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How species traits influence trophic interaction strength

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CONTENTS

ABSTRACT

An organism's traits affect how it interacts with the world and with other species. In a predator-prey interaction both the predator's and prey's traits affect the likelihood that a given predation attempt will be successful. Together multiple predation events determine the strength of the trophic interaction between these two species. A number of traits can be important in determining interaction strength. For trophic interactions, one of the best-studied traits is body size – which has proven so important that a significant portion of interactions within a food web can be predicted from this one trait alone. Beyond body size, other traits, such as prey defenses, mobility, feeding preference, and diet breadth also shape interactions between species.

Abiotic conditions shape and alter the relationship between species traits and interaction strength. This impact can be direct, where abiotic conditions change traits or their effectiveness, or indirect, where a species' ability to thrive in that environment – and thus interact with predators or prey – depends on its traits. Species respond to changes in abiotic conditions in different ways, potentially changing interaction strength. For example, temperature affects species at different rates depending on their body size, affecting interaction strength through changes in consumption rate, growth rate etc. Disturbances and changes in climate also affect species unequally, leading to mismatches in relative abundance, phenology or ranges. Such mismatches may lead to novel interactions, or the strengthening or weakening of interactions by altering overlap and encounter rates.

Together these trait-mediated interactions shape ecological communities. With a wealth of species interacting at the same time, the sum total of direct and indirect interactions determine community dynamics. Many traits and interactions have been studied, but there are still gaps in our understanding of how these interactions combine. A closer investigation of the mechanisms underpinning the relationship between traits and interaction strength will allow for more efficient quantification of food webs and predictions of how communities will respond to disturbances.

INTRODUCTION

Eat or be eaten. A simple expression which describes a great deal about the natural world around us. Energy flows from one organism to another by consumption, and an organism which does not consume others is itself consumed – although many both eat and are eaten. The traits we observe in organisms – those distinct characteristics which differ between organisms and especially between species; a cheetah's long legs or a snail's protective shell – are in large part formed in response to this two-way need to eat and avoid being eaten. But traits are not only shaped by these trophic interactions, they also shape them, influencing which species feed on each other and how strong the interaction is (Boukal 2014).

A multitude of traits shape trophic interaction strength and structure (henceforth 'TIS'). Some traits affect TIS by directly affecting how an individual of the predator species interacts with an individual of the prey species (Klecka & Boukal 2013; Kalinoski & DeLong 2016). Other traits affect TIS by determining how species interact with the environment, altering the spatiotemporal overlap of predator and prey and thus the likelihood that they will interact (Parmesan 2006; Dell, Pawar & Savage 2013). Traits which fall into the former category are largely those involved in the process of predation, while the latter can include traits affecting an organism's ability to survive and thrive in a particular environment (Parmesan 2006; Boukal 2014). There are also multiple types of consumer-resource interactions and traits which are highly relevant for one type of interaction may be unimportant for another. For example, body size is very important for predator-prey interactions (Brose 2010), can be important for parasitoids (Cohen *et al.* 2005), but is often not important for herbivory (Deraison *et al.* 2015). Due to the huge body of research on different types of interactions, it would be unwieldy to try and cover them all here. Thus, I will focus this review primarily on predator-prey interactions, but draw attention to other types of interaction where relevant.

The strength of a trophic interaction influences not only the two species involved in the interaction, but also the rest of the community and even the abiotic environment (Wootton 1997; Wootton & Emmerson 2005). Within an ecological community the strength and distribution of interactions can have critical effects on the stability of the community (McCann, Hastings & Huxel 1998; Berlow 1999; Wootton & Stouffer 2015). Changes in strength of even a single interaction can have wide-reaching and devastating effects (Watson & Estes 2011; Wootton &

Stouffer 2016). Unfortunately, quantifying trophic interactions can be difficult between two species, let alone across the entire community (figure 1). It requires a huge quantity of work, and different methods for quantifying interaction strength are not always directly comparable (Wootton & Emmerson 2005; Wirta *et al.* 2014). This forms a major bottleneck in the progress of studying ecological communities and their food webs - those networks of trophic interactions which make up the community. Using traits as a proxy to estimate whether two species will interact and, if so, how strongly, would form a major step forward in the study of food webs and how they will respond to changing conditions (Morales-Castilla *et al.* 2015). Quantifying every trait and how it affects interaction strength is, however, arguably more challenging than simply determining the interaction strength between two species. Therefore, we need to know *which* traits are the most important for influencing trophic interactions.

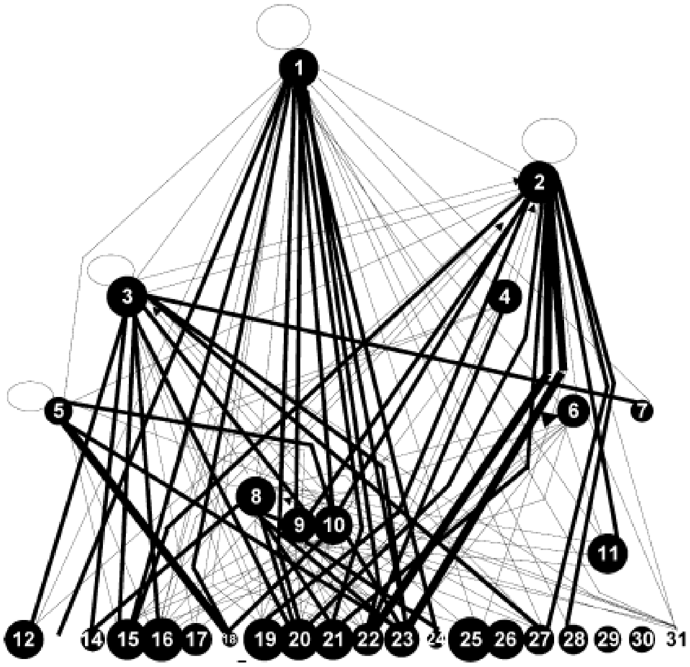

Figure 1. Quantifying the strength and structure of trophic interactions in any food web is a daunting task. Shown is the food web of Broadstone Stream, with line thickness indicating interaction strength. In this web, there are 496 potential pairwise interactions to be quantified. Source: Woodward et al. 2010, p. 117.

