# Toward a modular theory of trophic interactions

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## Author contributions

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,
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# 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.

*Key words: body size, ecological interaction networks, food webs, functional response, numerical response, trait-based approaches, predator-prey interactions*

# 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

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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 <u>Locate</u>, then <u>Attack</u>, and finally <u>Consume</u> its prey (e.g. Boukal, 2014; Griffiths, 1980; Holling, 1959; O'Brien et al., 1990). We additionally recognize the stage of <u>Decision</u> (Fig. 1). After locating its potential prey, a predator must <u>decide</u> that it is worth proceeding to attack it. We further break down each of the broad stages of <u>Locate</u>, <u>Decide</u>, <u>Attack</u>, and <u>Consume</u> 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: <u>Location</u> 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: <u>Decision</u> 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: <u>Attack</u> 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: <u>Consumption</u> 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.

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## 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 <u>Locates</u>, <u>Decides</u> to attack, and <u>Attacks</u> a prey individual. They further describe the cumulative proportion of <u>Consumption</u>, 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 <u>Location</u>, <u>Decision</u> and <u>Attack</u>, while the strength of the interaction, from the predator point of view, also includes the stage of <u>Consume</u>. 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

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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 ($\chi_5$, 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 $\varphi_{forage}$, 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 $\varphi_{search}$ is the proportion of foraging time spent searching, such that:

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

We can express the functional response, $FR$ as a function of total time by multiplying $\chi_5$ by the proportion of total time spent foraging $\varphi_{forage}$:

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

The remaining three steps of foraging not included in the functional response comprise the stage <u>Consume</u> (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, $\epsilon$, 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 ($\epsilon$) and made into functions to allow a more detailed representation of how traits affect these final

steps of a trophic interaction:

$$NR = \epsilon \cdot \chi_5 \cdot \varphi_{forage} = f_6 \cdot f_7 \cdot f_8 \cdot \chi_5 \cdot \varphi_{forage} \tag{3}$$

The functional response in equation (2) is expressed in relation to the proportion of foraging time available for searching, $\varphi_{search}$. However, $\varphi_{search}$ 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 $t_{handle}$):

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

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 $\varphi_{forage}$ a function of digestion time (e.g. Jeschke et al., 2002). The equation for $\varphi_{search}$ 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):

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

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):

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

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):

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

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 $A_{search}$:

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

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:

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

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 ($\varphi_{forage}$) varies with temperature (Ben Feit & Mattias Jonsson *pers. comm.*). This is a critical factor as rising temperatures may 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 $\varphi_{forage}$ (Rall et al., 2012):

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

Where $temp$ is the temperature, $\mu$ is the species optimum temperature, and $\sigma$ is the standard deviation of the predator's temperature niche. Individuals spend the most time foraging (largest $\varphi_{forage}$) when at their temperature optimum.

Combined and simplified, our model would look like this:

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

Where:

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

$f_{3,0}$, $A_0$, $t_{6,0}$ and $\varphi_0$ are all scaling parameters. We can now insert empirically measured values for body size ($B_C$ and $B_N$) and thermal niche optima ($\mu$) and thermal niche standard deviations ($\sigma$) 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 $\varphi_{forage}$) 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) |
| --- | --- | --- | --- |
| *Bembidion lampros*   | 23.5 | 9.9 | 1.61  |
| *Trechus secalis*     | 15.6 | 5.7 | 1.96  |
| *Agonum dorsale*      | 19.9 | 9.0 | 10.53 |
| *Pterostichus vernalis* | 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

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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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## References

Bartomeus, I., Gravel, D., Tylianakis, J. M., Aizen, M. A., Dickie, I. A., & Bernard-Verdier, M. (2016). "A common framework for identifying linkage rules across different types of interactions". *Functional Ecology, 30*(12), 1894–1903.

Bateman, A. W., Vos, M., & Anholt, B. R. (2014). "When to Defend : Antipredator Defenses and the Predation Sequence". *The American Naturalist, 183*(6).

Begon, M., Townsend, C. R., & Harper, J. L. (2005). *Ecology: from individuals to ecosystems* (4th). Wiley-Blackwell.

Berlow, E. L. (1999). "Strong effects of weak interactions in ecological communities". *Nature, 398*, 330–334.

Berlow, E. L., Dunne, J. A., Martinez, N. D., Stark, P. B., Williams, R. J., & Brose, U. (2009). "Simple prediction of interaction strengths in complex food webs". *Proceedings of the National Academy of Sciences*, *106*(1), 187–91.

Binz, H., Bucher, R., Entling, M. H., & Menzel, F. (2014). "Knowing the risk: Crickets distinguish between spider predators of different size and commonness". *Ethology*, *120*(1), 99–110.

