interactions to community dynamics, allowing for predictions

of food-web structure and dynamics based only on the measurement of a few traits, or predicting the effect of changing environmental conditions. To relate the functional response to the steps of the foraging cycle, we can consider the total number of prey that are subdued (killed) per predator (χ_5 , Fig. 1) during a foraging time interval as the proportion of prey which pass through steps 1-5, times the number of prey present within the area searched, A_{search} (scanned) by a predator per unit foraging time. The first parameter potentially affected by traits or the environment is φ_{forage} , the proportion of total time the predator spends foraging (Jeschke et al., 2002). Once foraging, the predation cycle starts with searching and here f_1 is the proportion of all prey individuals (N) present that are encountered within the area searched by a predator (A_{search}) per unit available search time. f_2 is the proportion of encountered prey that are detected and so on, and φ_{search} is the proportion of foraging time spent searching, such that:

$$\begin{aligned}
\chi_1 &= f_1 \cdot A_{search} \cdot N \cdot \varphi_{search} \\
\chi_2 &= f_2 \cdot \chi_1 = f_1 \cdot f_2 \cdot A_{search} \cdot N \cdot \varphi_{search} \\
&\dots \\
\chi_5 &= f_5 \cdot \chi_4 = f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot \varphi_{search}
\end{aligned} \tag{1}$$

We can express the functional response, FR as a function of total time by multiplying χ_5 by the proportion of total time spent foraging φ_{forage} :

$$FR = \chi_5 \cdot \varphi_{forage} \tag{2}$$

The remaining three steps of foraging not included in the functional response comprise the stage Consume (although, as mentioned previously, there may be cases where step 6, *ingestion* should be considered part of the functional response). These are part of the numerical response of the predator and do not directly affect the prey population. Indirectly, however, the stage Consume often affects the prey population due to its effect on handling time (see appendix S1). The three steps of Consume are often aggregated into a single parameter, ϵ , collectively describing the processes of ingestion (f_6), digestion and assimilation (f_7), and allocation to reproduction (f_8) and thus the proportion of a killed prey that are converted into new predators (or efficiency in doing so). However, as above, the steps 6-8 can easily be factored out from this parameter (ϵ) and made into functions to allow a more detailed representation of how traits affect these final

steps of a trophic interaction:

$$NR = \epsilon \cdot \chi_5 \cdot \varphi_{forage} = f_6 \cdot f_7 \cdot f_8 \cdot \chi_5 \cdot \varphi_{forage} \quad (3)$$

The functional response in equation (2) is expressed in relation to the proportion of foraging time available for searching, φ_{search} . However, φ_{search} is negatively affected by the proportion of time spent handling prey and therefore is not normally constant. In the simplest case, this results in a type II functional response, i.e. when there are more prey, more time is spent handling and the predator consumes a smaller proportion of the total prey population. Therefore, to understand how the above equations will change depending on prey density, it is better to express them as functions of average time spent handling each consumed prey (t_{handle}) rather than search time. Handling time is also often easier to measure and more constant than search time. If we consider that handling time is the average total time required for detection (t_2), decision (t_3), pursuit (t_4), subjugation (t_5) and ingestion (t_6) for each successfully consumed prey (by taking the probabilities of detection, decision, pursuit and subjugation into account), we arrive at the following definition of t_{handle} (see Eq. SI-10 in appendix S1 for derivation of t_{handle}):

$$t_{handle} = \frac{t_2}{f_2 \cdot f_3 \cdot f_4 \cdot f_5} + \frac{t_3}{f_3 \cdot f_4 \cdot f_5} + \frac{t_4}{f_4 \cdot f_5} + \frac{t_5}{f_5} + t_6 \quad (4)$$

This means that $\varphi_{search} = 1 - (t_{handle} \cdot \chi_5)$. In some cases, when predators decrease foraging when full or digesting, it may be appropriate to also include t_7 , digestion, as part of t_{handle} or to make φ_{forage} a function of digestion time (e.g. Jeschke et al., 2002). The equation for φ_{search} can be inserted into equation (2) above, rearranged and solved for FR , arriving at the following final formulation (see equations SI-12 - SI-14 in appendix S1 for details):

$$FR = \chi_5 \cdot \varphi_{forage} = \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{1 + f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot t_{handle}} \quad (5)$$

Here it is clear that if $f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search}$ is replaced by Holling's encounter rate a , and t_{handle} is replaced by Holling's handling time h , we obtain the familiar functional response found in many textbooks

(e.g. Begon et al., 2005; Case, 2000):

$$FR = \frac{a \cdot N \cdot T_{forage}}{1 + a \cdot h \cdot N} \quad (6)$$

However, this only applies if handling time is defined as above (i.e. average time spent handling each *ingested* prey, or if $f_2=f_3=f_4=f_5=1$, i.e. the predator successfully detects, decides to attack, pursues, and subdues all encountered prey, so that $a=f_1 \cdot A_{search}$ and $h=t_2+t_3+t_4+t_5+t_6$). If handling time instead is defined as the average time spent handling each *encountered* prey this has important consequences for how the rest of the functional response is formulated (see section 3 of appendix S1).

Below we suggest an approach for linking traits or other factors to trophic interactions. It builds on the ATN approach of linking ‘success’ and ‘encounter’ to body size (Schneider et al., 2012, 2014; Vucic-Pestic et al., 2011), but expands this approach with the more explicit formulation of the functional response above. It thereby allows traits other than body size to affect these and additional steps of a trophic interaction. We show how this can be done by linking relevant traits or other factors directly and quantitatively to parameters ($f_k, A_{search}, t_{handle}, \varphi_{forage}$) of the functional and numerical response terms of a trophic interaction.

5. A worked-through example

When faced with an ecological community for which we want to explain trophic-interaction structure and dynamics, we begin by determining which steps to include as modules for a particular trophic interaction. Then, one can proceed by determining which factors affect the chosen modules and how they do so. An alternative is to determine which modules are impacted by the observed factor(s) and how, thereby explicitly relating this factor(s) to parameters. The model can be refined, if necessary, by adding further factors to the selected modules in the same manner, or by adding further modules, until the community is adequately described. To exemplify, we next use empirical data on four similar ground-beetle predators preying on aphids to demonstrate the approach. We identify the relevant modules and return to the frequently-used trait body size (see “Trait-based models”), and then illustrate how adding an environmental factor — temperature — can have a dramatic effect on the resulting trophic interaction strength.

Here we present a worked-through example for how a modular theory of trophic interactions may be applied (see Fig. 2 for the visual summary of this example). Note that this is not intended as an empirical test of the theory and that the model we arrive at is simply one possibility. Rather, this example is intended

to illustrate the process through which modules are selected and the relationship between modules and the factors affecting them is estimated and parameterized. A true application of this theory would, of course, need to be followed up by application to empirical data on interaction strengths or population dynamics. See Box 1 for a discussion of how to empirically estimate parameter values.

For our specific example, we use two similarly-sized small predators (*Bembidion lampros* and *Trechus secalis*) and two similarly-sized large predators (*Agonum dorsale* and *Pterostichus vernalis*) and their prey (aphids of species *Rhopalosiphum padi*). Trait values (i.e., body sizes, thermal optima, and thermal breadth of the predators) are shown in table 1; other parameters are in the supplementary material (table S1 and S2).

We start from the common realization (discussed above) that for many interactions, the ratio between predator and prey body size is a major determinant for interaction strength (e.g. Schneider et al., 2012, 2014) and appears to be a major factor driving trophic interactions in this system. This is largely due to metabolic requirements and the cost-benefit balance of consuming different sized prey. While these impacts relate to the steps pursuit and subjugation, predators need to be efficient in how they use their energy, so the body-size ratio presents a filter at the crucial, but frequently over-looked, step of *decision*: i.e., predators are more likely to *decide* to attack prey close to their optimal body-size ratio (R_{opt}). Predators will have weaker interactions the further prey are from that optimal size because they *decide* to attack them less frequently. Therefore, we could end up with the following parameterization of step 3, decision, based on predator and prey body size (B_C and B_N respectively):

$$f_3(B_C, B_N) \propto \frac{B_C}{B_N R_{opt}} e^{1 - \frac{B_C}{B_N R_{opt}}} \quad (7)$$

Body size is also relevant for the area searched by a predator in a given foraging interval, A_{search} , in the case of active foraging strategies, as larger predators and prey are more mobile. Mobility is here assumed to scale with the quarter power of body size (following Schneider et al., 2012, 2014). In our example, the prey, aphids, are largely stationary and their body size does not contribute to A_{search} :

$$A_{search}(B_C) \propto B_C^{0.25} \quad (8)$$

Because the aphid prey are largely stationary, mostly do not evade capture, and have limited camouflage

or refuge, we can use the simplifying assumption that all prey within the search area are encountered ($f_1 = 1$) and detected ($f_2 = 1$) and all prey the predator decides to attack are successfully pursued and subjugated ($f_4 = f_5 = 1$). This is clearly an oversimplification, but allows a simpler model focused on those modules and factors which have the largest impact on the interaction.

Handling time is also affected by body size. In this case, because the aphids are mostly stationary and do not evade capture, the time for detection, decision, pursuit, and subjugation are minimal relative to the time for searching and consumption (i.e., $t_2 \approx t_3 \approx t_4 \approx t_5 \approx 0$, $t_6 > 0$). Time taken for consumption (t_6) depends on the body-size ratio between predator and prey, where larger predators are faster at consuming prey, and smaller prey are faster to consume:

$$t_6(B_C, B_N) \propto \frac{B_N}{B_C} \quad (9)$$

Now the general framework has been parameterized by one factor, body size, and we can next explore which interactions are not explained adequately and which factors could be added to explain those. For example, these interactions occur across a range of temperatures and species differ in their thermal tolerances, impacting trophic interactions (Grigaltchik et al., 2012). Each of the four predators has a different thermal niche, and their activity level and proportion of time spent foraging (φ_{forage}) varies with temperature (Ben Feit & Mattias Jonsson *pers. comm.*). This is a critical factor as rising temperatures may result in otherwise unexplained changes in trophic interaction strengths. Temperature can also affect handling time and mobility due to its effect on metabolism (e.g. Sentis et al., 2012; Vucic-Pestic et al., 2011), but here we focus on the effect on foraging time as the driving factor affecting interaction strength. With field-measured data on the optimum and standard deviation of each predator’s thermal niche, we can as a first approximation, use the probability density function of a normal distribution to determine the effect of temperature ($temp$) on φ_{forage} (Rall et al., 2012):

$$\varphi_{forage}(temp) \propto \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{1}{2}\left(\frac{temp-\mu}{\sigma}\right)^2} \quad (10)$$

Where $temp$ is the temperature, μ is the species optimum temperature, and σ is the standard deviation of the predator’s temperature niche. Individuals spend the most time foraging (largest φ_{forage}) when at their temperature optimum.

Combined and simplified, our model would look like this:

$$FR = \chi_5 \cdot \varphi_{forage} = \frac{f_3 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{1 + f_3 \cdot t_{handle} \cdot A_{search} \cdot N} \quad (11)$$

Where:

$$\begin{aligned} f_3(B_C, B_N) &= f_{3,0} \frac{B_C}{B_N R_{opt}} e^{1 - \frac{B_C}{B_N R_{opt}}} \\ A_{search}(B_C) &= A_0 B_C^{0.25} \\ t_{handle}(B_C, B_N) &= t_{6,0} \frac{B_N}{B_C} \\ \varphi_{forage}(temp) &= \varphi_0 \frac{1}{\sigma \sqrt{2\pi}} e^{-\frac{1}{2} \left(\frac{temp - \mu}{\sigma} \right)^2} \end{aligned} \quad (12)$$

$f_{3,0}$, A_0 , $t_{6,0}$ and φ_0 are all scaling parameters. We can now insert empirically measured values for body size (B_C and B_N) and thermal niche optima (μ) and thermal niche standard deviations (σ) into the model to predict how prey consumption will change across temperature and body size and realize that including temperature niches in the model has a dramatic effect (Fig. 3). Especially at low temperatures, where *Pterostichus vernalis*, one of the larger predators, is mostly inactive, predictions using only body size dramatically overestimate its impact on aphids (Fig. 3). Note that this is simply a rough first prediction using previous knowledge of the effect of body size on mobility and handling time, and empirical observations of the effect of temperature on foraging time. To test this model or make quantitative inferences would require a fit to data (see Box 1 for a discussion of how to do so).

Overall, this example illustrates the process of breaking down the interaction into steps, deciding which steps to include as modules, considering which factors affect those modules, and the importance of being able to add additional factors such as temperature niches. Additionally, it shows how interaction strengths can be a function of the environment, and how to incorporate that relationship into a model. This is a crucial element when studying communities in a changing climate. Finally, this example illustrates how we may take information from multiple sources (e.g. previously published relationships between body size and *decision* and *ingestion* from Schneider et al. 2012 and empirically measured activity data for temperature's effect on φ_{forage}) to put together the modular model.

In parameterizing this model, we have made several assumptions and simplifications. The strength of this approach, however, is that it requires one to be very clear about what assumptions are being made.