To understand how and why species interact and, from there, how ecological communities are shaped and will respond to disturbances, requires a greater understanding of the mechanisms behind species interactions (Morales-Castilla *et al.* 2015). An understanding of which traits influence TIS and how this is moderated by changes in abiotic conditions will go a long way toward filling this gap. This information can then be used to further understanding and study of communities, inform models predicting how communities will respond to disturbances and change as well as actions to manage that change. Here I discuss the most important traits affecting TIS, both directly and indirectly, and the mechanisms behind the relationship. I then discuss how the relationships between traits and TIS may be modulated by the abiotic environment, and finally, the impact of these traits beyond pairwise interactions.

TRAITS WHICH DIRECTLY AFFECT TROPHIC INTERACTION STRENGTH

Many traits are important for TIS by directly altering the likelihood of success of a predation event between an individual of the predator species and an individual of the prey species (Boukal 2014). These traits act by affecting one or more stages of the process of predation; either by making the predator better at capturing and consuming their prey or by making prey better at avoiding being captured and consumed. For predators, the process of predation can be broken down into three stages; encountering the prey, attack time, and handling and digestion, collectively known as the foraging ability of the predator. For prey, the stages of predation include encountering the predator, escape from the attack and escape after being caught, collectively known as the vulnerability of the prey (Greene 1983; Boukal 2014). Traits which affect any of these stages can impact TIS, such as a more mobile predator having greater success at capturing their prey than a less mobile predator. Some traits only impact one or a few stages while others, such as body size, impact multiple (Petchey *et al.* 2008; Schneider, Scheu & Brose 2012). A larger predator usually has a larger range and thus increased chance of encountering the prey (Ottaviani *et al.* 2006), while attack rate and handling time are usually decreased as the predator-prey body size ratio increases (Brose 2010). While larger prey may encounter the predator more frequently, their greater body mass increases their chances of escaping the attack or escaping after being captured (Yodzis & Innes 1992; Brose 2010). Because many traits are specific to the system or organism involved, it is difficult to discuss all traits which affect interaction strength. Here I discuss a number of the most commonly studied traits, as well as the different categories of traits which affect TIS and the types of impacts they can have.

BODY SIZE

Body size is a hugely important trait affecting many aspects of a species' ability to survive and thrive, including its trophic interactions (Brose *et al.* 2005; Schneider *et al.* 2012). Many of the most important effects of body size are due to its impact on metabolism, the biological processing of energy and materials (Gillooly *et al.* 2001). Larger individuals require more resources to meet their metabolic requirements and thus have stronger interactions with their prey. However, metabolism does not scale linearly with body size, but rather as a ¾ exponential (Brown *et al.* 2004). This means that a single large consumer requires less resources than two consumers half its size. In addition to larger predators requiring more resources, it is also easier and safer for a larger predator to subdue and consume smaller prey (Svanbäck *et al.* 2015). This is particularly prominent in aquatic systems where predation is largely gape limited, such that the larger a consumer is, the larger its gape and the larger its prey (Brose *et al.* 2006). While large prey may require too much energy to capture, handle and consume, prey that are too small are not worth the energy invested to capture them (Svanbäck *et al.* 2015). This results in a unimodal relationship between predator and prey body size (figure 2) (Brose, 2010b) where the optimal prey size is usually 1-3 orders of magnitude smaller than the predator (Woodward, Speirs & Hildrew 2005b; Woodward *et al.* 2005a). Indeed, by basing model parameters on body mass and the unimodal relationship between predator and prey body size, Schneider et al. (2012) were able to predict population dynamics in a simple four-species system. In addition to metabolic requirements, body size underlies many other traits and physical constraints which affect TIS. For example, diet generality tends to increase with body size, allowing larger predators to exploit a wider range of prey (Gilljam *et al.* 2011). Clearly, there are multiple ways in which body size affects trophic interactions between predators and prey, and this scales up to affect the structure of the network as a whole. In fact, a number of studies have shown that a significant portion of structural information within a food web can be predicted from body size alone (Williams & Martinez 2000; Stouffer, Rezende & Amaral 2011).

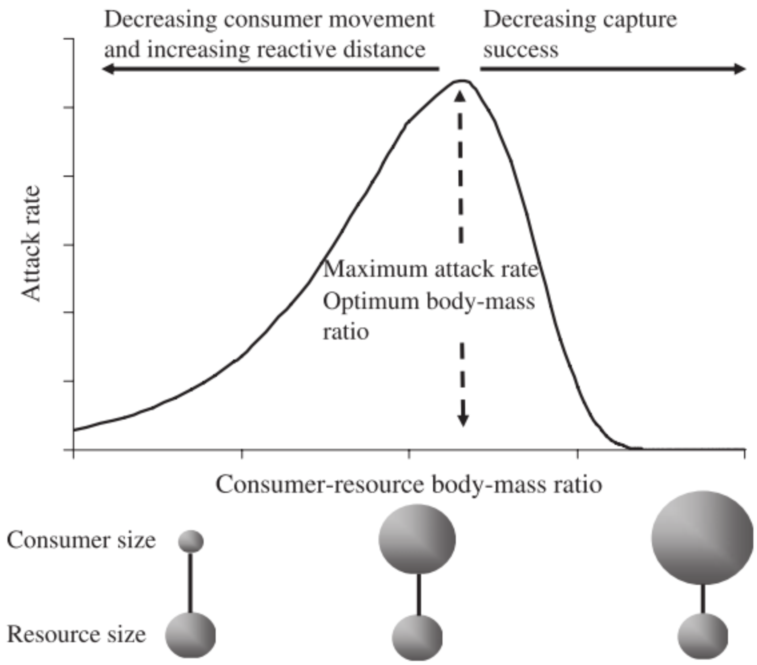

Figure 2; Attack rate and consumer-resource body-mass ratio have a hump-shaped relationship, with the highest attack rate occurring at the optimal body-mass ratio. Below this ratio consumers are too small to effectively capture their prey, while above this ratio prey are more difficult to capture and the energetic pay-off is low. Source: Brose 2010, p. 30.