Boukal, D. S. (2014). "Trait- and size-based descriptions of trophic links in freshwater food webs: Current status and perspectives". *Journal of Limnology*, *73*(s1), 171–185.

Brose, U. (2010). "Body-mass constraints on foraging behaviour determine population and food-web dynamics". *Functional Ecology*, *24*(1), 28–34.

Brose, U., Archambault, P., Barnes, A. D., Bersier, L. F., Boy, T., Canning-Clode, J., Conti, E., Dias, M., Digel, C., Dissanayake, A., Flores, A. A., Fussmann, K., Gauzens, B., Gray, C., Häussler, J., Hirt, M. R., Jacob, U., Jochum, M., Kéfi, S., . . . Iles, A. C. (2019). "Predator traits determine food-web architecture across ecosystems". *Nature Ecology and Evolution*, *3*(6), 919–927.

Brose, U., Jonsson, T., Berlow, E. L., Warren, P. H., Banasek-Richter, C., Bersier, L.-F., Blanchard, J. L., Brey, T., Carpenter, S. R., Cattin Blandenier, M.-F., Cushing, L., Ali Dawah, H., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M. E., Martinez, N. D., Memmot, J., . . . Cohen, J. E. (2006). "Consumer-resource body-size relationships in natural food webs". *Ecology*, *87*(10), 2411–2417.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, B. (2004). "Toward a metabolic theory of ecology". *Ecology*, *85*(7), 1771–1789.

Case, T. J. (2000). *An Illustrated Guide to Theoretical Ecology*. Oxford University Press.

Cohen, J. E., & Newman, C. M. (1985). "A Stochastic Theory of Community Food Webs: I. Models and Aggregated Data". *Proceedings of the Royal Society B: Biological Sciences*, *224*(1237), 421–448.

Corcoran, A. J., & Conner, W. E. (2012). "Sonar jamming in the field: effectiveness and behavior of a unique prey defense". *Journal of Experimental Biology*, *215*, 4278–4287.

Couture, J. J., Servi, J. S., & Lindroth, R. L. (2010). "Increased nitrogen availability influences predator – prey interactions by altering host-plant quality". *Chemoecology*, *20*, 277–284.

Curtsdotter, A., Banks, H. T., Banks, J. E., Jonsson, M., Bommarco, R., Jonsson, T., Laubmeier, A. N., & Traugott, M. (2019). "Ecosystem function in predator-prey food webs — confronting dynamic models with empirical data". *Journal of Animal Ecology*, *88*, 196–210.

Dell, A. I., Pawar, S., & Savage, V. M. (2014). "Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy". *Journal of Animal Ecology*, *83*(1), 70–84.

Elliott, J. M. (2004). "Prey switching in four species of carnivorous stoneflies". *Freshwater Biology*, *49*(6), 709–720.

Evans, M. R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C. M., Merz, M., O'Malley, M. A., Orzack, S. H., Weisberg, M., Wilkinson, D. J., Wolkenhauer, O., & Benton, T. G. (2013). "Do simple models lead to generality in ecology?" *Trends in Ecology and Evolution*, *28*(10), 578–583.

Gilbert, B., Tunney, T. D., Mccann, K. S., Delong, J. P., Vasseur, D. A., Savage, V., Shurin, J. B., Dell, A. I., Barton, B. T., Harley, C. D. G., Kharouba, H. M., Kratina, P., Blanchard, J. L., Clements, C., Winder, M., Greig, H. S., & O'Connor, M. I. (2014). "A bioenergetic framework for the temperature dependence of trophic interactions". *Ecology Letters*, *17*(8), 902–914.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). "Effects of size and temperature on metabolic rate." *Science*, *293*(5538), 2248–51.

Gownaris, N. J., Pikitch, E. K., Ojwang, W. O., Michener, R., & Kaufman, L. (2015). "Predicting species' vulnerability in a massively perturbed system: The fishes of Lake Turkana, Kenya". *PLoS ONE*, *10*(5), e0127027.

Gravel, D., Albouy, C., & Thuiller, W. (2016). "The meaning of functional trait composition of food webs for ecosystem functioning". *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1694).

Gravel, D., Poisot, T., Albouy, C., Velez, L., & Mouillot, D. (2013). "Inferring food web structure from predator-prey body size relationships". *Methods in Ecology and Evolution*, *4*(11), 1083–1090.

Griffiths, D. (1980). "Foraging Costs and Relative Prey Size". *The American Naturalist*, *116*(5), 743–752.

Grigaltchik, V. S., Ward, A. J. W., & Seebacher, F. (2012). "Thermal acclimation of interactions: differential responses to temperature change alter predator-prey relationship." *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 4058–64.

Holling, C. (1959). "The components of predation as revealed by a study of small-mammal predation of the European pine sawfly". *The Canadian Entomologist*, *93*(5), 293–320.