This is true of both the biological knowledge about the species and the mathematical formulation of both which module(s) is affected and how the factor(s) affects this module(s). Such a transparent and systematic approach comes with the inherent advantage of creating a strong and explicit link between the biology of species, the environmental context, and the dynamical model. These links are often unclear, hampering the application of models to real communities. If the predictions from our framework do not match the empirical data, the next factor or module to add should be easier to find because the assumptions were clear from the start.

Table 1: Body size, thermal optima and thermal breadth (standard deviation) for four predator carabid beetles.

	Optimum (°C)	Breadth (°C)	Size (mg)
<i>Bembidion lampros</i>	23.5	9.9	1.61
<i>Trechus secalis</i>	15.6	5.7	1.96
<i>Agonum dorsale</i>	19.9	9.0	10.53
<i>Pterostichus vernalis</i>	31.0	7.2	9.55

6. Next steps

The value of a modular approach to trophic interactions will increase the more it is applied and as we thereby increase the reference library against which we can compare an interaction. The obvious next step, therefore, is to apply it to a range of interactions. To truly test this approach requires first building the models while being explicit in their assumptions and simplifications, as we did in section 5, then applying the predictions of the models to empirical data, and finally refining the model in a modular fashion as required. In Box 1 we outline how our framework can be put to use by describing how parameters of the functional response function can be empirically estimated (Fig. 5) and the effect of traits analyzed (Fig. 6). As this approach is applied across different interaction types and environments, it will increase our fundamental understanding of trophic interactions. This in turn will improve our predictions of trophic interactions subjected to global change and the resulting impacts on community structure and dynamics.

To increase our fundamental understanding of how trophic interactions work and why and how they differ across species and environments, the modular approach should be applied across different interaction types, such as predation, pollination and herbivory, and in different types of ecosystem, e.g. aquatic and terrestrial. This will reveal which steps are most important generally and whether some steps are more important for certain interactions than others. An example could be that pursuit is more important in predator-prey interactions than for herbivorous interactions, with implications for the traits expressed by herbivores versus

predators. We will learn whether certain steps are more dependent on traits or on environmental factors (and therefore more susceptible to environmental change), whether traits or environmental factors can be grouped based on the steps they affect, and if the shape of the response function differs among steps (e.g. saturating vs sigmoid responses, Fig. 4). Currently, without the structuring framework of the modular approach, it is difficult to glean this fundamental understanding, as it is unclear whether an observed occurrence and outcome of an interaction depends on particular traits, the environment, type of interaction, step affected, or something else.

The modular approach can be used to identify knowledge gaps. When deciding which steps and factors are important for a particular trophic interaction or food web, any time the answer is "we don't know" is a potential new research question. This is true at a broad scale; rather than looking at the impact of, for example, a trait on the interaction as a whole, research can be more directly focused on the effect of the trait in a given step. It is similarly true at a narrow scale. If a model needs refining, an experiment can be focused on a particular step and the trait(s) affecting it, leading to a clearer, and/or more cost-effective, outcome than an experiment focused on the interaction as a whole. Results from previous research in similar ecosystems or on similar traits could be used as a baseline for a particular module, even if other modules need to be tailored specifically for the community at hand.

The modular approach can further be used to investigate interactive effects of traits, environmental factors, the presence of other individuals or species, and the internal state of the predator on each other and on the interaction (e.g. Jeschke et al., 2002; McCluney and Sabo, 2009; Schmitz, 2007; Terry et al., 2017). Traits and environment both affect trophic interactions, but environmental factors can also impact the effectiveness of traits (Sentis et al., 2014) as traits can alter susceptibility to environmental factors (e.g. Gownaris et al., 2015; Jacob et al., 2011). Such interactive effects can be incredibly difficult to understand in relation to trophic interactions or food-web dynamics. A modular approach provides a solution, as any module can easily be made into a function of one of these factors or their interaction. Clearly, the model can rapidly become unwieldy and, as with any model, the complexity level of the model should depend on the question and community of interest.

Through an increased fundamental understanding of trophic interactions and more directed research, the modular approach should produce better understanding and predictions of food-web structure and dynamics and the effect of climate change. A modular approach should greatly facilitate the formalisation of hypothesis testing the role of traits for determining trophic interactions into models. This is a hot topic in ecology for their promise of accurate predictions of trophic interactions without measuring each interaction separately

(Bartomeus et al., 2016; Morales-Castilla et al., 2015). Environmental factors affect different species and different steps in different ways. With a modular approach it becomes manageable to formalise, model, and predict the resultant impact on food-web dynamics.

The modular approach should be evaluated based on how it helps increase our fundamental understanding of trophic interactions, helps direct future research, helps us understand and model interactive effects, and to make more accurate predictions. The results of these applications will reveal whether trophic interactions really are the sum of their parts. Undoubtedly, our tentative theory can – and should – be extended and built upon. By laying out explicitly how we have broken down the predation process, and then how we have used those steps to build up a modular dynamic-model framework. Finally, a core strength of a modular theory of trophic interactions is that it is designed to be progressively built upon. It provides a format where predictions can be made now with available information on how traits or other factors affect interactions and refined as more information becomes available. The resulting models can be as simple or complex as need be.

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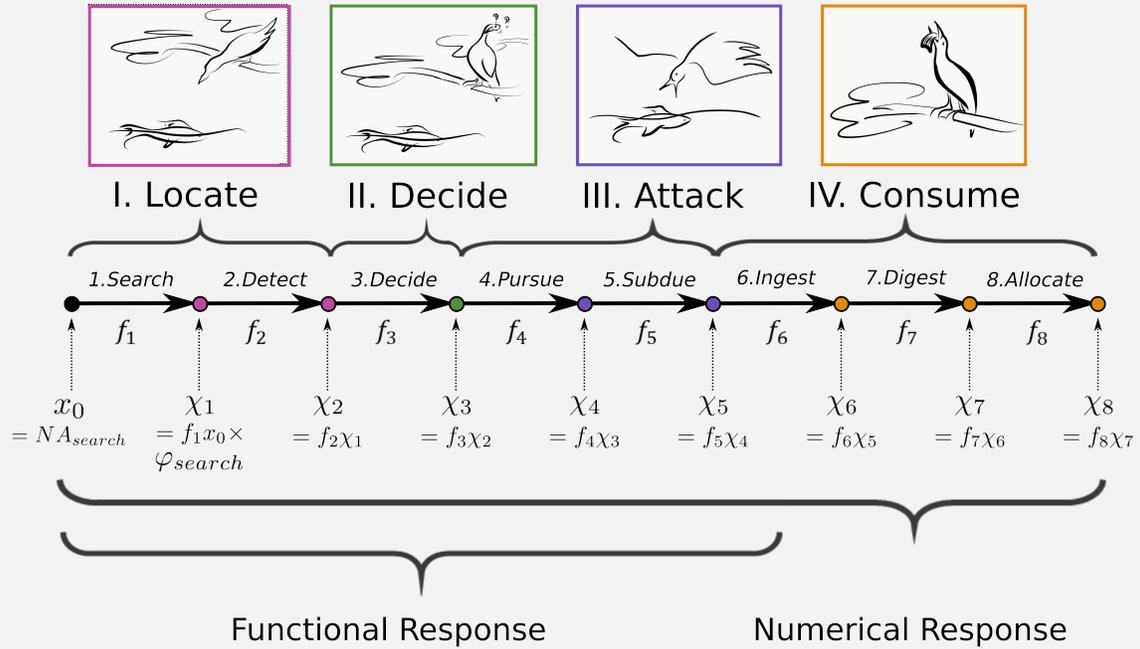
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Steps in a trophic interaction and their parameters



Examples of traits affecting each step

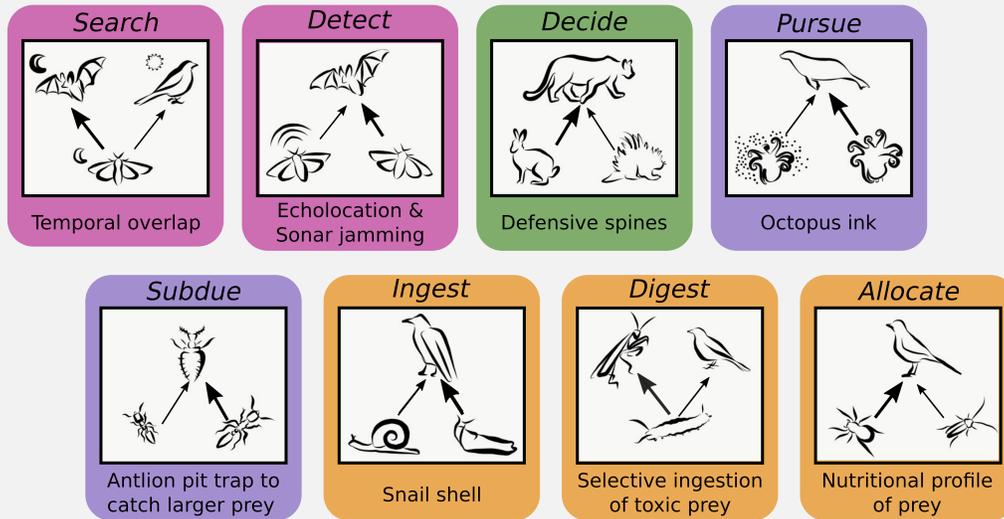
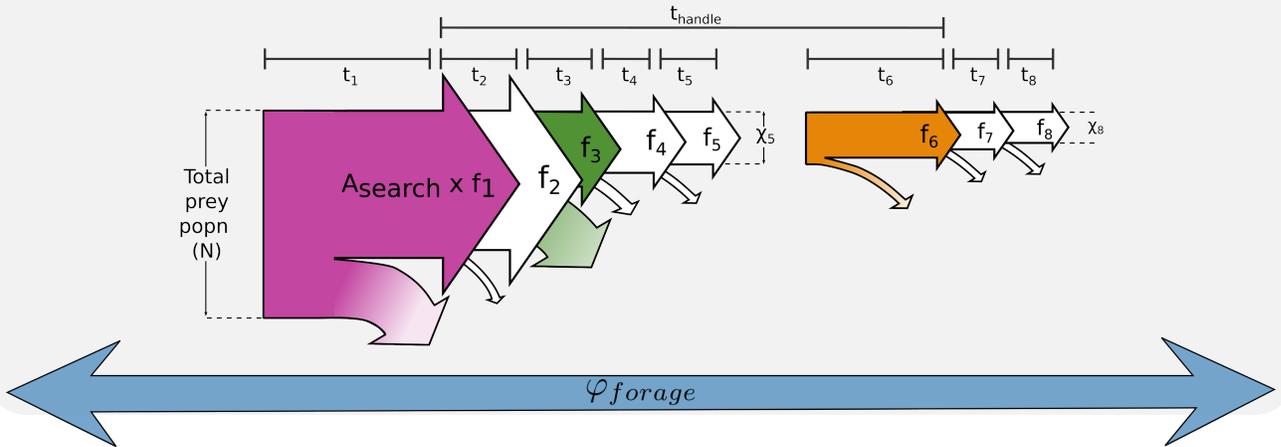


Figure 1: (Continued on the following page)

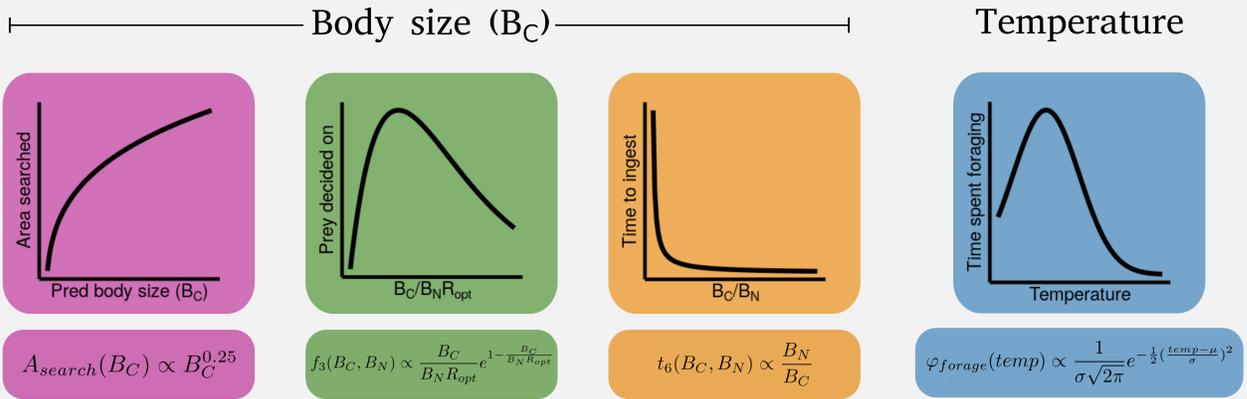
Figure 1: The eight steps (1. *search*, 2. *detect*, 3. *decide*, 4. *pursue*, 5. *subdue*, 6. *ingest*, 7. *digest*, and 8. *allocate*) of the pre-consumption (Functional response) and post-consumption (Numerical response) phases of a foraging cycle, and the four main stages (capitalized: I Locate, II Decide, III Attack, and IV Consume) that these steps can be aggregated into. N is the prey population, f_1 , f_2 , f_3 , f_4 , and f_5 describe the conditional probability that each prey individual is encountered, detected, decided upon, pursued, and subdued, while f_6 , f_7 , and f_8 describe the proportion of subdued prey (χ_5) that are ingested, digested, and allocated to reproduction respectively, per area searched (A_{search}) and per proportion of foraging time spent searching (φ_{search}). Steps 1-5 make up the functional response (here expressed per unit available foraging time), while the final three steps are also included in the numerical response. (Note that to be expressed on a per unit total time the functional and numerical response equations also need to be multiplied by φ_{forage} , the proportion of total time available for foraging).