Although body size is an important trait structuring trophic interactions, it is not a fixed trait. Most organisms grow during their life time and as a result pass through many different body sizes (Gilljam *et al.* 2011). In some species this is especially pronounced and individuals experience an ontogenetic shift in diet, moving from one prey type as a juvenile to a completely different prey type as an adult (Werner & Gilliam 1984). Many studies aggregate individuals into species and use an average body size to estimate interactions, but this risks missing the importance of this diet shift. As a result, these studies sometimes find a weaker relationship between body size and TIS or no relationship at all, even where it does exist (Gilljam *et al.* 2011). Woodward et al. (2005b) show the importance of individual variation in body size in an invertebrate stream food web. When examined at species level, they found a weaker effect of body size and a different scaling relationship than when examined at individual level. They also found that observations of interactions where a smaller species consumed a larger species did not mean a smaller *individual* consumed a larger *individual.* In all of these cases, the individual from the “large” species was a small individual of that species and the individual from the “small” species was a large individual such that the predator individual was actually larger than the prey individual.

Body size is a very important trait governing trophic interactions and a useful one to study as it affects organisms in all systems, is easy to measure, and easy to directly compare across systems. It does not, however, capture everything. There are a number of cases where body size is either not important or acts primarily as a filter, such that two individuals can have a trophic interaction if they are within a relatively broad size spectrum. Within that spectrum, however, other traits dictate the occurrence and strength of the interaction (Klecka & Boukal 2013). For example, in herbivorous or parasitic interactions the cost-benefit relationship is not affected by body size and other traits dictate TIS (Deraison *et al.* 2015). Within predator-prey interactions, other traits, such as hunting mode or prey defenses, can be more important for determining TIS across a smaller size spectrum. These traits can allow a smaller predator to overcome a larger prey or protecting a smaller prey from predation (Kalinoski & DeLong 2016).

OTHER TRAITS

Although body size may put limitations on which species can interact, other traits can modify that relationship, sometimes quite extensively (figure 3). This usually occurs when the impact of another trait changes the cost-benefit quotient or the predator and thus the most beneficial body size ratio of predator and prey (Svanbäck *et al.* 2015). Many traits have been studied in this context, however a number of these traits are specific to the ecosystem, organism or even consumer-resource pair. This makes it difficult to generalize as to which traits are most important for TIS, or even to compile a complete list of those studied. The effect of these traits, however, is to alter an individual’s foraging ability or vulnerability to predation, and can be broadly grouped within a handful of categories affecting one or the other. Here I discuss first those traits affecting a prey individual’s vulnerability to predation (defenses, behavior, morphology and mobility), and then those affecting a predator’s foraging ability (behavior, morphology, mobility and foraging mode).

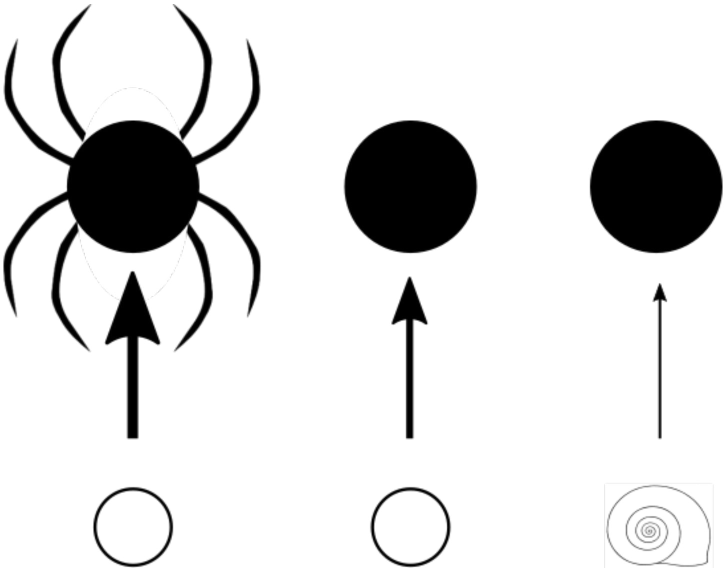

Figure 3: Within a particular predator-prey body-mass ratio, other species traits can alter TIS. Traits increasing predator foraging ability (such as increased mobility) will increase TIS. Traits which decrease prey vulnerability (such as defenses) decrease TIS.