Ibanez, S., Millery, A., D'ottavio, M., Guilhot, R., & Vesin, E. (2017). "Phosphorus-rich grasshoppers consume plants high in nitrogen and phosphorus". *Ecological Entomology*, *42*(5), 610–616.

Jacob, U., Thierry, A., Brose, U., Arntz, W. E., Berg, S., Brey, T., Fetzer, I., Jonsson, T., Mintenbeck, K., Möllmann, C., Petchey, O. L., Riede, J. O., & Dunne, J. A. (2011). *The role of body size in complex food webs: a cold case* (Vol. 45).

Jeschke, J. M., Kopp, M., & Tollrian, R. (2002). "Predator functional responses: Discriminating between handling and digesting prey". *Ecological Monographs*, *72*(1), 95–112.

Jonsson, T., Kaartinen, R., Jonsson, M., & Bommarco, R. (2018). "Predictive power of food web models based on body size decreases with trophic complexity". *Ecology Letters*, *21*(5), 702–712.

Kalinoski, R. M., & DeLong, J. P. (2016). "Beyond body mass: how prey traits improve predictions of functional response parameters". *Oecologia*, *180*(2), 543–550.

Klecka, J., & Boukal, D. S. (2013). "Foraging and vulnerability traits modify predator-prey body mass allometry: freshwater macroinvertebrates as a case study". *Journal of Animal Ecology*, *82*(5), 1031–1041.

Koen-Alonso, M. (2007). "A Process-Oriented Approach to the Multispecies Functional Response". In N. Rooney, K. S. McCann, & D. L. G. Noakes (Eds.), *From energetics to ecosystems: The dynamics and structure of ecological systems* (pp. 1–36). Springer Netherlands.

Kuszewska, K., Miler, K., Filipiak, M., & Woyciechowski, M. (2016). "Sedentary antlion larvae (Neuroptera: Myrmeleontidae) use vibrational cues to modify their foraging strategies". *Animal Cognition*, *19*(5), 1037–1041.

Lafferty, K. D., DeLeo, G., Briggs, C. J., Dobson, A. P., Gross, T., & Kuris, A. M. (2015). "A general consumer-resource population model". *Science*, *349*(6250), 854–857.

Laigle, I., Aubin, I., Digel, C., Brose, U., Boulangeat, I., & Gravel, D. (2018). "Species traits as drivers of food web structure". *Oikos*, *127*(2), 316–326.

Laubmeier, A., Wootton, K., Banks, J., Bommarco, R., Curtsdotter, A., Jonsson, T., Roslin, T., & Banks, H. (2018). "From theory to experimental design—Quantifying a trait-based theory of predator-prey dynamics". *PLoS ONE*, *13*(4).

Losey, J. E., & Denno, R. F. (1998). "Positive predator-predator interactions: Enhanced predation rates and synergistic suppression of aphid populations". *Ecology*, *79*(6), 2143–2152.

Lotka, A. J. (1920). "Analytical Note on Certain Rhythmic Relations in Organic Systems." *Proceedings of the National Academy of Sciences*, *6*(7), 410–415.

McCluney, K. E., & Sabo, J. L. (2009). "Water availability directly determines per capita consumption at two trophic levels". *Ecology*, *90*(6), 1463–1469.
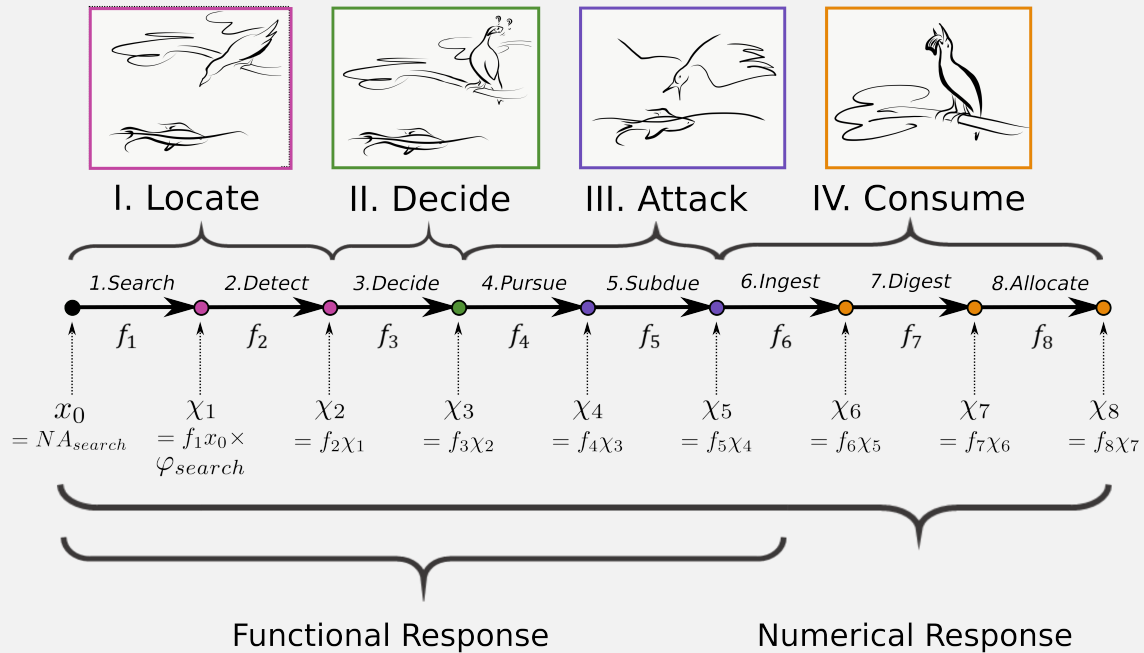
Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). "Inferring biotic interactions from proxies". *Trends in Ecology and Evolution, 30*(6), 347–356.