Sketches in the lower half of the figure give examples of interactions where the conditional probability or proportion of the step occurring (i.e. f_x) is strongly dependent on the illustrated predator and/or prey traits. The thicker arrow in each example shows which of the two interactions has a higher probability of that step occurring, based on the match between predator and prey traits. *Search*: Moths are active at night, avoiding temporal overlap and therefore encounter with birds, but retaining it with nocturnal bats. *Detect*: Bats have developed sonar to help locate their prey in the dark, but some moths have developed methods of jamming sonar, essentially becoming invisible to the bat (Corcoran and Conner, 2012). *Decide*: Porcupines have spines that dissuade potential predators from attacking them, relative to unprotected prey such as hares (Mori et al., 2014). *Pursue*: Octopi release ink to distract and confuse their predators, making pursuit more difficult. *Subdue*: Ant lions have pits to capture their ant prey, enabling them to catch and subdue larger individuals than they otherwise would (Kuszevska et al., 2016). *Ingest*: The shell of a snail makes them more difficult to ingest than unprotected slugs. *Digest*: Monarch caterpillars are toxic, preventing most predators from successfully attacking them. Chinese praying mantises, however, remove the gut of the caterpillar and discard the toxic plant compounds, enabling them to digest and assimilate the otherwise toxic prey (Rafter et al., 2013). *Allocate*: By consuming prey of higher nutritional content, including protein, fat, and also micronutrients (e.g., spiders and Coleoptera rather than Blattodea), insectivorous birds allocate more nutrients to growth and reproduction per unit of consumed prey (Razeng and Watson, 2015).

Selection of modules



Effect of traits and environment on selected modules



A modular functional response

$$FR = \frac{f_3 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{1 + f_3 \cdot t_{handle} \cdot A_{search} \cdot N}$$

$A_{search}(B_C) = A_0 B_C^{0.25}$

$f_3(B_C, B_N) = f_{3,0} \frac{B_C}{B_N R_{opt}} e^{1 - \frac{B_C}{B_N R_{opt}}}$

$t_{handle}(B_C, B_N) = t_{6,0} \frac{B_N}{B_C}$

$\varphi_{forage}(temp) = \varphi_0 \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{1}{2}(\frac{temp-\mu}{\sigma})^2}$

Figure 2: (Continued on the following page)

Figure 2: An overview of how the modular theory of trophic interactions may be applied to build a modular dynamic model parameterized by traits (here, body size) and environmental factors (here, temperature). This example is fully described in section 5 "A worked-through example". The effect of the eight modules are suggested by the arrows in the top panel (the exact effect depending on which trait or environmental variables are involved). The width of the arrow indicates the cumulative probability of the predation process succeeding up until that step (f_x), while the length of the arrow gives a rough indication of how long the step takes (t_x). Those steps with a low probability of success are indicated by a wider arrow diverting from the predation process (relative to the width of the arrow continuing forward). In this particular example, we select three important steps as well as φ_{forage} , the proportion of time the predator spends foraging (selected steps and φ_{forage} shown in color in the first panel), where body size and temperature make a substantial impact on the probability of the step occurring, or time taken, and these we select as modules to build the model from. These three steps are: search (f_1), decision (f_3), and ingestion (f_6). Body size affects search area (A_{search}), because larger species move further. Body size is important for decision because predators *decide* to attack prey close to their optimum body size. Body size affects the time required for ingestion (as suggested by the longer arrow), which limits a predator's ability to exploit other prey. The primary effect of temperature is on time spent foraging, φ_{forage} . Close to the optimum of their thermal niche, predators spend more time foraging (larger φ_{forage}), which means more time repeating the foraging process and therefore a stronger interaction. Once modules are selected, we estimate the shape of the relationship between the trait (body size) or environmental factor (temperature) and the probability of the step occurring or time taken. These modules are then put together into a full model.

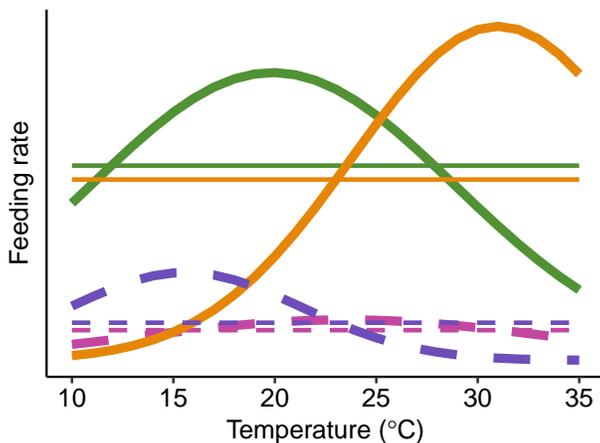
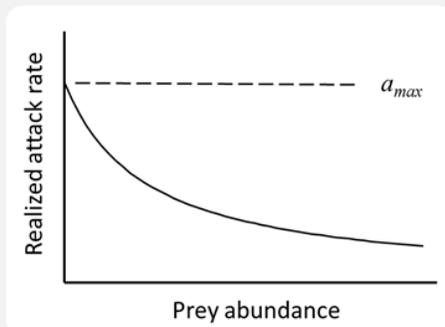


Figure 3: Model-predicted feeding rates (number of prey individuals - aphids of species *Rhopalosiphum padi*, 0.155mg - consumed per unit time by an individual predator) for four different predatory ground beetles as a function of temperature, using the model in Eq. (11) parameterized by empirical values. The thinner, horizontal lines show the predicted number of prey consumed if temperature niche is not included in the model. *Bembidion lampros* (pink) and *Trechus secalis* (purple) are similar size and are indicated by dashed lines. *Agonum dorsale* (green) and *Pterostichus vernalis* (orange) are similar size, and indicated by solid lines. Each predator has a different thermal niche (Table 1) leading to differences in interaction strength across temperature.

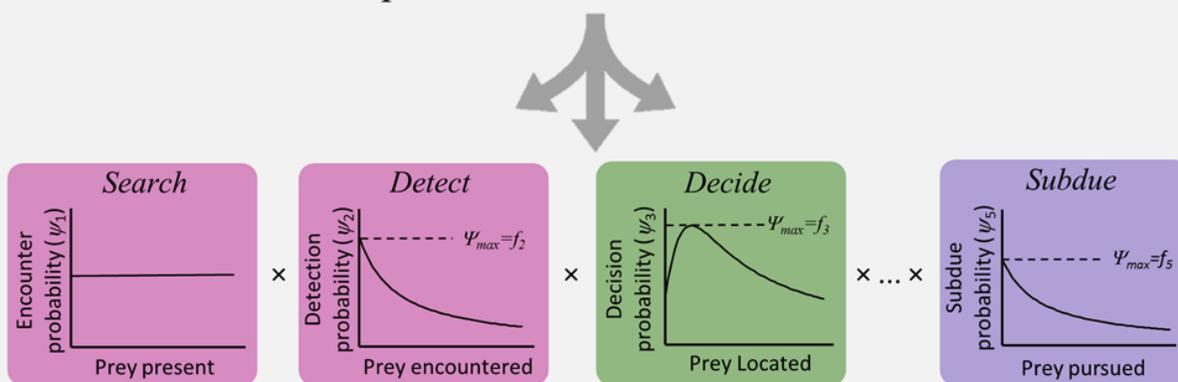
Traditional composite proportional functional response function:

One function to summarize the result of all steps in a trophic interaction



Or, one function to describe the process in one step of a trophic interaction that is believed to be of overwhelming importance (e.g. subjugation)

Trophic interaction factorization



Acknowledgement that multiple steps in a trophic interaction may be important and that focusing on each step will lead to a more nuanced understanding of trophic interactions and what drives them

Figure 4: Hypothetical factorization of a composite functional response into separate predator success rates (or proportional functional responses) for individual steps of the predation cycle. This can be an approach for studying and acknowledging various response functions for different foraging steps. In this example, *search* is assumed to display a more or less type I response (so that the proportion of prey present per unit area that are encountered is constant), while *decision* and *subjugation* follow a type II responses (with the success rate decreasing monotonically) and *Detection* displaying a type III response. Note that here, f_k is a *parameter* describing the probability of that step occurring successfully for a particular predator-prey combination (see Box 1).

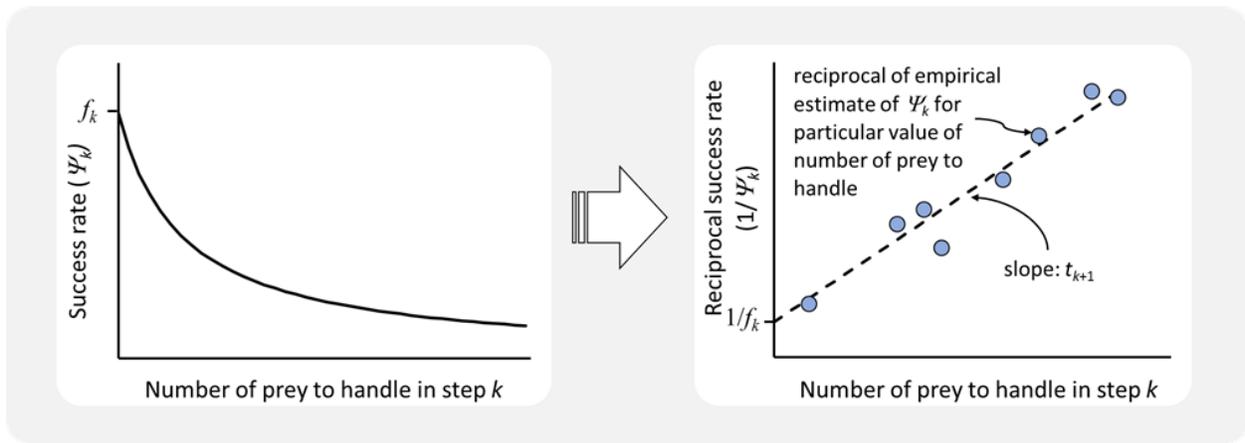


Figure 5: Illustration of an approach for estimating f_k and t_{k+1} of a saturating response function from empirical data using linear regression. Note that here f_k and t_{k+1} are *parameters* for a particular predator-prey combination (see Box 1).