The most important traits for prey species in relation to TIS are those related to its vulnerability to predation, including prey defenses, mobility and antipredator behavior. Defenses increase a prey individual's ability to evade predation by making it harder for the predator to capture and consume them (figure 3). For example, Kalinoski & DeLong (2016) found that the toughness of the prey's integument could increase handling time, which then decreased TIS. Using defenses to decrease interaction strength can have effects beyond the two species directly involved in the interaction; Kratina et al. (2010) found that inducible defenses of intraguild prey decreased interaction strength sufficiently to allow persistence of omnivory and coexistence of three species which could otherwise not coexist. Prey can also change their mobility in response to predation (Binz *et al.* 2014). This is often a trade off with defenses, as a more heavily defended prey tends to be less mobile. The effectiveness of mobility vs defenses can depend on the type of predators the prey is exposed to (Peckarsky *et al.* 2015). In damselflies, the ability to outswim their dragonfly predators enhances their chance of survival, and dragonfly predation has been shown to exert selection pressure for both morphological (McPeek 1997) and biochemical (Strobbe *et al.* 2010) traits which enhance swimming speed. In other cases, higher mobility can increase a prey species' ability to find food, but actually increases the prey's susceptibility to predation. For example, Woodward et al. (2005b) found that the highly mobile, epibenthic stonefly *N. pictetii* are consumed at a higher rate than the slow moving, interstitial species *L. nigra,* despite the numerical dominance of the latter. Some prey species change their behavior in response to predator cues. For example, wood crickets modify their behavior (by increasing or decreasing mobility) to evade predation in response to chemical predator cues from spiders (Binz *et al.* 2014). Furthermore, the way in which the crickets modify their behavior depends on the size ratio between predator and prey, the commonness of the predator, and the maturity of both the predator and prey. In each case, this ensures the optimal escape response. There are a multitude of ways in which prey can decrease their susceptibility to predation, frequently involving a combination of the above categories. In addition to avoiding predation, however, prey individuals must also eat and reproduce and their traits frequently reflect a trade-off between these competing requirements.

For predators, the most important traits are those related to their foraging ability, in particular their hunting or foraging mode, mobility, diet breadth, and behavior. Two contrasting classes of foraging mode for predators include sit-and-wait and active-capture. The effectiveness of each method depends on the type of prey targeted (Preisser, Orrock & Schmitz 2007). Active-capture predators tend to have more success against prey which are less mobile than themselves, while for more active prey, the ambush strategy of sit-and-wait predators is more effective (Scharf *et al.* 2006). Predators can either specialize on a particular prey or adopt a generalist behavior and take advantage of a wide range of prey items. While the former allows greater efficiency or the ability to exploit resources that other predators may not be capable of, predators with a wide diet breadth are frequently better prepared to survive in variable or competitive environments by exploiting whatever resources are most abundant (Coll & Guershon 2002). Co-operation between individuals of the predator and/or prey species can modify TIS. Pack hunting animals are able to hunt much larger prey together than they would alone due to their behavior of working together, and larger prey require a larger pack (Barber-Meyer *et al.* 2016). Because the most effective traits for capturing prey depend on the type of prey, most predators must specialize to some degree on the type of prey they hunt. In some cases, this results in a specialist species, while in other cases, individuals of a species specialize on different prey and the species as a whole is generalist (Bolnick *et al.* 2003; Pettorelli *et al.* 2015).

In most cases, the effectiveness of a particular trait depends on how it matches the traits of the interacting species. This has been likened to a “lock and key” mechanism, whereby the consumer traits are the keys that unlock the prey’s traits (Boukal 2014). While some keys are effective at opening a large number of locks (i.e. some traits increase interaction strength on a wide range of resources) and some locks are easier to open than others (i.e. some prey are easier to consume regardless of consumer traits), some locks and keys are highly specialized, requiring a close coupling between consumer and resource traits (Pouilly *et al.* 2003). For freshwater fish from the Mamore River in the Bolivian Amazon, the morphology of the fish was relatively unimportant for the consumption of terrestrial invertebrates and zooplankton (suggesting that these prey types are easy locks to open). Soft substratums, algae, and fishes, on the other hand, were trickier locks and required more specific morphology (Pouilly *et al.* 2003). In a similar way, traits which affect TIS in one predator-prey couple may be unimportant when combined with a different predator or prey. For example, in a study of consumer fish and their resources in Lake Tana, Ethiopia, Nagelkerke & Rossberg (2014) found that one of the most important traits predicting a feeding interaction was barbel length, but that this depended strongly on the main habitat of the resource. Barbels were useful for detecting resources in the sediment, but of less use in the water column – fish which do not feed in the sediments have no need of barbels. In a study of freshwater macroinvertebrates, Klecka and Boukal (2013) found that the interaction between predator foraging mode (searching/ambush), prey escape behavior (slow/fast) and prey activity (sedentary/active) had significant effects on TIS; searching predators had weak TIS with fast escape prey while ambush predators had higher TIS than searching prey, especially for active prey. Furthermore, the effectiveness of a particular trait is often enhanced by the presence of other traits, such that a “cluster” of traits within a single species is important. For example, Green and Côté (2014) studied the vulnerability of prey to the Indo-Pacific Lionfish and found that a combination of body size, body shape, position in the water column and aggregation behavior could heighten the risk of predation by a factor of nearly 200. This vulnerability, however, is inherently tied to the traits of Lionfish. A different cluster of traits would confer a different level of vulnerability to a consumer with different predatory traits. The combination of predator-prey trait matching and trait clustering can make it difficult to determine which traits are most important in a given interaction, let alone to infer the effect of a particular predator on a prey species with which it has not previously interacted.

PHYLOGENY

As a species evolves, certain traits change and diverge, but many other traits are conserved. As a result, phylogeny --- the evolutionary history and relationships among organisms --- can be an important element in determining TIS between species (Bersier & Kehrli 2008). Traits and evolution are inextricably linked to each other; as individuals struggle to survive, those with the most beneficial traits which increase TIS with prey or decrease TIS with predators are the individuals to survive and pass on their traits to their offspring. The effects of these traits and altered TIS then drive further evolution of both interacting species in an endless loop of eat, escape or evolve. While this makes it difficult to separate and compare the relative roles of phylogeny versus present-day traits in driving TIS, a phylogeny depicting present-day relationships among species can be a useful tool in predicting TIS, much as present-day traits, such as body size, are used (Cattin *et al.* 2004; Naisbit *et al.* 2012). Because many traits are conserved to some degree as species evolve, phylogenetic relationships encapsulate information about a number of present-day traits driving present-day TIS and can make for an effect trait proxy (Bersier & Kehrli 2008; Eklöf & Stouffer 2016). This is particularly relevant due to the difficulty of determining which traits are relevant; phylogeny can be a useful substitute to measuring a multitude of traits directly.