Mori, E., Maggini, I., & Menchetti, M. (2014). "When quills kill: The defense strategy of the crested porcupine Hystrix cristata L., 1758". *Mammalia, 78*(2), 229–234.

Morozov, A., & Petrovskii, S. (2013). "Feeding on Multiple Sources: Towards a Universal Parameterization of the Functional Response of a Generalist Predator Allowing for Switching". *PLoS ONE, 8*(9).

Neubert, M. G., Blumenshine, S. C., Duplisea, D. E., Jonsson, T., & Rashleigh, B. (2000). "Body size and food web structure: testing the equiprobability assumption of the cascade model". *Oecologia, 123,* 241–251.

O'Brien, W. J., Browman, H. I., & Evans, B. I. (1990). "Search Strategies of Foraging Animals". *American Scientist, 78*(2), 152–160.

Otto, S. B., Rall, B. C., & Brose, U. (2007). "Allometric degree distributions facilitate food-web stability." *Nature, 450*(7173), 1226–1229.

Preisser, E. L., Orrock, J. L., & Schmitz, O. J. (2007). "Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions." *Ecology, 88*(11), 2744–51.

Rafter, J. L., Agrawal, A. A., & Preisser, E. L. (2013). "Chinese mantids gut toxic monarch caterpillars: Avoidance of prey defence?" *Ecological Entomology, 38,* 76–82.

Rall, B. Ö. C., Vucic-Pestic, O., Ehnes, R. B., Emmerson, M., & Brose, U. (2010). "Temperature, predator-prey interaction strength and population stability". *Global Change Biology, 16*(8), 2145–2157.

Rall, B. C. B., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., & Petchey, O. L. (2012). "Universal temperature and body-mass scaling of feeding rates". *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1605), 2923–34.

Razeng, E., & Watson, D. M. (2015). "Nutritional composition of the preferred prey of insectivorous birds: popularity reflects quality". *Journal of Avian Biology, 46,* 89–96.

Roitberg, B. D., & Myers, J. H. (1979). "Behavioural and physiological adaptations of pea aphids (Homoptera: Aphididae) to high ground temperatures and predator disturbance". *The Canadian Entomologist, 111*(4), 515–519.

Ruxton, G. D. (2009). "Non-visual crypsis: A review of the empirical evidence for camouflage to senses other than vision". *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1516), 549–557.

Schmitz, O. J., & Suttle, K. B. (2001). "Effects of top predator species on direct and indirect interactions in a food web". *Ecology, 82*(7), 2072–2081.

Schmitz, O. J. (2007). "Predator diversity and trophic interactions". *Ecology, 88*(10), 2415–2426.

Schneider, F. D., Scheu, S., & Brose, U. (2012). "Body mass constraints on feeding rates determine the consequences of predator loss". *Ecology Letters, 15*(5), 436–443.

Schneider, F. D., Scheu, S., & Brose, U. (2014). "Corrigendum to Schneider, Scheu & Brose (2012) DOI: 10.1111/j.1461-0248.2012.01750.x". *Ecology Letters, 17*(10), 1339–1340.

Sentis, A., Hemptinne, J. L., & Brodeur, J. (2014). "Towards a mechanistic understanding of temperature and enrichment effects on species interaction strength, omnivory and food-web structure". *Ecology Letters, 17*(7), 785–793.

Sentis, A., Hemptinne, J.-L., & Brodeur, J. (2012). "Using functional response modeling to investigate the effect of temperature on predator feeding rate and energetic efficiency." *Oecologia, 169*(4), 1117–25.

Solomon, M. E. (1949). "The Natural Control of Animal Populations". *Journal of Animal Ecology, 18*(1), 1–35.