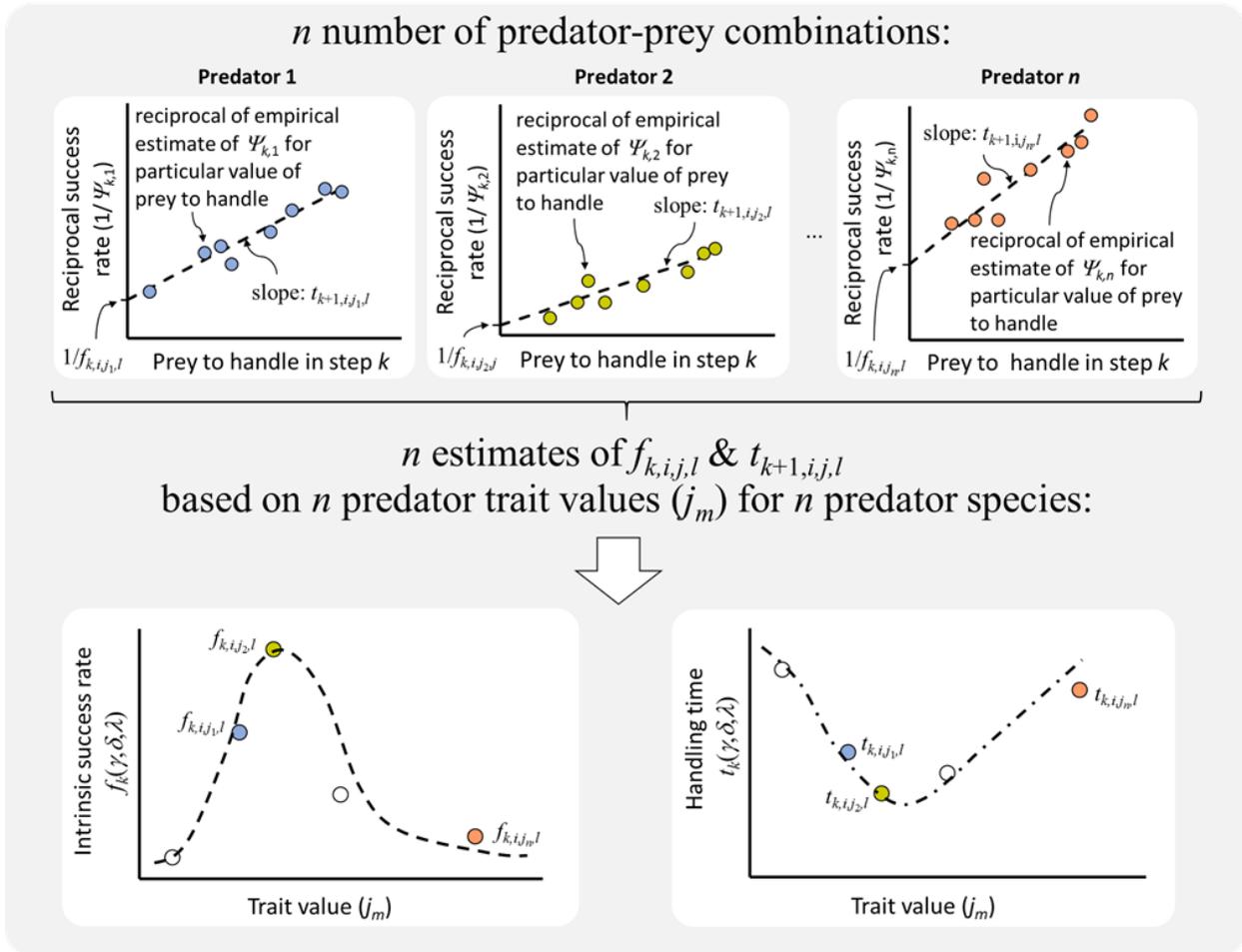


Figure 6: An approach for testing theoretical predictions of how species traits may affect $f_k(\gamma, \delta, \lambda)$ and $t_k(\gamma, \delta, \lambda)$. Combining the results of multiple estimates of $f_{k,i,j,l}$ and $t_{k+1,i,j,l}$ under the influence of different values of a relevant trait (upper subplots) will provide data for inferring how a trait value affects $f_k(\gamma, \delta, \lambda)$ and $t_k(\gamma, \delta, \lambda)$ (lower subplots). The form of the relationship between trait value and $f_k(\gamma, \delta, \lambda)$ and $t_k(\gamma, \delta, \lambda)$ is here only hypothetical. Furthermore, here, the potential effect of only one predator trait is illustrated, but it could as well be a prey trait (or both) and in theory the combined effects of several traits could be analysed in a similar way (using multivariate techniques)

Box 1 - How to empirically estimate parameter values

The modular functional response (Eq. 5) we lay out in section 4.2 assumes that, for each step k included as a module, we know or can measure f_k (the probability that step k is successful) and t_k (how long step k takes). Measuring f_k and t_k is not always trivial, and in this box we outline an approach for estimating them empirically. Here it is important to make a distinction between $f_k(\gamma, \delta, \lambda)$ and $t_k(\gamma, \delta, \lambda)$ as *functions of variable* prey traits (γ), predator traits (δ) and/or environmental factors (λ), versus $f_{k,i,j,l}$ and $t_{k,i,j,l}$ as *parameters* for *fixed* prey (i) and predator (j) traits and/or environmental factors (l). If we have a model applicable to multiple species with different trait values and/or across a range of one or more environmental conditions, $f_k(\gamma, \delta, \lambda)$ and $t_k(\gamma, \delta, \lambda)$ are *functions* of those traits and environmental variables. We can then apply these functions to a specific predator-prey pair with fixed traits and at fixed environmental conditions, to obtain the *parameters* $f_{k,i,j,l}$ and $t_{k,i,j,l}$. Alternatively, by measuring the values of $f_{k,i,j,l}$ and $t_{k,i,j,l}$ at multiple trait and/or environmental conditions, we can establish the shape of $f_k(\gamma, \delta, \lambda)$ and $t_k(\gamma, \delta, \lambda)$ as *functions* of those factors.

$f_{k,i,j,l}$ (the *parameter*) describes the *intrinsic* success of step k . This means $f_{k,i,j,l}$ quantifies the success of step k when unaffected by handling time. To accurately measure $f_{k,i,j,l}$ directly, therefore, requires measuring the success rate with a very small number of prey (approaching zero) to be handled, which may not always be feasible. An alternative approach, which also allows for the simultaneous estimation of $t_{k+1,i,j,l}$, is to measure the *realized* success rate (ψ_k) at a range of prey densities, and then use linear (or non-linear) regression to estimate both $f_{k,i,j,l}$ and $t_{k+1,i,j,l}$ (See Fig. 5 for an example using linear regression). This approach is similar to how attack rate (a) and handling time (h) of Holling's 'composite' Type II functional response are often estimated (e.g. Vucic-Pestic et al., 2011). The advantage of our approach, however, is the explicit recognition that steps may have different functional response shapes (Fig. 4).

We start by factorizing the composite functional response (Eq. 5) into separate *proportional* functional responses (ψ_k) for each step (Eq. 13 is equivalent to Eq. 5, see appendix S2):

$$FR = \psi_1 \cdot \psi_2 \cdot \psi_3 \cdot \psi_4 \cdot \psi_5 \cdot N \cdot A_{search} \cdot \varphi_{forage} \quad (13)$$

ψ_k describes how the success of step k depends on the number of prey entering step k from step $k - 1$

(χ_{k-1}) and the time available for step k (which is negatively affected by t_{k+1} , the time consumed by the following step, see appendix S2). Assuming a saturating form of the response function:

$$\psi_k = \frac{f_{k,i,j,l}}{1 + f_{k,i,j,l} \cdot t_{k+1,i,j,l} \cdot \xi_{k-1}} \quad (14)$$

where ψ_k is the ‘realized success function’ of step k , or the actual (as opposed to intrinsic) proportion of prey that are ‘handled successfully’ in step k . By regressing empirical data for $1/\psi_k$ on ξ_{k-1} , one can obtain $1/f_{k,i,j,l}$ and $t_{k+1,i,j,l}$ as the intercept and slope, respectively, of the regression line (Fig. 5).

Factorizing the functional response function as in Eq. (13) also allows for different forms of the proportional response functions (ψ_k) for separate steps of the predation cycle, e.g. combining saturating and sigmoid responses for separate steps (Fig. 4).

This procedure could be used to estimate values for $f_{k,i,j,l}$ and $t_{k+1,i,j,l}$ of each module k included in the model. More importantly, however, this also allows experimental tests of theoretical predictions of how species traits or other factors may affect f_k and t_{k+1} . To do this, $f_{k,i,j,l}$ and $t_{k+1,i,j,l}$ for a certain step k should be estimated for different values of important traits or other factors. The estimated values of $f_{k,i,j,l}$ and $t_{k+1,i,j,l}$ (using the approach in Fig. 5) can then be plotted as functions of the trait(s) to determine the shape of the functions $f_k(\gamma, \delta, \lambda)$ and $t_k(\gamma, \delta, \lambda)$ (Fig. 6).

We believe that the approach outlined here can provide a strategy for advancing trophic ecology by starting to build a library for how species traits (and other factors) affect trophic interaction strengths for major types of predator-prey combinations. This approach allows for the incorporation of traits of particular importance to a given interaction, in contrast to the super-generality of the current ATN approach across all kinds of predator and prey interactions. At the same time, it allows for comparison across diverse interactions to find generalities, rather than advocating for the idiosyncrasy of individual interactions. Experiments as outlined above should provide empirical data to make scientifically based conclusions on the existence of such generalities.

SUPPORTING INFORMATION FOR:

Toward a modular theory of trophic interactions

K. L. Wootton, A. Curtsdotter, T. Roslin, R. Bommarco, and T. Jonsson

This Supporting Information includes the following:

1. **Appendix S1.** Derivation of the functional response of predators from basic principles and its implications.
2. **Appendix S2.** Factorization of the functional response by separating steps of the predation cycle.
3. **Table S1.** Effect of body size and thermal niche on parameter values of the dynamic model described in the main text.
4. **Table S2.** Parameter values for the model represented in figure 3 of the main text.

Appendix S1. Derivation of the functional response of predators from basic principles and its implications

Summary

Here we define the basic steps of foraging, use these to revisit the derivation of the functional response of predators and arrive at a formulation of the single predator-single prey functional response that is more process explicit than the classic formulation (Holling 1959a). We then show how this formulation can be extended to situations with multiple prey or predators. Finally, we indicate briefly how the allometric trophic network (ATN) model approach (Otto et al. 2007, Berlow et al. 2009, Schneider et al. 2012) which links body size to underlying parameters of the functional response, fits with this revised formulation of the functional response.

1. Background

Solomon (1949) introduced the term ‘functional response’ to describe the change in the number of prey consumed by individual predators in response to ‘increased availability of victims’ (i.e. prey density) and Holling (1959b) identified three basic forms: a linear response, a saturating response and a sigmoid response (later termed type I, type II and type III, Fig S1). In the original mathematical derivation of the functional response (Holling, 1959a, based on a now classic experiment using sandpaper dishes), two main processes of foraging were considered: searching for prey, and handling of discovered prey. These led to the standard formulation of the saturating (type II) functional response (FR), for the number of prey killed per predator, replicated in many textbooks (e.g., Case 2000, Begon et al. 2005):

$$(SI-1) \quad FR = \frac{aNT_{forage}}{1+ahN}$$

Here a was termed the ‘discovery rate of prey’ (or by later authors ‘encounter rate’ or ‘attack rate’), while h is the ‘handling time’ of prey, N the density of prey, and T_{forage} the time available for foraging. Handling time can either be defined as (i) the average time to handle each *encountered* prey, or (ii) the average time to handle each *ingested* prey. As will be seen below, how handling time (h) is defined has important consequences for how the rest of the functional response equation should be formulated. For reasons outlined below, we advocate defining handling time in terms of the average time to handle each *ingested* prey.

Although highly influential (by capturing the essence of the saturating functional response and being able to replicate empirically observed data), this formulation is based on a series of simplifying assumptions that hampers development of quantitative, process-explicit models, where model parameters have been linked to species traits. More specifically, this formulation lumps a number of steps of the foraging process (predation cycle) that may need to be separated to see how parameters could be linked to traits. Here, we derive the functional response of predators from basic principles, essentially following T. J. Case (An illustrated guide to theoretical ecology, 2000, Ch. 11), but without lumping potentially important steps or assuming that all encountered prey are detected, decided upon, and successfully pursued

and subjugated. This leads to a modified, more explicit, and potentially more mechanistically useful formulation of the functional response relative to the classic formulation (Holling 1959a), with implications for how to develop the ATN model approach (Schneider et al. 2012) by including (additional) traits that are explicitly linked to different sequential parts of a predators foraging activity.

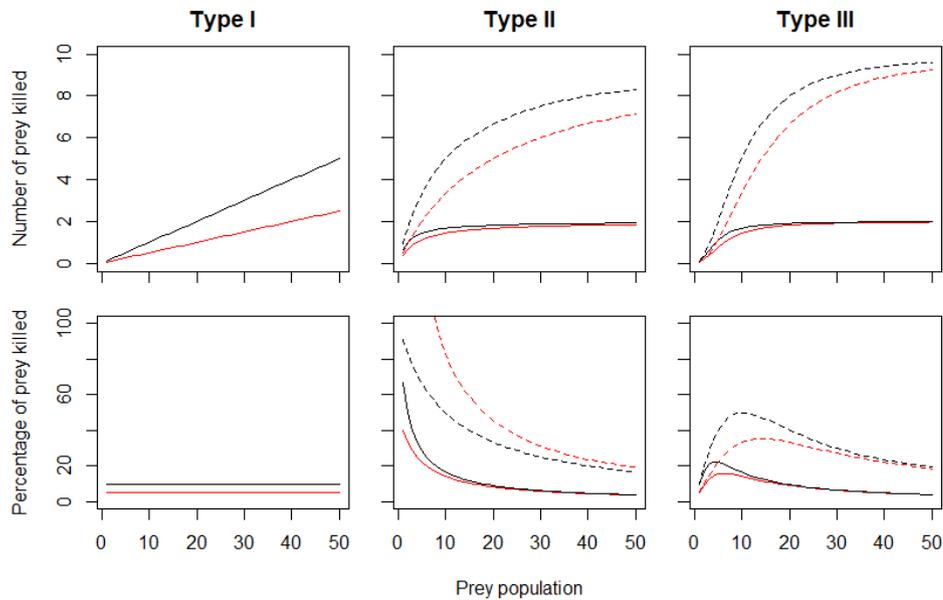


Fig S1. The three different functional responses and how they respond to different parameter values. The first row shows the number of prey consumed, while the second row shows the percentage of the prey population consumed. Black lines indicate an attack rate twice the magnitude of red lines (0.1 and 0.05 respectively for Type I and II, 0.01 and 0.05 respectively for Type III). Solid lines indicate a handling time five times the magnitude of dashed lines (0.5 and 0.1 respectively).