The predictive power of phylogeny is comparable to that of body size, although this can depend on the community or species of interest (Naisbit *et al.* 2012). Furthermore, phylogeny does not always explain the same aspects of TIS as present-day traits such as body size and the two can therefore complement each other. Eklöf & Stouffer (2016) found that phylogeny could explain "a significant background" of interactions, but after this "background" was explained, the use of specific traits, body size in particular, could still explain a lot of added information. They hypothesize that the reason body size in particular can add so much information is because it is less phylogenetically conserved than other traits. It is therefore less likely to be encapsulated in, and explaining the same variation as, the phylogeny. Furthermore, the effect of phylogeny is asymmetric; prey tended to interact with related predators more than predators interacted with related prey (Bersier & Kehrli 2008; Naisbit *et al.* 2012; Eklöf & Stouffer 2016). For prey, phylogeny is more important than body size in determining which predators they interacted with, while for predators, body size and phylogeny are of similar importance. A possible explanation may relate to the way in which predators vs prey compete with each other. Predators compete directly for shared prey, while prey compete indirectly by sharing predators (apparent competition). The former is likely to be a stronger driver for divergence than the latter (Naisbit *et al.* 2012). An alternative explanation is that traits related to a predator's foraging ability adapt more easily than traits determining prey vulnerability. This contention is supported by Rossberg et al. (2006) who found that foraging traits need to evolve faster than vulnerability traits to produce food webs like the ones that we find in nature. Where the measurement of traits is difficult, or when it is unclear which traits are most important to be measured, phylogeny may be a useful step in determining whether species traits are driving TIS.

THE ABIOTIC ENVIRONMENT CHANGES THE RELATIONSHIP BETWEEN TRAITS AND TROPHIC INTERACTION STRENGTH

Although it is clear that a species' traits affect its trophic interactions with other species, the nature of this relationship is largely dependent on the abiotic environment (figure 4). The abiotic environment can alter the relationship in two ways; (i) by altering a species' traits directly or altering the effectiveness of their traits (Brown *et al.* 2004; Grigaltchik, Ward & Seebacher 2012), or (ii) by affecting the spatiotemporal overlap between predator and prey (Parmesan 2006); before two individuals can have a trophic interaction, they must first encounter each other, so species with high spatiotemporal overlap are more likely to have a stronger interaction (Williamson 1993). An understanding of the effects of climate change on species interactions requires an understanding of both of these mechanisms, and because a change in abiotic environment affects both interaction partners to different extents, it can be difficult to predict the outcome of the change on TIS (Dell *et al.* 2013).

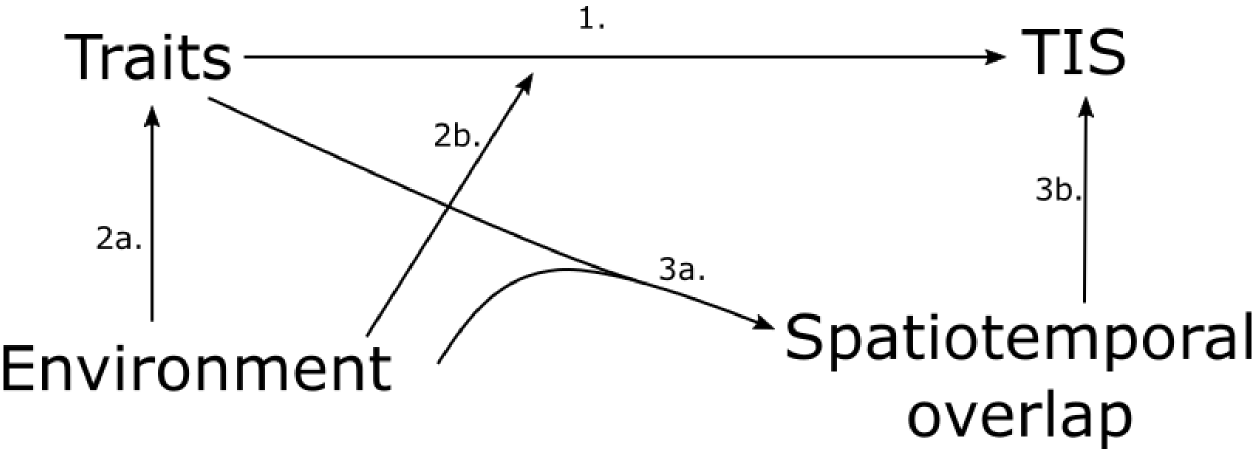

Figure 4: Traits directly influence TIS (1), but this relationship also depends on the abiotic environment. The environment can directly alter traits (2a) or the effectiveness of traits (2b). The environment can also indirectly affect the relationship between traits and TIS by interacting with traits to affect the spatiotemporal overlap of predator and prey (3a) which then determines TIS (3b).