Spitz, J., Ridoux, V., & Brind'Amour, A. (2014). "Let's go beyond taxonomy in diet description: Testing a trait-based approach to prey-predator relationships". *Journal of Animal Ecology, 83*(5), 1137–1148.

Stouffer, D. B., & Novak, M. (2021). "Hidden layers of density dependence in consumer feeding rates". *Ecology Letters*, 520–532.

Terry, J. C. D., Morris, R. J., & Bonsall, M. B. (2017). "Trophic interaction modifications: an empirical and theoretical framework". *Ecology Letters, 20*(10), 1219–1230.

Violle, C., Navas, M.-l., Vile, D., Kazakou, E., & Fortunel, C. (2007). "Let the concept of trait be functional!" *Oikos, 116*, 882–892.

Volterra, V. (1926). "Fluctuations in the abundance of a species considered mathematically". *Nature, 118*(2972), 558–560.

Vucic-Pestic, O., Ehnes, R. B., Rall, B. C., & Brose, U. (2011). "Warming up the system: higher predator feeding rates but lower energetic efficiencies". *Global Change Biology, 17*(3), 1301–1310.

Vucic-Pestic, O., Rall, B. C., Kalinkat, G., & Brose, U. (2010). "Allometric functional response model: Body masses constrain interaction strengths". *Journal of Animal Ecology, 79*(1), 249–256.

Williams, R. J., & Martinez, N. D. (2000). "Simple rules yield complex food webs." *Nature, 404*(6774), 180–183.

Yodzis, P., & Innes, S. (1992). "Body size and consumer-resource dynamics". *The American Naturalist*, *139*(6), 1151–1175.

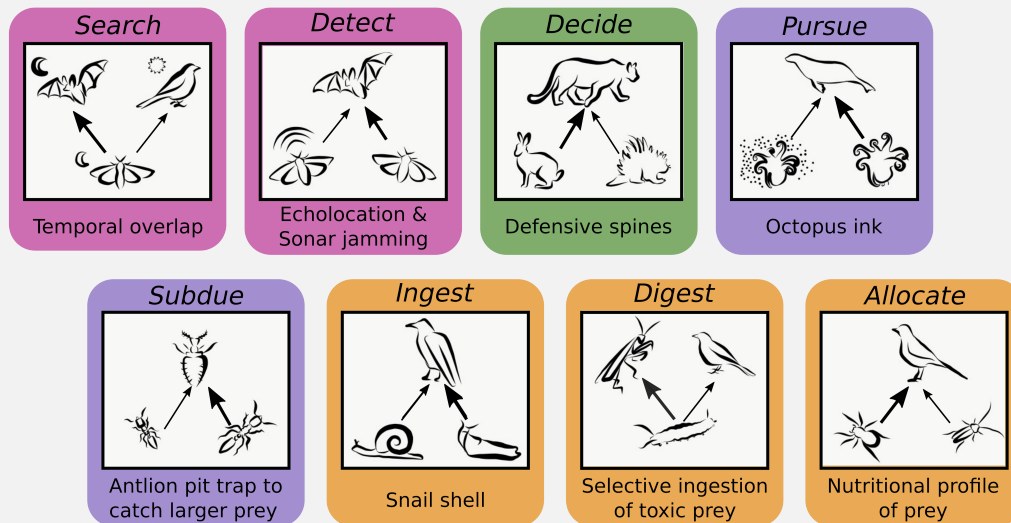# Steps in a trophic interaction and their parameters

I. Locate  II. Decide  III. Attack  IV. Consume

1.Search  2.Detect  3.Decide  4.Pursue  5.Subdue  6.Ingest  7.Digest  8.Allocate

$f_1$  $f_2$  $f_3$  $f_4$  $f_5$  $f_6$  $f_7$  $f_8$

$x_0$  $\chi_1$  $\chi_2$  $\chi_3$  $\chi_4$  $\chi_5$  $\chi_6$  $\chi_7$  $\chi_8$

$= NA_{search}$  $= f_1 x_0 \times$  $= f_2\chi_1$  $= f_3\chi_2$  $= f_4\chi_3$  $= f_5\chi_4$  $= f_6\chi_5$  $= f_7\chi_6$  $= f_8\chi_7$

$\varphi_{search}$

Functional Response   Numerical Response

# Examples of traits affecting each step

**Search** — Temporal overlap

**Detect** — Echolocation & Sonar jamming

**Decide** — Defensive spines

**Pursue** — Octopus ink

**Subdue** — Antlion pit trap to catch larger prey

**Ingest** — Snail shell

**Digest** — Selective ingestion of toxic prey

**Allocate** — Nutritional profile of prey

Figure 1: (Continued on the following page)