When foraging, a predator must (1) *search* for, (2) *detect*, (3) *decide* to exploit, (4) *pursue*, and (5) *subdue* a potential prey item, and then (6) *ingest*, (7) *digest*, and (8) *allocate* the immobilized prey to growth and reproduction (Fig. 1, main text). These eight steps can be aggregated into four stages; (I) Location, (II) Decision, (III) Attack and (IV) Consumption. In addition to simplifying for conceptual purposes, these four stages (with the exception of Decision, which tends to be overlooked) more closely match the way the predation process is broken up in the literature (e.g., Griffiths 1980, O’Brien et al. 1990, Jescke et al 2002, Vucic-Pestic et al 2011, Bateman et al. 2014). Many studies do break one or more of these stages into finer steps (and each of the eight steps we use have at least been mentioned by previous work), but for tractability, many studies implicitly do as we advocate here; omit steps, assume they equal one, and/or aggregate steps. The element that we advocate that these studies often miss is the explicit acknowledgement of which steps they are omitting or aggregating. The eight steps we use here are the coarsest division of the predation process that takes into account all steps we found mentioned in the literature. Although the predation process could be sliced into ever thinner pieces, the eight steps we present here are sufficiently specific that they capture each important element of a trophic interaction, and yet are sufficiently broad to apply to any type of trophic interaction, including predation,

herbivory, parasitism, and pollination. However, should further steps be necessary, by explicitly laying out our framework here it should be clear how to add steps as required.

The basic assumptions here, as with Holling (1959a) and Case (2000), are that predators, while foraging, move randomly in search of prey (or prey move randomly to encounter a sit-and-wait predator), and that the time available for searching for prey is negatively affected by the other activities of foraging. The more time that is spent on handling prey, the less is available for searching for new prey. These assumptions can be relaxed by appropriate formulations of relevant parameters, as discussed below. Thus, crucial to the derivation presented below is if and how the different activities of the predation cycle may affect one another. In general, one step will influence another step if (i) it determines the number of prey that will enter the next step (the flow-through rate from one step to another), or (ii) it affects the time available for the other step. Here, every step has the potential to affect the following step by controlling the number of prey that will enter the next step, and thus also the time that will be spent on handling prey in that step. Consequently, with a limited time for a predator to forage (T_{forage} , itself potentially a function of traits), the more time that is spent on one activity the less will be available for another. The time spent on searching is the most important for our derivation because this is the gateway to all subsequent activities of foraging; in other words, without searching there will be no prey to attack or consume. For the derivation of the functional response, we (and Holling 1959a and Case 2000) focus on how the time available for foraging is divided among the different activities of the predation cycle and, more specifically, how the time available for searching (T_{search}) is affected by the time spent handling prey in the other steps of the predation cycle.

Of the eight steps of foraging identified here, only the second to sixth (detection to ingestion), directly affect the time available for searching, while the last, allocation, does not (in most cases). This is because when the predator is handling a prey item in any of step 2-6 it (normally) cannot search for new prey, while it can when in step 8 (but see Stouffer & Novak 2021 for a discussion of when this assumption may not apply. Such scenarios can be accounted for here by changing the formulation of t_{handle} (Eq. SI-10).). The effect of digestion (step 7) might be intermediate, or reach a threshold, with small amounts of prey to digest not significantly affecting foraging, but larger amounts effectively stopping a predator from searching for new prey. Digestion may also affect the time spent foraging (T_{forage}) by its effect on hunger (see Jeschke et al 2002 for how to integrate this into a model). Acknowledging these caveats, for the derivation below, we assume that only the first six steps of a predators' foraging are relevant, because the total time available for searching for prey will be negatively affected by the amount of time spent handling prey in step two to six, but not by step seven and eight. This assumption can easily be modified to the predation type in question.

2. Derivation of the functional response

Here, we focus on how to combine the steps of the predation cycle into a description of a 'single predator-single prey functional response', i.e. how the number of prey of one type (species) that one predator individual subjugates, changes with the abundance of the prey. This can then easily be expanded to include presence of alternative prey as well as effects of

multiple predators (e.g interference competition and fear of intraguild predation; see section 3.2-3.3 below).

The predation cycle starts with the activity of searching and here f_1 is the proportion of all prey individuals ($x_0 = x_{Tot}$) present within the area searched (scanned) by a predator that are encountered¹ per unit available search time. x_1 is the number of prey successfully searched for (encountered) per unit available search time. f_2 is the proportion of encountered prey that are detected, f_3 is the proportion of detected prey that the predator decides to pursue, f_4 is the proportion of decided upon prey that are successfully pursued and caught and f_5 is the proportion of caught prey that are successfully subdued. Thus (per unit search time):

$$(SI-2) \quad \begin{cases} (2a): x_{Encountered} = x_1 = f_1 \cdot x_0 \\ (2b): x_{Detected} = x_2 = f_2 \cdot x_1 \\ (2c): x_{Decided} = x_3 = f_3 \cdot x_2 \\ (2d): x_{Pursued} = x_4 = f_4 \cdot x_3 \\ (2e): x_{Subdued} = x_5 = f_5 \cdot x_4 \end{cases}$$

The total number of prey individuals present (x_0) within the area searched (A_{search}) per unit available search time by a predator is simply: $x_0 = A_{search} \cdot N$ (where N is the density of prey)². Thus, (assuming random movement of a predator species and/or its prey in a single uniform habitat) the number of individuals of the prey encountered per predator, χ_1 , per unit foraging time, should depend on (i) the area scanned per unit available search time per predator (A_{search}), (ii) the density of prey (number of individuals per unit area, N), (iii) the encounter probability of present prey (f_1) and (iv) the proportion of foraging time spent

searching, $\varphi_{search} = \frac{T_{search}}{T_{forage}}$, as:

$$(SI-3) \quad \chi_{Encountered} = \chi_1 = f_1 \cdot x_0 \cdot \varphi_{search} = f_1 \cdot A_{search} \cdot N \cdot \varphi_{search}.$$

Note that from here and onwards we switch from “ x_k ”, denoting the number of prey encountered/detected/decided on/pursued/subdued in step k per unit *search* time, to “ χ_k ”, denoting step success per unit *foraging* time. The reason not all prey present within A_{search} are encountered may be because prey have access to safe hiding places (refuges) where they are completely hidden and thus safe from a predator. This may include differences in phenology or diurnal activity if prey are hidden and inactive while the predator is searching. The encounter probability (f_1) can therefore be interpreted as the proportion of prey that are out of hiding (i.e. $1 - f_1$ would be a measure of prey in safe refuges) and x_1 as the number of prey

¹ The proportion of the individuals within the scanned area that a predator could potentially detect and kill. The predator and prey do not need to meet each other, be in physical contact with each other, or detect each other.

² If A_{search} equals the unit of area used to describe population abundance then $x_0 = N$.

which come within the sensory range of the predator, even if they are not necessarily detected.

Assuming that the predator is not perfectly efficient in detecting all the encountered prey, the detection probability (f_2) is the proportion of prey that are exposed (not in a safe refuge) that the predator detects³. This means that the number of prey individuals detected (per unit foraging time), χ_2 , is⁴:

$$(SI-4) \quad \chi_2 = f_2 \cdot \chi_1 = f_1 \cdot f_2 \cdot A_{search} \cdot N \cdot \varphi_{search}$$

We assume that the predator will decide to attack a proportion f_3 of all detected prey, that a proportion f_4 of these will be successfully pursued, and that a proportion f_5 of these will be subdued (generally killed in a predator-prey interaction). This means that (a) the number of prey individuals that a predator decides to pursue (χ_3), (b) the number of prey caught (χ_4), and (c) the number of prey subdued (χ_5), respectively, per predator (per unit foraging time), can be described as⁵:

$$(SI-5) \quad \begin{cases} (5a): & \chi_3 = f_3 \cdot \chi_2 = f_1 \cdot f_2 \cdot f_3 \cdot A_{search} \cdot N \cdot \varphi_{search} \\ (5b): & \chi_4 = f_4 \cdot \chi_3 = f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot A_{search} \cdot N \cdot \varphi_{search} \\ (5c): & \chi_5 = f_5 \cdot \chi_4 = f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot \varphi_{search} \end{cases}$$

Because time available for searching, T_{search} , is dependent on the time taken to handle prey during other steps and therefore the number of prey a predator handles, it can be useful to express χ_5 in terms of the more consistent handling time. Although we in our contribution argue that $A_{search}, f_1, f_2, f_3, f_4$ and f_5 , will be functions of species traits and settings when considering multiple predator-prey combinations and environmental conditions, for a given predator-prey combination (i.e. fixed traits) and consistent environmental conditions they will evaluate to constants and can be considered parameters (see Box 1 in the main text for further discussion). Thus, during the derivation of the functional response below, we assume the latter (i.e. the terms $A_{search}, f_1, f_2, f_3, f_4$ and f_5 are parameters that represent fixed average values across all predator individuals for particular predator-prey combination that are not affected by prey or predator abundance).

The time available for searching, T_{search} , is the amount of time left when total time for handling prey (T_{handle} = time for detection, decision, pursuit, subjugation and ingestion) has been subtracted from the total time spent foraging, T_{forage} :

$$(SI-6) \quad T_{search} = T_{forage} - T_{handle} = T_{forage} - T_{detect} - T_{decide} - T_{pursue} - T_{subjugate} - T_{ingest}$$

If the total time for handling prey (T_{handle}) is a positive linear function of the number of prey to be handled in the respective steps, so that time available for searching (T_{search}) becomes a

³ In Case (2000) no distinction is made (as is here) between prey in refuges and exposed prey difficult to detect.

⁴ In Case (2000) $f_1 \cdot f_2 \cdot A_{search}$ is denoted by a and termed 'the prey encounter rate'.

⁵ In Case (2000) it is assumed that all encountered prey are detected, deemed suitable and profitable to pursue and successfully subjugated (=killed), i.e. $f_2 = f_3 = f_4 = f_5 = 1$.

negative linear function of the number of prey to be handled, this will result in a saturating type II functional response. A sigmoid type III functional response may occur if, for example, f_2 , detection, is positively related to prey abundance. Assuming that total time for detection, decision, pursuit, subjugation and ingestion all are linearly related to the average times to (i) detect each encountered prey individual (t_2), (ii) decide on each detected prey individual (t_3), (iii) pursue each decided upon prey (t_4), (iv) subjugate each caught prey (t_5) and (v) ingest each subjugated (killed) prey respectively (t_6), then:

$$(SI-7) \quad \left\{ \begin{array}{l} (7a): T_{detect} = t_2 \cdot \chi_1 \cdot T_{forage} \Rightarrow \varphi_{detect} = \frac{T_{detect}}{T_{forage}} = t_2 \cdot \chi_1 \\ (7b): T_{decide} = t_3 \cdot \chi_2 \cdot T_{forage} \Rightarrow \varphi_{decide} = \frac{T_{decide}}{T_{forage}} = t_3 \cdot \chi_2 \\ (7c): T_{pursue} = t_4 \cdot \chi_3 \cdot T_{forage} \Rightarrow \varphi_{pursue} = \frac{T_{pursue}}{T_{forage}} = t_4 \cdot \chi_3 \\ (7d): T_{subjugate} = t_5 \cdot \chi_4 \cdot T_{forage} \Rightarrow \varphi_{subjugate} = \frac{T_{subjugate}}{T_{forage}} = t_5 \cdot \chi_4 \\ (7e): T_{ingest} = t_6 \cdot \chi_5 \cdot T_{forage} \Rightarrow \varphi_{ingest} = \frac{T_{ingest}}{T_{forage}} = t_6 \cdot \chi_5 \end{array} \right.$$

Note that T_k is the *total* time required for step k (and has the units of ‘total time’) and thus increases as the number of prey entering that step increases. t_k , in contrast, is the *average* time taken for step k per prey individual “handled” in step k (and thus has units of time per prey).