DIRECT EFFECT ON (EFFECTIVENESS OF) TRAITS

In some cases, the abiotic environment can alter species traits directly. Temperature is a prime example of this. The direct effect of temperature on individual interactions is largely due to temperature's effect on a species metabolism, which, as outlined above, is closely tied to body size (Gillooly *et al.* 2001; Brown *et al.* 2004). As temperature increases, a predator's attack rate tends to increase (as it requires more food to meet its increased metabolic demands), handling time decreases and mobility of both predator and prey increase (Brown *et al.* 2004; Sentis, Hemptinne & Brodeur 2012). The sum total of all of these changes on TIS can be difficult to predict, as differential responses in the predator and prey can lead to significantly variant outcomes, and can depend on the foraging mode of the predator and type of interaction (Dell *et al.* 2013). For example, Grigaltchik et al. (2012) found that increasing temperature increased the velocity of both predators and prey, but the escape velocity of prey increased more than the attack velocity of predators, leading to a decrease in TIS. This kind of response can also depend on other traits, such as the foraging mode of the predator. Interactions with sit-and-wait predators will be affected primarily by changes in the prey's velocity, while active-capture predators will be affected by velocity of both predator and prey (Dell *et al.* 2013). The type of interaction may also be important; Legagneux et al. (2014) found that predation intensity increased by 4.5% per degree C increase in temperature in Arctic ecosystems, whereas plant-herbivore TIS decreased with temperature. This may be due to herbivores being unable to increase their feeding rate to the same extent as plant growth increased with temperature, but may also be caused by decreased herbivore population size as a result of increased predation. In addition, in warmer environments, individuals of some species grow to a smaller size than in colder environments (Daufresne, Lengfellner & Sommer 2009). Smaller-sized individuals also tend to thrive better in colder environments than larger individuals. Combined, this leads to a shift in body size ratio between predator and prey and an overall shift is size structure within the food web, both of which alter TIS (Yvon-Durocher *et al.* 2011; Brose *et al.* 2012).

Abiotic conditions can also influence the *effectiveness* of traits in relation to TIS. For example, camouflage is only effective in an environment which matches the camouflage. If the environment changes, camouflage is no longer effective and TIS will increase. This is illustrated by the classic example of the increase in darker morphs of the peppered moth, *Biston betularia,* as a result of industrialization darkening the trees they habitually rested on with soot (Kettlewell 1958). The more common light-colored morphs suddenly experienced stronger TIS from birds who could now spot them with greater ease (Cook 2003). Similarly, species with the behavior to respond to predation risk by hiding in refuges will have a lower TIS with their predators when in a habitat with ample refuges (Stuart-Smith *et al.* 2007; Pozzebon, Loeb & Duso 2015). The effectiveness of defenses also depends on the environment; in highly disturbed environments, defenses which decrease mobility are likely to be a liability and less defended but more mobile species will thrive (Peckarsky *et al.* 2015) .

In addition to meeting energy requirements, organisms (largely) meet their nutritional needs through consumption. Particularly in herbivorous interactions, the stoichiometry of a consumer's resources may not be equivalent to that required by the consumer. To remedy the resulting imbalance, consumers can actively choose to consume other resources with complementary stoichiometry. Raubenheimer & Simpson (2004) demonstrate that it is not only the ratio of different nutrients which is important, but also the absolute quantities. They show that locusts will regulate their consumption to meet their optimum intake of both protein and carbohydrates, and when fed food with a lower concentration of protein and carbohydrate, they would consume a greater quantity of the food to reach the same optimal intake. This leads to a stronger TIS with the resource. In some cases, species can drastically shift their diet to take advantage of abundant resources. Omnivores such as crayfish can move from an almost entirely herbivorous diet to an entirely predaceous one depending on the availability of each resource (Olsson *et al.* 2008; Arbačiauskas, Lesutiene & Gasiūnaite 2013). In some cases this flexibility depends on life stage and the requirement for certain nutrients for development, and/or can impact reproductive capacity (Coll & Guershon 2002). Water is a similarly essential component of an organism's diet and its availability can affect TIS. McCluney and Sabo (2009) show that in dry conditions, wolf spiders consume significantly more field crickets than when water is abundant, in which case they consume almost none at all. Furthermore, the crickets consume 31 times as much moist leaf material in dry conditions (strong TIS) than when water is abundant. As environmental conditions change and the availability of water and nutrients alters, this may have cascading effects on herbivores and their predators.

In summary, changing climate and habitat alteration have major effects on community structure. In many cases this is largely mediated by the altered effectiveness of species traits and therefore TIS. Prey which were once adequately defended against their predators, or predators who once had an effective hunting mechanism suddenly find themselves overexploited or starving as their previous strategies are no longer effective.

Spatiotemporal overlap

In addition to its direct effect on traits or trait effectiveness, the abiotic environment can affect TIS by altering the spatiotemporal overlap of interaction partners (Parmesan 2006). This is largely due to traits which affect how an organism interacts with the abiotic environment. For example, an organism with traits that make it more tolerant of cold weather is unlikely to have a strong trophic interaction with an organism with traits best suited for living in the tropics. In fact, a neutral model accurately predicted interaction strength in host-parasitoid networks by only including local population abundances (Canard *et al.* 2014). A species' traits dictate whether it will survive or thrive in a particular environment, and a combination of traits and environment which leads to a high spatiotemporal overlap of two species will increase their TIS. Traits which fall into this category include habitat domain, phenology, range and diurnal behavior (Boukal 2014). Changes in the environment, either seasonally, stochastically or long-term, will frequently have knock-on effects on TIS as species respond to the change at different rates, magnitude or direction (Parmesan 2006).

The way different species interact with their habitat can impact TIS. This can occur because of species spending time in different habitat types and thus being more or less likely to encounter each other. For example, Rusch et al. (2015) found that spiders with a stronger preference for arable land had a stronger TIS with aphids in agroecosystems. Schneider et al (2012) hypothesized that spiders' preference for hunting on top of the litter layer rather than in the interspace between soil and litter where their springtail and mite prey dwelled might explain the weaker than expected TIS between spiders and their prey. Because of the importance of habitat, TIS between two species can differ widely across habitat gradients.