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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 ($\chi_5$) that are ingested, digested, and allocated to reproduction respectively, per area searched ($A_{search}$) and per proportion of foraging time spent searching ($\varphi_{search}$). 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 $\varphi_{forage}$, 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 (Kuszewska 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).
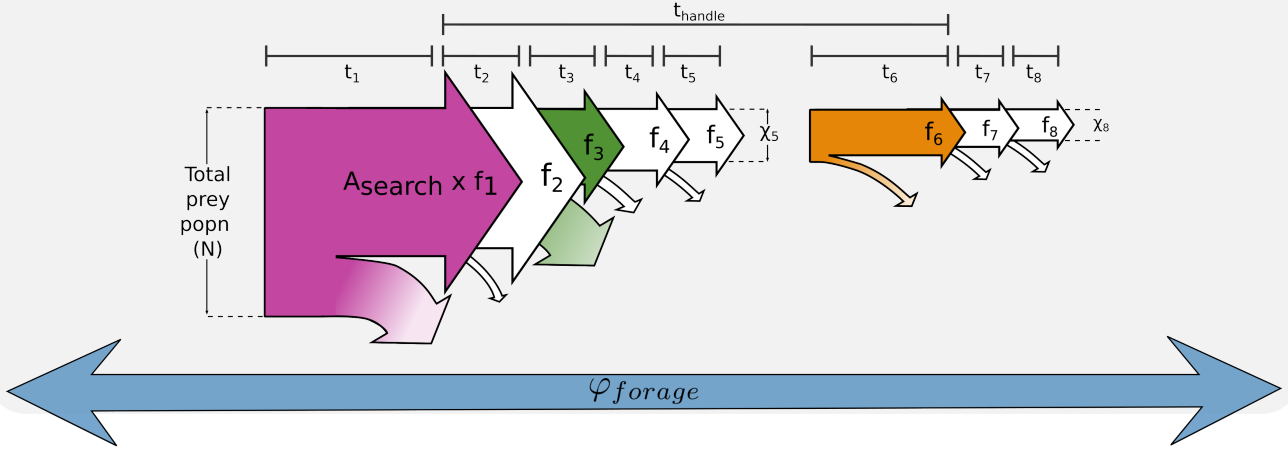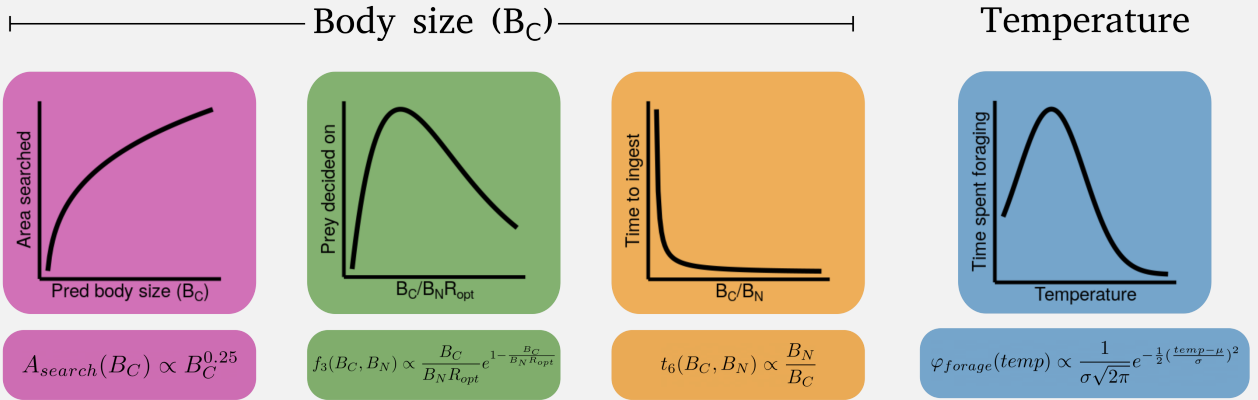
Figure 2: (Continued on the following page)