Since

$$(SI-8) \quad \chi_{k+1} = f_{k+1} \times \chi_k \Leftrightarrow \chi_k = \frac{\chi_{k+1}}{f_{k+1}},$$

equation SI-7 can be reformulated, all as functions of χ_5 :

$$(SI-9) \quad \left\{ \begin{array}{l} (9a): T_{detect} = \frac{t_2}{f_2 \cdot f_3 \cdot f_4 \cdot f_5} \cdot \chi_5 \cdot T_{forage} \\ (9b): T_{decide} = \frac{t_3}{f_3 \cdot f_4 \cdot f_5} \cdot \chi_5 \cdot T_{forage} \\ (9c): T_{pursue} = \frac{t_4}{f_4 \cdot f_5} \cdot \chi_5 \cdot T_{forage} \\ (9d): T_{subjugate} = \frac{t_5}{f_5} \cdot \chi_5 \cdot T_{forage} \\ (9e): T_{ingest} = t_6 \cdot \chi_5 \cdot T_{forage} \end{array} \right.$$

Eqs. SI-9a – SI-9e can be collected to describe the total foraging time not spent on searching, but that is spent on handling prey, as a function of the ‘average handling time’ (t_{handle}):

$$\begin{aligned}
(SI-10) \quad T_{handle} &= T_{detect} + T_{decide} + T_{pursue} + T_{subjugate} + T_{ingest} = \\
&= \left(\frac{t_2}{f_2 \cdot f_3 \cdot f_4 \cdot f_5} + \frac{t_3}{f_3 \cdot f_4 \cdot f_5} + \frac{t_4}{f_4 \cdot f_5} + \frac{t_5}{f_5} + t_6 \right) \cdot \chi_5 \cdot T_{forage} = \\
&= t_{handle} \cdot \chi_5 \cdot T_{forage}
\end{aligned}$$

Here t_{handle} is the average handling time per ingested prey (= the time that on average has been spent on detection, decision, pursuit, subjugation and ingestion to result in one ingested prey). Note that t_2 (detection) and t_3 (decision) include the time for ‘negative detections’ and ‘negative decisions’, respectively, and similarly that t_4 , t_5 and t_6 include the time for unsuccessful pursues, unsuccessful subjugations and incomplete ingestion respectively. Inserting Eq. SI-10 into Eq. SI-6 yields:

$$(SI-11) \quad T_{search} = T_{forage} - t_{handle} \cdot \chi_5 \cdot T_{forage} = T_{forage} (1 - t_{handle} \cdot \chi_5) \Rightarrow \varphi_{search} = 1 - t_{handle} \cdot \chi_5$$

Now, inserting Eq. SI-11 into Eq. SI-5c gives:

$$\begin{aligned}
(SI-12) \quad \chi_5 &= f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot \varphi_{search} = \\
&= f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot (1 - t_{handle} \cdot \chi_5) = \\
&= f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N + \\
&\quad - f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot t_{handle} \cdot \chi_5
\end{aligned}$$

Rearranging Eq. SI-12 results in a somewhat familiar expression for a saturating type II functional response, expressed per unit available foraging time:

$$(SI-13) \quad \chi_5 = \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N}{1 + f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot t_{handle} \cdot N}$$

Thus, expressing the functional response (FR) as the number of prey killed per predator per unit total time, T_{Tot} , (where $\varphi_{forage} = T_{forage}/T_{Tot}$):

$$(SI-14) \quad FR = \chi_5 \cdot \varphi_{forage} = \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot \varphi_{forage}}{1 + f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot t_{handle} \cdot N}$$

Eq. SI-14 is the general relationship for the functional response of every foraging process that can be decomposed into the basic steps outlined in Fig. 1, main MS,

assuming (i) that the number of prey to be handled in every step is a cumulative proportion of the prey being handled in the preceding steps (= Eq. SI-5), (ii) that total handling time in every step is linearly related to the average time to handle a single prey individual in each step (= Eq. SI-7) and (iii) that A_{search} , f_1 , f_2 , f_3 , f_4 and f_5 are constants and with t_{handle} defined as in Eq. SI-10.

2.1. ALTERNATIVE FORMULATION OF THE FUNCTIONAL RESPONSE BY AGGREGATING STEPS OF THE PREDATION CYCLE INTO STAGES

Instead of using all eight steps, we can simplify the derivation by using only the four stages Location, Decision, Attack, and Consumption. Using only four stages may be appropriate in some cases, but limits the ability to link different traits to particular parameters and so, in general, we recommend starting from all eight steps and then deciding to remove those steps which are least relevant. However, because previous research frequently utilizes groupings of steps similar to these four stages, we present this option here for comparison with that research. Eq. SI-14 can be rewritten (and simplified) by grouping the steps *search* and *detect* into the stage of Location and grouping the steps *pursuit* and *subjugation* into Attack. That is, denoting $A_{search} \cdot f_1 \cdot f_2$ with γ_{Loc} , and $f_3 \cdot f_4$ with γ_{Att} , SI-Eq. 14 reads:

$$(SI-15) \quad FR = \chi_5 \cdot \varphi_{forage} = \frac{\gamma_{Loc} \cdot f_3 \cdot \gamma_{Att} \cdot N \cdot \varphi_{forage}}{1 + \gamma_{Loc} \cdot f_3 \cdot \gamma_{Att} \cdot t_{handle} \cdot N}$$

3. Implications of more explicit formulation of functional response

3.1. COMPATIBILITY WITH CLASSIC HOLLING FORMULATION AND EXISTING ATN MODEL APPROACH

How the foraging cycle of a predator is split into stages or steps and how handling time is defined, have important implications for the final formulation of the functional response equation, and should depend on the type of predator considered. Essentially, there are two ways to reach the classic Holling equation (SI-1) from our modular functional response (SI-14). Either we assume that attack rate, a , from SI-1 is the aggregate of the success of each step (i.e. $a = f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5$), OR we assume that $f_2 = f_3 = f_4 = f_5 = 1$, and that $a = f_1$. In the latter case, it does not matter how handling time is defined. In the former case, however, SI-14 can only be equivalent to SI-1 if handling time is defined as the average handling time per *ingested* prey (taking failures in each step into account, Eq. SI-10), not per *located* prey. It may seem like a trivial difference, but here we demonstrate its implications.

For a consumer with a very simple foraging behaviour, such as sedentary filter feeders (e.g. sponges and bivalves), the processes of detection, decision, pursuit and subjugation may be irrelevant so that $f_2 = f_3 = f_4 = f_5 \approx 1$ and $t_2 = t_3 = t_4 = t_5 \approx 0$. This implies that $t_{handle} \approx t_6$ (i.e. the average time to ingest a captured food particle) and means that Eq. 14 simplifies to (with $A_{search} = 1$):

$$(SI-16) \quad FR = \chi_5 \cdot \varphi_{forage} = \frac{f_1 \cdot N \cdot \varphi_{forage}}{1 + f_1 \cdot t_{consume} \cdot N}$$

This recovers the classic Holling equation perfectly. However, in many cases, predators have a more complex foraging behaviour where detection, decision, pursuit and/or subjugation are separate processes in the foraging cycle, clearly distinguishable from consumption (so that $f_2 \neq f_3 \neq f_4 \neq f_5 < 1$ and $t_2 \neq t_3 \neq t_4 \neq t_5 > 0$). In these cases, the full version of the functional response equation (Eq. SI-14) provides a more realistic representation of the ingestion rate of

these predators. This will also aid in linking species traits in a more nuanced way to parameters of the functional response. Here it is important to also note that handling time as

defined in Eq. SI-14 (where $t_{handle,1} = \frac{t_2}{f_2 \cdot f_3 \cdot f_4 \cdot f_5} + \frac{t_3}{f_3 \cdot f_4 \cdot f_5} + \frac{t_4}{f_4 \cdot f_5} + \frac{t_5}{f_5} + t_6$), is the

average handling time per ingested prey. This is the sum of the time it takes for a predator to detect, decide on, pursue, subjugate and ingest a prey item. The time for each of these activities increases as the proportions of prey not detected, decided on, pursued, and subjugated increases. In the ecological literature, however, handling time is often not clearly defined (i.e. what it includes and/or what the prey unit is) or sometimes (e.g., Case 2000) defined as the average handling time of each encountered prey. The latter definition, which here corresponds to:

$$(SI-17) \quad t_{handle,2} = t_2 + t_3 \cdot f_2 + t_4 \cdot f_2 \cdot f_3 + t_5 \cdot f_2 \cdot f_3 \cdot f_4 + t_6 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5$$

is the sum of the proportion of foraging time it takes for a predator to identify, detect, decide on, pursue, subjugate and ingest each *encountered* prey. The smaller the proportion of success for each step, the smaller $t_{handle,2}$ becomes, relative to $t_{handle,1}$. The definition of handling time (as the average time to handle each encountered or the average time to handle each killed prey) is crucial because this has important consequences for how the rest of the functional response equation is formulated. Defining handling time as in Eq. SI-17 leads to a functional response formulation significantly different from Eq. SI-14:

$$(SI-18) \quad FR = \chi_5 \cdot \varphi_{forage} = \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot \varphi_{forage}}{1 + f_1 \cdot A_{search} \cdot t_{handle,2} \cdot N}$$

If $f_2 \cdot f_3 \cdot f_4 \cdot f_5$ does not equal one, then SI-18 is not equivalent to SI-1, because $f_1 \neq f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5$ and thus they cannot both be denoted with a . In most real situations (for predators which are not passive filter-feeders), $f_2 \cdot f_3 \cdot f_4 \cdot f_5 < 1$, illustrating that if handling time is defined as $t_{handle,2}$ above, the classic Holling expression is a simplification based on potentially unrealistic assumptions.

Because Eq. SI-14 is a more explicit formulation of the functional response than Eq. SI-1, it allows species traits to more easily be linked to parameters of the functional response (see below). Attempts in this direction have already been developed, most notably within the framework of the ATN model approach (Otto et al. 2007, Berlow et al. 2009, Schneider et al. 2012). We argue, however, that, although laudable, this effort now needs to be developed (and possibly also adjusted depending on how handling time is defined). More specifically, Vucic-Pestic et al. (2011) and Schneider et al. (2012) argued that a in Eq. SI-1 could be described as the product of two processes: ‘success’ \times ‘encounter’, with Eq. SI-1 interpreted as (with $T_{forage} = 1$):

$$(SI-19) \quad FR = \frac{\text{'encounter'} \cdot \text{'success'} \cdot N}{1 + \text{'encounter'} \cdot \text{'success'} \cdot \text{'handling time'} \cdot N}$$

Encounter was argued to depend on predator and prey speed, and Schneider et al. (2012) suggested that it should scale allometrically with predator (W_j) and prey (W_i) body size as:

$a_0 W_i^{0.25} W_j^{0.25}$ (where a_0 is a scaling constant). *Success* was argued to describe the predators’

‘ability to subdue prey of different sizes’ and suggested to scale as $\left(\frac{W_j/W_i}{R_{opt}}\right) e^{\left(1-\frac{W_j/W_i}{R_{opt}}\right)^\theta}$

(where R_{opt} is the optimal predator-prey body mass ratio of the predator, and θ a constant determining the width of the success curve). *Handling time* was the time required for processing and digesting one prey item’, and suggested to scale as $h_0 W_i^{0.25} W_j^{-0.25}$. It is unclear if this means the average handling time per encountered prey or the average handling time per ingested prey (see above for mathematical definitions). As discussed above, how handling time is defined is crucial since it affects how the rest of the functional response equation is formulated (either as Eq. SI-14 or SI-18). If handling time is defined as the average time per *encountered* prey, then we would expect to only see “encounter” in the denominator of SI-19. The ATN model approach clearly represents a significant and important step towards linking parameters of predator-prey models to species traits and several studies have used this approach to parameterize models that attempt to replicate observed predator-prey dynamics, either from controlled experiments (Schneider et al. 2012, 2014, Jonsson et al. 2018) or from field surveys (Curtsdotter et al. 2019). If γ_{Loc} and γ_{Att} in Eq SI-16 are interpreted as ‘encounter’ and ‘success’, respectively, in Schneider et al. (2012), and f_3 is assumed to equal unity, Eq. SI-20 (the Schneider et al. formulation) is identical to Eq. SI-14 (our more detailed formulations of the functional response, with $\phi_{forage} = 1$).

On the one hand, suggesting how trophic interaction strengths may be affected by body sizes, the approach of Schneider et al (2012) represents a significant step forward by showing how ‘success’, ‘encounter’ and handling time may quantitatively be linked to predator and prey body sizes. This will be very useful for future research. On the other hand, we show here that unless handling time is defined as in Eq. SI-10, and f_3 assumed to equal unity, Eq. SI-14 cannot be recovered from Eq. SI-19. Furthermore, by aggregating steps search and detect into ‘location’ and steps pursuit and subjugation into ‘success’ important details on how various species traits affect different parts of the foraging of a predator may be obscured

3.2. MULTIPLE SPECIES

The presence of other species can affect trophic interactions in a number of different ways (Terry et al. 2017, Jonsson et al. 2018) and the dynamic model and functional response we describe above can easily be extended to include some effects of multiple prey and/or predators. As examples of such effects, (i) the time spent handling one prey species will usually leave less time to handle other prey species (see e.g. Koen-Alonso, 2007) (ii) the chance of encountering prey may increase if the prey’s response to a second predator makes them more visible to the focal predator (e.g. Losey & Denno, 1998; Prasad & Snyder, 2010), thus affecting f_1), (iii) predators may decrease the proportion of time they spend foraging if they are avoiding their own predators or interfering with other predators (e.g. Preisser et al. 2007), thus affecting ϕ_{forage} and/or ϕ_{search} , and (iv) predators may strategically choose one

prey species over another based on their nutritional needs and the availability of alternate prey (e.g. McCluney & Sabo, 2009; Razeng and Watson, 2015), thus affecting f_3 . Each of these effects, and others, can be incorporated into a model by making the appropriate terms of the general model (i.e. φ_{forage} , φ_{search} , f_k , t_k , A_{search}) a function of the presence of other species. Here we explicitly demonstrate this for handling multiple resources (3.2.1), predator interference (3.2.2), and fear of predation (3.2.3).

3.2.1. MULTIPLE PREY

If the predator has several different prey types (species) to choose from, this can affect the predator's foraging in many ways. The predator may develop preferences for different prey or become more experienced at handling a particular prey depending on their abundances. This could be incorporated in the functional response by allowing one or more of the probability parameters (i.e. $f_1 - f_5$), and/or the time components of t_{handle} (i.e. $t_2 - t_6$), to be functions of prey abundance. This has the capacity of turning a type II functional response into a type III functional response. However, the simplest and most straightforward effect of multiple prey on the foraging of a predator is its effect on searching time (see Koen-Alonso, 2007).