Many species respond to a warmer climate by altering their range or phenology (Parmesan 2006). Some species have traits which allow them to emerge earlier in the spring or to remain active during winter. This decreases interaction strength, at least at certain times, with species which are only active during the summer or emerge later in spring. How species respond to seasonal changes – which is dictated by their traits – can have important implications for interactions. For example, in Broadstone Stream, an increase in small prey during summer led to a shift in the diet of tanypod midges (Chironomidae) to become more predatory and exploit the higher density of prey (Woodward *et al.* 2005b). Similarly, a species' diurnal behavior can alter its spatiotemporal overlap with potential predators or prey, altering their TIS. Many species adopt nocturnal behavior to avoid potential predators (Berger & Gotthard 2008). Changing spatiotemporal overlap with interaction partners can be an effective mechanism to capture more prey or avoid predation, but when spatiotemporal overlap changes due to external forces it can drastically change the success or survival of both species.

Due to the dependence of the trait-TIS relationship on the environment, changes in conditions can have severe consequences for trophic interactions and communities as a whole. There are multiple factors of the abiotic environment which can change and affect species interactions, including temperature, climate, disturbance and enrichment. These changes are increasing in frequency and magnitude due to current levels of anthropogenic impacts, and frequently multiple changes occur and interact at the same time (IPCC 2007). Because a change in the abiotic environment may affect both interaction partners but to different extents, it can be difficult to predict the effect of the change on TIS. If two species respond to an environmental change in the same way, rate and extent, then static properties of the interaction, such as relative population sizes and coexistence at equilibrium, should remain constant (Dell *et al.* 2013). However, because species differ in their traits, and their traits dictate how they respond to environmental change, a given change is highly unlikely to affect all species or individuals identically. Mismatching responses to changing abiotic conditions can occur in a number of ways. Species can respond to the change to a different extent, such that one may have a strong response and the other a weak or nonexistent response. Species can respond at different rates, or their response may peak at different conditions (Dell *et al.* 2013). Frequently two or three of these mechanisms occur at the same time, complicating predictions of how organisms will respond to environmental change. When mismatches occur, consumers struggle to survive without their food resources, prey populations can explode when released from predation, or crash under increased pressure from new predators.

Disturbance and enrichment can also impact trophic interaction strength. Depending on their traits, disturbance can have stronger effects on some species than others. For example, in steam systems, larger and more mobile species can withstand disturbances better than highly defended but immobile species (Power, Holomuzki & Lowe 2013; Peckarsky *et al.* 2015). After a disturbance, therefore, the population sizes of the interacting species will be very different than prior to the disturbance, impacting TIS. Similarly, ecosystems which are frequently disturbed have a different community of species than those which are rarely disturbed (Townsend *et al.* 1998). This results in not only a difference in TIS between specific species due to altered population sizes, but also a difference in TIS between different trophic levels, such as herbivores and plants, due to different traits of species present in disturbed compared to undisturbed environments. For example, Peckarsky et al. (2015) found that highly disturbed streams were dominated by mayflies, a more mobile species which can withstand disturbances, while more stable streams were dominated by caddisflies, a highly defended species which cannot easily escape disturbances. TIS with resources therefore decreased as disturbance increased, because mayflies had a weaker impact on resources than caddisflies, in addition to being recruitment limited at the highest levels of disturbance. However, this relationship was moderated by levels of productivity. In enriched streams, grazers had low impact on the resource regardless of disturbance level, because their feeding rate did not increase to the same extent as primary producer productivity did. Sentis et al. (2014) also found decreasing TIS with enrichment in a terrestrial tritrophic system. This was due to a nonlinear feeding rate of the predator which could not keep up with the increase in prey at higher levels of enrichment.

Trophic interactions do not occur in a vacuum and the role of the environment cannot be ignored. However, the high level of spatial and temporal variation in environmental conditions, as well as the myriad ways in which species can respond to this variation, significantly complicate matters. For conservation and management, it is often important to understand how species will interact based on their traits, the role and effect a new species will take if it invades a community, and how communities will respond to a changing climate. To do so, however, requires that we understand the role environment plays and how traits and interactions will respond, both directly and as a result of changing spatiotemporal overlap.

BEYOND PAIRWISE INTERACTIONS

Species do not occur in isolated pairs, and the flow-on effects from and to other species are also relevant. A number of different mechanisms cause flow-on effects including impacts on abundance, movement between local food webs, non-trophic interactions with other species, and behavioral responses to one predator increasing vulnerability to another predator. Within a community, the sum total of these direct and indirect effects determine the success and survival of each species.

Similar to spatiotemporal overlap, the abundance of interacting populations is an essential component affecting interaction strength – the more abundant a species is, the more likely it is to encounter and interact with other species (Canard *et al.* 2014). When considering a simple predator-prey pair, the abundance of the two species should reflect TIS. Each species should respond to abundance changes of the other species in a relatively predictable manner. In reality however, most species interact with more than one partner, and it is the sum of these interactions which dictates the dynamics of the interacting populations. This can be to either the benefit or detriment of a species. For example, when two prey species share a predator (apparent competition), increases in one prey species can lead to increases in the predator population (Holt 1977). This in turn increases TIS with the second prey species. On the other hand, predators which focus their efforts on the most abundant prey species can release rare prey. Frost et al. (2016) demonstrated that this mechanism can occur both within a habitat and across habitat borders; apparent competition, mediated by shared parasitiods, predicted a significant portion of future parasitism rates and herbivore abundances. Trophic cascades, where the abundance of predators in one trophic level controls the abundance of their prey, which in turn controls the abundance of *their* prey, are a similar phenomenon (Watson & Estes 2011). Abundances of one species and its resultant TIS flow on beyond their immediate interaction partners.