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 $\varphi_{forage}$, the proportion of time the predator spends foraging (selected steps and $\varphi_{forage}$ 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, $\varphi_{forage}$. Close to the optimum of their thermal niche, predators spend more time foraging (larger $\varphi_{forage}$), 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.
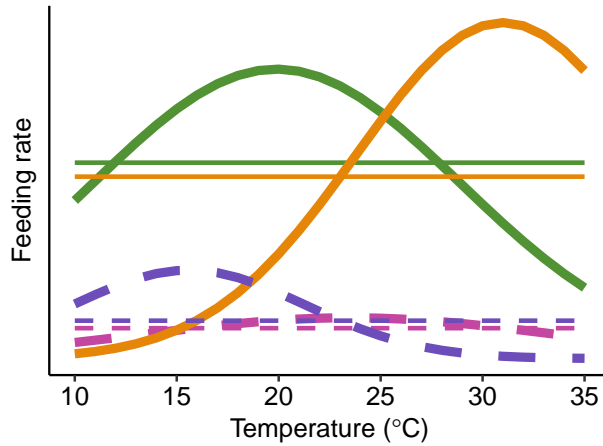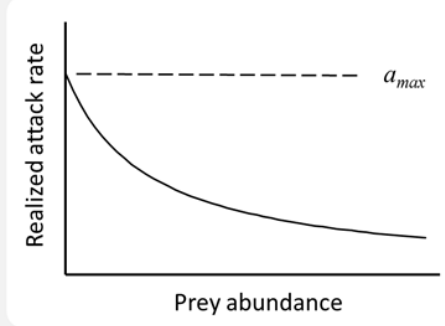