If additional prey only affect the time available to predator j for searching for prey (with m different prey types available to predator j) and assuming that the predator searches for all prey at the same time, Eq. SI-14 can easily be extended to account for multiple prey (note that this is not always the case (Stouffer & Novak 2021), and what follows could be parameterized differently to account for different scenarios). This is done in the traditional way by adding an expression for the time spent handling other prey items (species) to the denominator of the functional response equation. To show this, first, modify the expression for available search time (Eqs. SI-6 & SI-7) by taking time to handle all types of prey into account (here, R_j is the set of resource species to species j):

$$\begin{aligned}
 T_{search} &= T_{forage} - \sum_{m \in R_j} T_{handle,m} = T_{forage} - \sum_{m \in R_j} (t_{handle,m} \cdot \chi_{m,5} \cdot T_{forage}) = \\
 \text{(SI-20)} \quad &= T_{forage} \left(1 - \sum_{m \in R_j} (t_{handle,m} \cdot \chi_{m,5}) \right)
 \end{aligned}$$

Now, inserting Eq. SI-20 into Eq. SI-6c (and observing that components of $f_1 - f_5$ are predator-prey specific) gives (per unit foraging time):

(SI-21)

$$\begin{aligned}
\chi_{i,j,5} &= f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i \cdot \varphi_{search} = \\
&= f_{5,i,j} \cdot f_{4,i,j} \cdot f_{3,i,j} \cdot f_{2,i,j} \cdot f_{1,i,j} \cdot A_{search,i,j} \cdot N_i \cdot \left(1 - \sum_{m \in R_j} (t_{handle,m,j} \cdot \chi_{m,j,5}) \right) = \\
&= f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i \cdot \left(1 - t_{handle,i,j} \cdot \chi_{i,j,5} + \right. \\
&\quad \left. - \sum_{m \neq i} (t_{handle,m,j} \cdot \chi_{m,j,5}) \right) = \\
&\quad \left[\begin{aligned}
\chi_{m,j,5} &= \frac{\chi_{i,j,5}}{\chi_{i,j,5}} \cdot \chi_{m,j,5} = \chi_{i,j,5} \cdot \frac{\chi_{m,j,5}}{\chi_{i,j,5}} = \\
&= \chi_{i,j,5} \cdot \frac{f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot A_{search,m,j} \cdot N_m \cdot \varphi_{search}}{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i \cdot \varphi_{search}} = \\
&= \chi_{i,j,5} \cdot \frac{f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot A_{search,m,j} \cdot N_m}{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i} \end{aligned} \right] = \\
&\quad = A_{search,i,j} \cdot N_i \cdot f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot \\
&\quad \cdot \left(1 - t_{handle,i,j} \cdot \chi_{i,j,5} + \right. \\
&\quad \left. - \sum_{m \neq i} \left(t_{handle,m,j} \cdot \chi_{i,j,5} \cdot \frac{f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot A_{search,m,j} \cdot N_m}{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i} \right) \right) = \\
&\quad = A_{search,i,j} \cdot N_i \cdot f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot \\
&\quad \cdot \left(1 - \chi_{i,j,5} \cdot \sum_{m \in R_j} t_{handle,m,j} \cdot \frac{f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot A_{search,m,j} \cdot N_m}{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i} \right) = \\
&\quad = A_{search,i,j} \cdot N_i \cdot f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} + \\
&\quad - \chi_{i,j,5} \cdot \sum_{m \in R_j} t_{handle,m} \cdot f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot A_{search,m,j} \cdot N_m
\end{aligned}$$

Rearranging Eq. SI-21 (and multiplying by φ_{forage}) results in an expression for a saturating type II functional response with multiple prey (per unit total time):

$$\text{(SI-22) } FR = \chi_{i,j,5} \cdot \varphi_{forage} = \frac{A_{search,i,j} \cdot N_i \cdot f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot \varphi_{forage}}{1 + \sum_{m \in R_j} (t_{handle,m,j} \cdot f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot A_{search,m,j} \cdot N_m)}$$

Now, $A_{search,i,j} \neq A_{search,m,j}$ if mobility of prey m is different from that of prey i . Thus, if mobility of prey m is NOT different from that of prey i (so that $A_{search,i,j} = A_{search,m,j} = A_{search}$) and with $A_{search} = 1$ this simplifies to:

$$(SI-23) \quad FR = \chi_{i,j,5} \cdot \varphi_{forage} = \frac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot N_i \cdot \varphi_{forage}}{1 + \sum_{m \in R_j} (f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot t_{handle,m,j} \cdot N_m)}$$

The implication of this is that in a ‘multiple prey species situation’, differences in mobility of the different prey species become important, since they affect the encounter rates between the predator and the different prey species and need to be accounted for.

3.2.2. PREDATOR INTERFERENCE

Predators can interact in many different ways, for example indirectly via resource competition, directly via interference competition or by affecting the behaviour of one another (e.g. due to ‘fear of predation’). Indirect resource competition (where consumption of prey species i by predator species j reduces the availability of prey species i to predator species m , and vice versa) will immediately be covered by a predator-prey model based on Eq. SI-14 and expanded to multiple species where several predators feed on the same prey type. Focusing on predator interference (where predators interact physically) and assuming that it only affects a predator’s foraging by reducing the time available for searching, this can easily be accommodated in Eq. SI-14 (as mentioned above, however, interference may affect time for foraging as well, or instead). We do this in a similar way as accounting for multiple prey, by describing the decrease in available search time due to contacts with intra- and/or interspecific competitors. This results in an expression for a saturating type II functional response with multiple interacting predators. First, modify the expression for available search time (Eq. SI-6 and SI-7) by taking time to interfere with other predators into account (here, I_j is the set of species that species j has interference competition with):

$$(SI-24) \quad \begin{aligned} T_{search} &= T_{forage} - T_{handle,i,j} - \sum_{m \in I_j} T_{interfere,m,j} = \\ &= T_{forage} - T_{handle,i,j} - \sum_{m \in I_j} (t_{interfere,m,j} \cdot \chi_{m,j,Interfere} \cdot T_{forage}) \end{aligned}$$

Here, $\chi_{m,j,Interfere}$ is the number of individuals of species m that an individual of species j interferes with per unit time. Here it is assumed that for interference between predator species j and k to occur, the predator needs to encounter, detect and decide to interfere with the other species (while no steps similar to pursuit and immobilization should occur for interference). Now, inserting Eq. SI-24 into Eq. SI-6c (and performing the same steps as in Eq. SI-21 gives (per unit total time):

$$(SI-25) \quad FR = \chi_{i,j,5} \cdot \varphi_{forage} = \frac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i \cdot \varphi_{forage}}{1 + \left(f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot t_{handle,i,j} \cdot A_{search,i,j} \cdot N_i + \sum_{m \in I_j} (f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot t_{interfere,m,j} \cdot A_{search,m,j} \cdot N_m) \right)}$$

Similarly as above for multiple prey, $A_{search,i,j} \neq A_{search,m,j}$ if mobility of predators m that predator j interferes with is different from that of prey i . Conversely, if mobility of predators m is NOT different from that of prey i (so that $A_{search,i,j} = A_{search,m,j} = A_{search}$) and with $A_{search} = 1$ this simplifies to:

$$(SI-26) \quad FR = \chi_{i,j,5} \cdot \varphi_{forage} = \frac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot N_i \cdot \varphi_{forage}}{1 + \left(f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot t_{handle,i,j} \cdot N_i + \sum_{m \in I_j} (f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot t_{interfere,m,j} \cdot N_m) \right)}$$

The implication of this is that in a ‘multiple predator species situation’ with interference taking place, differences in mobility of the different predator species become important, and need to be accounted for, since they affect the encounter rates between focal predator and the other predator species it interferes with.

To summarize, the result of interference competition is described as a time loss on search time. Replacing $f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot t_{interfere,m,j} \cdot A_{search,m,j}$ with the parameter $c_{m,j}$, results in a general reformulation of Eq. 26, for the effect of intra- and interspecific interference competition that is the same as that used for intraspecific competition in the ATN model (with $A_{search,i,j} = 1$):

$$(SI-27) \quad FR = \chi_{i,j,5} \cdot \varphi_{forage} = \frac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot N_i \cdot \varphi_{forage}}{1 + \sum_{m \in I_j} (c_{m,j} \cdot N_m) + f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot t_{handle,i,j} \cdot N_i},$$

suggesting that $c_{m,j}$ could be related allometrically to body size as in Schneider et al. (2012).

If predator interference also has other (secondary) effects on a predator’s foraging, such as increasing the risk of physical injuries, this could also affect one or more of the probability components (f_1 - f_5), and/or the time components of t_{handle} (i.e. $t_2 - t_6$). This development is, however, outside the scope of this paper.

3.2.3. FEAR OF PREDATION

‘Fear of predation’ is when the presence of a predator affects the behaviour of another predator (e.g. due to intraguild predation) or prey species. The effect of this should be more complex than the simple one described above as a result of interference competition, since it can be expected that the effect is not only on the time available for searching in both species. Instead, it could be assumed that the effect is a reduction in the time available for searching in one species (due to induced inactivity and hiding in the one experiencing the ‘fear of predation’), but a decrease in the encounter rate in the other species (due to less exposed prey for the one causing the ‘fear of predation’). Assuming increasing encounters with individuals of species j causes a linear increase in the time species i spends hiding, the effect on species i ’s foraging can either be described as a direct decrease in the proportion of time spent foraging (φ_{forage}) or as a decrease in available search time (T_{search}). Here we take the latter

approach and modify the expression for available search time (Eq. SI-7) by subtracting time spent hiding ($t_{inactive,m,j}$) from each individual of species m of the set P_j of species inducing fear in species j .

$$(SI-28) \quad \begin{aligned} T_{search} &= T_{forage} - T_{handle,i,j} - \sum_{m \in P_j} T_{inactive,m,j} = \\ &= T_{forage} - T_{handle,i,j} - \sum_{m \in P_j} \left(t_{inactive,m,j} \cdot \chi_{m,j,Fear} \cdot T_{forage} \right) \end{aligned}$$

Here, $\chi_{m,j,Fear}$ is the number of individuals of species m , that upon meeting an individual of species j induces inactivity in species j , due to fear of predation, per unit foraging time. Here it is assumed that for inactivity of species j due to fear of predation from species m to occur, species j needs to encounter, detect and decide to become inactive for a period of time (while no steps similar to pursuit and immobilization should occur for fear of predation). Now, inserting Eq. SI-28 into Eq. SI-6c (and performing the same steps as in Eq. SI-21 gives:

$$(SI-29) \quad FR = \chi_{i,j,5} \cdot \varphi_{forage} = \frac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i \cdot \varphi_{forage}}{\left(f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot t_{handle,i,j} \cdot A_{search,i,j} \cdot N_i + \sum_{m \in P_j} \left(f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot t_{inactive,m,j} \cdot A_{search,m,j} \cdot N_m \right) \right)} \cdot 1 +$$

Similarly as above for interference and multiple prey, $A_{search,i,j} \neq A_{search,m,j}$ if mobility of predators m that induces fear in predator j is different from that of prey i . Conversely, if mobility of predators m is NOT different from that of prey i (so that $A_{search,i,j} = A_{search,m,j} = A_{search}$) and with $A_{search} = 1$ this simplifies to:

$$(SI-30) \quad FR = \chi_{i,j,5} \cdot \varphi_{forage} = \frac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot N_i \cdot \varphi_{forage}}{\left(f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot t_{handle,i,j} \cdot N_i + \sum_{m \in P_j} \left(f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot t_{inactive,m,j} \cdot N_m \right) \right)} \cdot 1 +$$

The implication of this is that in a ‘fear of predator situation’, differences in mobility of the different predator species become important, since they affect the encounter rates between focal predator and the other predator species that induces fear of predation behaviour and need to be accounted for. To summarize, the result of ‘fear of predation’ is as above described as an added time loss on search time. Replacing

$f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot t_{inactive,m,j} \cdot A_{search,m,j}$ with $b_0 \times \rho_j$, results in a general formulation for the effect of ‘fear of predation’ on the species experiencing it, and would recover the basic formulation in Laubmeier et al. (2018):

$$(SI-31) \quad \begin{aligned} FR &= \chi_{i,j,5} \cdot \varphi_{forage} = \\ &= \frac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot N_i \cdot \varphi_{forage}}{1 + \sum_{m \in P_j} \left(b_0 \cdot \rho_j \cdot N_m \right) + f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot t_{handle,i,j} \times N_i} \end{aligned}$$

suggesting that this could be modelled as in Laubmeier et al. (2018).

Finally, assuming that ‘fear of predation’ also has an effect on the species causing it, we need to find a way to describe this. The simplest assumption is probably that this results in a decrease in the encounter rate the species experiencing ‘fear of predation’ (due to inactivity and/or hiding behaviour of the prey). This development is also outside the scope of this paper.

4. References

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Appendix S2. Factorization of the functional response by separating steps of the predation cycle.