Prey develop defensive traits in response to their predator's hunting tactics. The traits which provide protection from one predator, however, do not necessarily provide protection from another. In extreme cases, it can *increase* vulnerability to another predator. For example, some species of aphids will drop from the plant they are feeding on to avoid predation by lady beetles (Coccinellidae) (Losey & Denno 1998c). While this decreases their vulnerability to the lady beetles, it increases their likelihood of being preyed on by ground beetles (Carabidae) when they fall from the plant (Losey & Denno 1998a b; Grez, Rivera & Zaviezo 2007). A similar effect occurs in freshwater systems, where the combined effect of sculpins (*Cottus bairdi*) and stonefly larvae (*Agnetina capitata*) on mayfly larvae (*Ephemerella subvaria*) is higher than predicted. *Ephemerella* reacts to stonefly larvae by defensive posturing or crawling away which makes them more conspicuous to fish (Soluk 1993).

In contrast to the facilitative effects of multiple predators, predators can have negative effects on each other (Schmitz 2007; Frago & Godfray 2014). This frequently occurs because many predators are also prey to other predators. They need to balance their traits for foraging with traits for avoiding predation. In the above example consisting of sculpins and stonefly larvae, Soluk (1993) also tested the predators' impact on another mayfly species, *Baetis tricaudatus.* In this case, the combined effect of the two predators on *Baetis* was *lower* than predicted. In addition to feeding on mayflies, sculpin will also feed on the stonefly larvae; stoneflies respond to this threat by decreasing their movement and hiding on the underside of rocks which decreases their capacity to feed on *Baetis.*

In an ecological community, it is the outcome of all these interacting trophic and non-trophic interactions which ultimately shapes community dynamics. For example, Frago and Godfray

(2014) show how both the interaction between predators as well as apparent competition can impact population sizes of multiple interacting species across generations. They used a model insect community comprising of two plant species (*Vicia* and *Triticum*), two aphids (*Acyrthosiphon pisum* on *Vicia* and *Sitobion avenae* on *Triticum*), a parasitoid (*Aphidius ervi*) and a dominant intraguild predator (*Coccinella septempunctata*). *Coccinella* feeds on both species of aphids as well as on the parasitoid. As a result, the parasitoid will avoid chemical traces of *Coccinella.* In this experiment, application of *Coccinella* extracts to *Vicia* plants decreased parasitism of *A. pisum.* In the short term this had no effect on the other aphid species, *S. avenae*, despite the potential for them to be used as alternative prey to *A. pisum.* It did, however, result in decreased parasitoid recruitment. This then lead to an increase in population size of both aphid species. The behavioural response of the parasitoid to decrease TIS with its predator lead to altered TIS with both prey species which in turn would increase their impact on their host plant species.

CONCLUSIONS AND FUTURE DIRECTIONS

Clearly, traits are important for trophic interactions. While body size may be the most well studied trait and one easily measured and applied to a huge variety of systems and species, other traits are also important in dictating TIS. These traits are usually related to the foraging ability of the consumer or the vulnerability of the prey. The exact identity of the traits important in any given situation, however, depends on the identity of the interacting predator and prey and, frequently, on a match between their traits. The relationship between traits and TIS has been used, with a fair amount of success, to predict food web structure and interactions. The question of which traits affect interaction strength and how, though, is far from fully answered, and there remains a number of valuable avenues of research.

Firstly, it is important to determine which traits, other than body size, are important in dictating TIS. Ideally, this could be narrowed down to a handful of the most important traits, as measuring *all* traits is largely infeasible. While some traits are broadly relevant, most traits are specific to the system and organisms studied (e.g. marine fish or herbivorous insects in grasslands) and there is frequently a match between relevant consumer and resource traits. In many cases, a trait relevant for predation on one prey type may be irrelevant for predation on another prey type. A trait hierarchy may be one way to determine TIS using the minimum number of traits; one set of broad traits to categorize consumers and resources into relevant systems or guilds, then within those groups, a particular set of other traits can give more specific information on TIS.

Although it is generally accepted that traits are important for TIS, there are a number of gaps in our understanding which, if filled, would help clarify the trait-TIS relationship. Intraspecific, spatial, and temporal variation are some of the gaps which are beginning to be filled. Historically, most studies used species averages as trait values, however studies show that individual variation can impact TIS (Gibert & Brassil, 2014; Woodward et al., 2010). Food webs resolved at the individual scale are allowing further exploration of this concept (Woodward *et al.* 2010; Gilljam *et al.* 2011; Svanbäck *et al.* 2015). Population abundances change temporally and spatially, as do their ranges and even their traits (Parmesan 2006; Rudolf 2012). Some trophic interactions are more important at certain times or locations than others (Closs & Lake 1994). Increased spatial and temporal resolution of trophic interactions will enhance our understanding of this variation. Currently, the relationship between traits and TIS is most well understood for predator-prey interactions. These, however, consist only a small proportion of all trophic interactions. Understanding which traits are important for predicting TIS for herbivorous, parasitic and other trophic interactions is essential in order to quantify and understand food webs.

Ecological communities are experiencing high levels of change as a result of anthropogenic activity. An understanding of the relationship between traits and TIS would allow greatly increase the ability to study how communities will respond to these changes. For example, by predicting novel interactions where species ranges are shifting or new species are invading (Gravel, Poisot, Albouy, Velez, & Mouillot, 2013), or quantifying how a community may respond to disturbances (Wootton & Stouffer 2016). Finally, TIS is essential for the stability of ecological communities (McCann *et al.* 1998). By understanding the effect of traits on TIS, it may be possible to begin engineering simple communities with the addition or control of species with particular traits in order to enhance stability. With increasingly novel collections of species forming communities, it is more important than ever to understand the relationship between a species traits and TIS and what that means not only for the interacting populations, but also for the rest of the community.

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