Figure 3: Model-predicted feeding rates (number of prey individuals - aphids of species *Rhopalosiphum padi*, 0.155mg - consumed per unit time by an individual predator) for four different predatory ground beetles as a function of temperature, using the model in Eq. (11) parameterized by empirical values. 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.
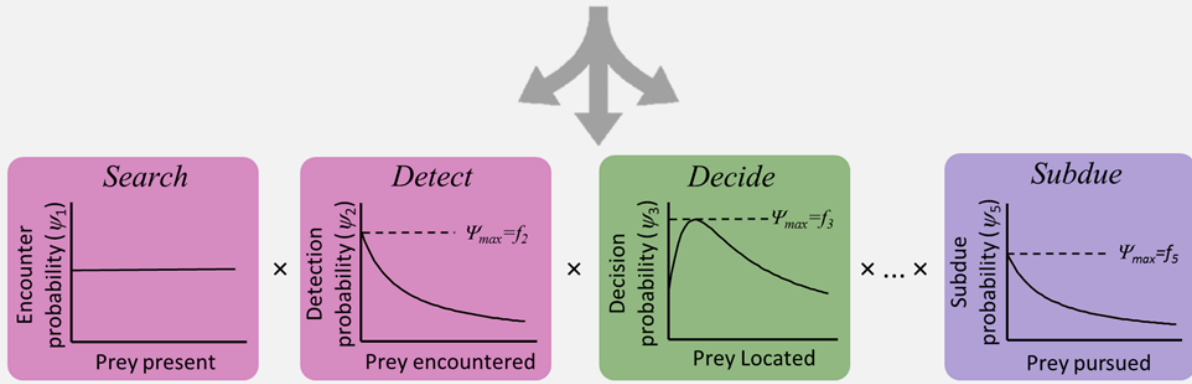
Figure 4: Hypothetical factorization of a composite functional response into separate predator success rates (or proportional functional responses) for individual steps of the predation cycle. This can be an approach for studying and acknowledging various response functions for different foraging steps. 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).
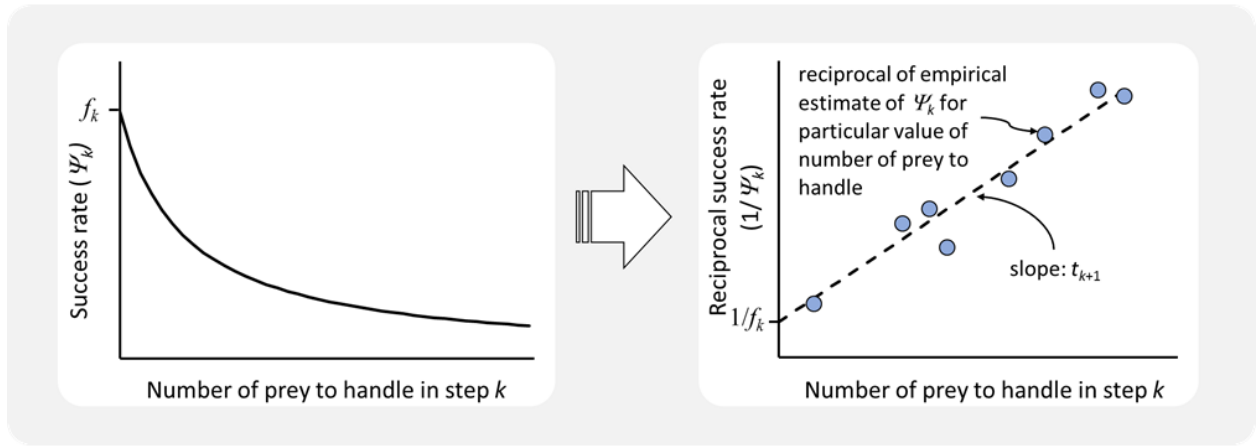
Figure 5: Illustration of an approach for estimating $f_k$ and $t_{k+1}$ of a saturating response function from empirical data using linear regression. Note that here $f_k$ and $t_{k+1}$ are *parameters* for a particular predator-prey combination (see Box 1).
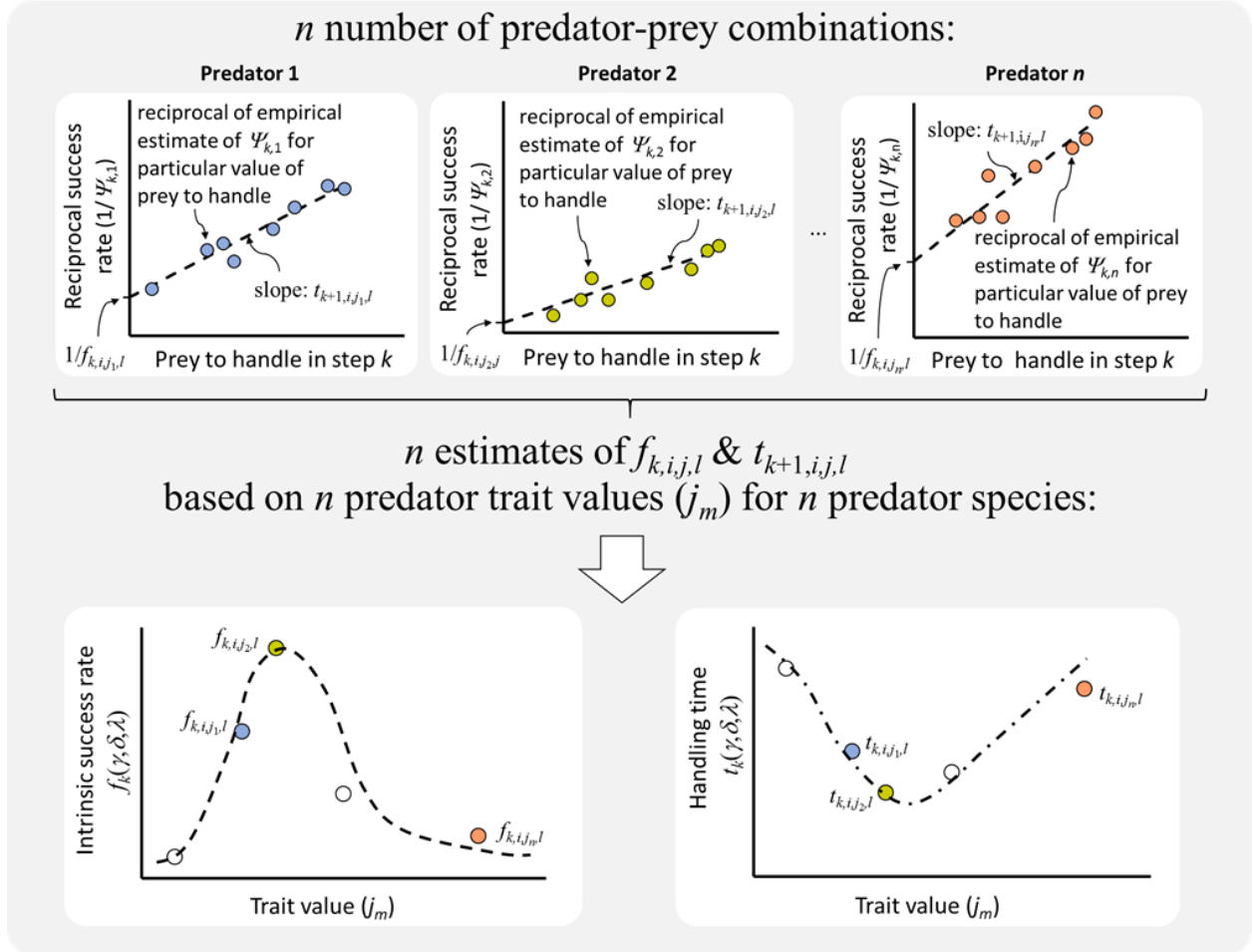
Figure 6: An approach for testing theoretical predictions of how species traits may affect $f_k(\gamma, \delta, \lambda)$ and $t_k(\gamma, \delta, \lambda)$. Combining the results of multiple estimates of $f_{k,i,j,l}$ and $t_{k,i,j,l}$ under the influence of different values of a relevant trait (upper 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 ($\gamma$), predator traits ($\delta$) and/or environmental factors ($\lambda$), 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 ($\psi_k$) 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 ($\psi_k$) for each step (Eq. 13 is equivalent to Eq. 5, see appendix S2):

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

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

$(\chi_{k-1})$ 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:

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

where $\psi_k$ 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 $\xi_{k-1}$, 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 $(\psi_k)$ 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 tropic 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.