Remembering the definition of t_{handle} (Eq. SI-10), the full composite functional response (Eq. SI-14) can be factorized to give main text Eq. 12 as follows:

(SI-32)

$$\begin{aligned}
 FR &= \chi_5 \cdot \varphi_{forage} = \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{1 + f_1 f_2 f_3 f_4 f_5 \cdot t_{handle} \times N \cdot A_{search}} = \\
 &= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{1 + f_1 f_2 f_3 f_4 f_5 \times \left(\frac{t_2}{f_2 f_3 f_4 f_5} + \frac{t_3}{f_3 f_4 f_5} + \frac{t_4}{f_4 f_5} + \frac{t_5}{f_5} + t_6 \right) \cdot N \cdot A_{search}} = \\
 &= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{1 + (f_1 \cdot t_2 + f_1 f_2 \cdot t_3 + f_1 f_2 f_3 \cdot t_4 + f_1 f_2 f_3 f_4 \cdot t_5 + f_1 f_2 f_3 f_4 f_5 \cdot t_6) \cdot N \cdot A_{search}} = [\xi_0 = N \cdot A_{search}] = \\
 &= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{1 + f_1 \cdot t_2 \cdot \xi_0 + f_1 f_2 \cdot t_3 \cdot \xi_0 + f_1 f_2 f_3 \cdot t_4 \cdot \xi_0 + f_1 f_2 f_3 f_4 \cdot t_5 \cdot \xi_0 + f_1 f_2 f_3 f_4 f_5 \cdot t_6 \cdot \xi_0} = \\
 &= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{(1 + f_1 \cdot t_2 \cdot \xi_0) \cdot \left(1 + \frac{f_1 f_2 t_3 \xi_0}{1 + f_1 t_2 \xi_0} + \frac{f_1 f_2 f_3 t_4 \xi_0}{1 + f_1 t_2 \xi_0} + \frac{f_1 f_2 f_3 f_4 t_5 \xi_0}{1 + f_1 t_2 \xi_0} + \frac{f_1 f_2 f_3 f_4 f_5 t_6 \xi_0}{1 + f_1 t_2 \xi_0} \right)} = \left[\xi_1 = \frac{f_1 \cdot \xi_0}{1 + f_1 \cdot t_2 \cdot \xi_0} \right] = \\
 &= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{(1 + f_1 \cdot t_2 \cdot \xi_0) \cdot (1 + f_2 \cdot t_3 \cdot \xi_1) \cdot \left(1 + \frac{f_2 f_3 t_4 \xi_1}{1 + f_2 t_3 \xi_1} + \frac{f_2 f_3 f_4 t_5 \xi_1}{1 + f_2 t_3 \xi_1} + \frac{f_2 f_3 f_4 f_5 t_6 \xi_1}{1 + f_2 t_3 \xi_1} \right)} = \left[\xi_2 = \frac{f_2 \cdot \xi_1}{1 + f_2 \cdot t_3 \cdot \xi_1} \right] = \\
 &= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{(1 + f_1 \cdot t_2 \cdot \xi_0) \cdot (1 + f_2 \cdot t_3 \cdot \xi_1) \cdot (1 + f_3 \cdot t_4 \cdot \xi_2) \cdot \left(1 + \frac{f_3 f_4 t_5 \xi_2}{1 + f_3 t_4 \xi_2} + \frac{f_3 f_4 f_5 t_6 \xi_2}{1 + f_3 t_4 \xi_2} \right)} = \left[\xi_3 = \frac{f_3 \cdot \xi_2}{1 + f_3 \cdot t_4 \cdot \xi_2} \right] = \\
 &= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{(1 + f_1 \cdot t_2 \cdot \xi_0) \cdot (1 + f_2 \cdot t_3 \cdot \xi_1) \cdot (1 + f_3 \cdot t_4 \cdot \xi_2) \cdot (1 + f_4 \cdot t_5 \cdot \xi_3) \cdot \left(1 + \frac{f_4 f_5 t_6 \xi_3}{1 + f_4 t_5 \xi_3} \right)} = \left[\xi_4 = \frac{f_4 \cdot \xi_3}{1 + f_4 \cdot t_5 \cdot \xi_3} \right] = \\
 &= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{(1 + f_1 \cdot t_2 \cdot \xi_0) \cdot (1 + f_2 \cdot t_3 \cdot \xi_1) \cdot (1 + f_3 \cdot t_4 \cdot \xi_2) \cdot (1 + f_4 \cdot t_5 \cdot \xi_3) \cdot (1 + f_5 \cdot t_6 \cdot \xi_4)} = \\
 &= \frac{f_1}{1 + f_1 \cdot t_2 \cdot \xi_0} \cdot \frac{f_2}{1 + f_2 \cdot t_3 \cdot \xi_1} \cdot \frac{f_3}{1 + f_3 \cdot t_4 \cdot \xi_2} \cdot \frac{f_4}{1 + f_4 \cdot t_5 \cdot \xi_3} \cdot \frac{f_5}{1 + f_5 \cdot t_6 \cdot \xi_4} \cdot N \cdot A_{search} \cdot \varphi_{forage} = \\
 &= \psi_1 \cdot \psi_2 \cdot \psi_3 \cdot \psi_4 \cdot \psi_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}
 \end{aligned}$$

Here, $\psi_k = \frac{f_k}{1 + f_k \cdot t_{k+1} \cdot \xi_{k-1}}$ can be interpreted as ‘the proportional functional response of one step of the predation cycle’ with ξ_{k-1} being ‘the number of prey entering step k from step $k-1$ per unit aggregated step time up until step $k-1$ ’ and ξ_k thus being the rate of prey successfully handled in step k). Thus, ψ_k can be understood as ‘the realized proportion of prey handled in step k when handling in the following step is taken into account’ (since in a conveyer belt

system, to avoid pile-up/overflow, the numbers that can be processed in one station will ultimately be limited by the process rate in the following station).

To get a further understanding of the meaning of ψ_k and ξ_k above, the revised composite formulation of the functional response (Eq. SI-14) can be factorized along a different route, by remembering that

$$\frac{T_{search}}{T_{search} + T_2 + T_3 + T_4 + T_5 + T_6} = \frac{T_{search}}{T_{forage}} = \varphi_{search} = \frac{1}{1 + f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot t_{handle} \cdot N \cdot A_{search}}.$$

Thus:

(SI-33)

$$\begin{aligned} FR &= \chi_5 \cdot \varphi_{forage} = \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{1 + f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot t_{handle} \cdot N \cdot A_{search}} = \\ &= \frac{T_{Search}}{T_{Search} + T_2 + T_3 + T_4 + T_5 + T_6} \cdot f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage} = \\ &= \left[T_{forage} = T_{Search} + T_2 + T_3 + T_4 + T_5 + T_6 \right] = \\ &= \frac{T_{Search} \cdot (T_{Search} + T_2) \cdot (T_{Search} + T_2 + T_3) \cdot (T_{Search} + T_2 + T_3 + T_4) \cdot (T_{Search} + T_2 + T_3 + T_4 + T_5)}{(T_{Search} + T_2) \cdot (T_{Search} + T_2 + T_3) \cdot (T_{Search} + T_2 + T_3 + T_4) \cdot (T_{Search} + T_2 + T_3 + T_4 + T_5) \cdot T_{forage}} \\ &\quad \cdot f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage} = \\ &= \left[\frac{T_{Search}}{T_{Search} + T_2} \cdot f_1 \right] \cdot \left[\frac{T_{Search} + T_2}{T_{Search} + T_2 + T_3} \cdot f_2 \right] \cdot \left[\frac{T_{Search} + T_2 + T_3}{T_{Search} + T_2 + T_3 + T_4} \cdot f_3 \right] \cdot \\ &\quad \cdot \left[\frac{T_{Search} + T_2 + T_3 + T_4}{T_{Search} + T_2 + T_3 + T_4 + T_5} \cdot f_4 \right] \cdot \left[\frac{T_{Search} + T_2 + T_3 + T_4 + T_5}{T_{forage}} \cdot f_5 \right] \cdot N \cdot A_{search} \cdot \varphi_{forage} = \\ &= \zeta_1 \cdot \zeta_2 \cdot \zeta_3 \cdot \zeta_4 \cdot \zeta_5 \cdot N \cdot A_{search} \cdot \varphi_{forage} \end{aligned}$$

This implies that $\zeta_k = \psi_k$ or more specifically:

$$(SI-34) \quad \zeta_k = \frac{T_{Search} + \dots + T_k}{T_{Search} + \dots + T_{k+1}} \cdot f_k = \psi_k = \frac{f_k}{1 + f_k \cdot t_{k+1} \cdot \xi_{k-1}}$$

That $\zeta_k = \psi_k$ can be verified by noting that $\xi_k = \frac{T_{forage} \cdot \chi_k}{\sum_1^k T_i}$ and inserting this into Eq. SI-32.

This second factorization of the functional response suggests two alternative or complementary interpretations of $\frac{\psi_k}{f_k}$:

$$(SI-35) \quad \frac{\psi_k}{f_k} = \frac{1}{1 + f_k \cdot t_{k+1} \cdot \xi_{k-1}} = \frac{\zeta_k}{f_k} = \frac{T_{Search} + \dots + T_k}{T_{Search} + \dots + T_{k+1}}.$$

That is, either (i) as the ‘realized success function’ of step k (= the proportion of the intrinsic handling probability (f_k) that is realized’), or (ii) as ‘the proportion of foraging time from step 1 (= searching) to step $k+1$ that is available for steps 1 to k , (in other words, the proportion of foraging time from step 1 to step $k+1$ that is not ‘used’ by step $k+1$).

From the exercise above it can also be seen how χ_k (in Eqs. SI-3-5) is related to ξ_k :

$$(SI-36) \quad \xi_k = \frac{\chi_k}{\frac{1}{T_{forage}} \cdot \sum_1^k T_i} = \frac{\chi_k}{\varphi_{T_{search} \rightarrow T_k}} = x_k \cdot \frac{T_{search}}{\sum_1^k T_i}$$

This means that while χ_k is the rate of prey handling in step k per unit foraging time, ξ_k is the rate of prey handling in step k per unit step time up until step k .

To summarize, the proportional functional responses (ψ_k) above, factored out from the composite functional response, correspond to and have a similar meaning and form as the well-known ‘prey risk functions’ (i.e. FR/N , or the proportion of prey killed per predator) of a type II or type III functional response, albeit describing the realized predator success rate and prey risk for individual foraging steps.

Table S1. Effect of body size and thermal niche on parameter values of the dynamic model described in the main text.

Table S1. Effect of body size and thermal niche on parameter values of the dynamic model described in the main text, section “Assigning parameter values based on traits”. Data on temperature niches was obtained from B. Feit and M. Jonsson (pers. comm.). We calculated body masses from body lengths as reported in Banks et al (2016)¹.

Parameter	Effect	Explanation	Factor
A_{search}	$B_C^{0.25}$	Larger predators can cover more area when searching. This is scaled by metabolic rate. Prey are stationary. Based on ATN	Body size
f_1, f_2, f_4, f_5	1	Assuming stationary aphid prey which do not flee, all prey within the area searched will be encountered and detected, and all prey decided upon will be successfully pursued and subdued	NA
f_3	$\frac{B_C}{B_N R_{opt}} e^{-\frac{B_C}{B_N R_{opt}}}$	Predators will decide to attack prey close to their optimal prey size. Equation based on the Ricker function.	Body size
$t_2 - t_5$	0	Time for prey to detect and decide upon prey, and pursue and subjugate stationary aphid prey which they have encountered is sufficiently minimal that we can set these to zero to simplify our model.	NA
t_6	$\frac{B_N}{B_C}$	Larger prey take longer to handle and larger predators are faster at handling prey.	Body size
φ_{forage}	$\frac{1}{\sigma\sqrt{2\pi}} e^{-\left(\frac{temp-\mu}{2\sigma^2}\right)}$	Predators spend more time foraging when closer to the optimum of their thermal niche. Based on the probability density function for a normal distribution	Temperature

1: Banks, H. T. et al. (2016) Parameter Estimation for an Allometric Food Web Model. (Technical Report No. CRSC-TR16-03), CRSC Technical Reports. CRSC-TR16-03, Center for Research in Scientific Computation, North Carolina State University, Raleigh, May., Raleigh.

NA: Not applicable.

Table S2. Parameter values for the model represented in figure 3 of the main text.

Table S2. Parameter values for the model represented in figure 3 of the main text.

Parameter	Value
B_C	<i>Bembidion lampros</i> = 1.61 mg <i>Trechus secalis</i> = 1.96 mg <i>Agonum dorsale</i> = 10.53 mg <i>Pterostichus vernalis</i> = 9.55 mg
B_N	<i>R. padi</i> = 0.1550mg
R_{opt}	118 (from Jonsson et al 2018) ¹
σ	<i>Bembidion lampros</i> = 9.9 °C <i>Trechus secalis</i> = 5.7 °C <i>Agonum dorsale</i> = 9 °C <i>Pterostichus vernalis</i> = 7.2 °C
μ	<i>Bembidion lampros</i> = 23.5 °C <i>Trechus secalis</i> = 15.6 °C <i>Agonum dorsale</i> = 19.9 °C <i>Pterostichus vernalis</i> = 31.0 °C
<i>temp</i>	10-35°C
N	10 individuals

1: Jonsson, T. et al. (2018) Predictive power of food web models based on body size decreases with trophic complexity. *Ecology Letters* 21: 702–712.