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Trait-matching and phylogeny as predictors of predator-prey interactions involving ground beetles

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Running-Head: Trait-matching & phylogeny

Summary

1. With global change modifying species assemblages, our success in predicting

    ecosystem level consequences of these new communities will depend, in part, on our

    ability to understand biotic interactions. Current food web theory considers

    interactions between numerous species simultaneously, but descriptive models are

    unable to predict interactions between newly co-occurring species. Incorporating

    proxies such as functional traits and phylogeny into models could help infer predator/

    prey interactions.

2. Here we used trait-matching between predator feeding traits and prey vulnerability traits, along with phylogeny (used as a proxy for chemical defence and other traits difficult to document), to infer predatory interactions using ground beetles as model organisms.

3. A feeding experiment was conducted involving 20 ground beetle and 115 prey species to determine which pair of species did or did not interact. Eight predator and four prey functional traits were measured directly on specimens. Then, using a modeling approach based on the matching-centrality formalism, we evaluated 511 predictive ecological models that tested different combinations of all predator and prey functional traits, and phylogenetic information.

4. The most parsimonious model accurately predicted 81 % of the observed realized and unrealized interactions, using phylogenetic information and the trait-matches predator biting force/ prey cuticular toughness and predator/ prey body size ratio. The best trait-based models predicted correctly >80 % which species interact (realized interactions), but predict <58 % of which species did not interact (unrealized interactions). Adding a phylogenetic term representing the evolutionary distance within each trophic level increased the ability to predict which species did not interact to >75 %.

5. The matching of predator biting force and prey cuticular toughness demonstrated a better predictive power than the commonly used predator/ prey body size ratio. Our novel model combining both functional traits and phylogeny extends beyond existing descriptive approaches and could represent a valuable tool to predict consumer/ resource interactions of newly introduced species and to resolve cryptic food webs.

Introduction

Predicting the dynamics of novel communities arising with global change will depend on our

ability to understand interactions between species (Van der Putten, Macel & Visser 2010).

Current food web theory considers simultaneous interactions between a high number of

species and is useful to anticipate the consequences of species extinction on the structure of

food webs (Dunne, Williams & Martinez 2002). Its predictive ability is however limited to

known interacting species and is thus unable to predict interactions between newly co-

occurring species resulting from a recent invasion or a range shift (Gravel et al. 2013). A

further problem is that food web models are limited by the documentation of interactions. It is

not feasible to document all potential interactions between species of a region with traditional

techniques (direct observation, DNA analysis of gut content, etc.), making it important to

develop inference tools (Morales-Castilla et al. 2015).

Recent descriptive models of food web structure rely on two important sources of

information; functional traits (Petchey et al. 2008; Allesina 2011) and phylogeny (Cattin et al.

2004; Bersier & Kehrli 2008). Functional traits represent any characteristics measurable at

the individual level influencing the fitness of an organism (Violle et al. 2007) and could be

instrumental to determine foraging ability of a consumer and the vulnerability of the resource.

Previous studies demonstrate that most ecological networks can be represented in a three to

five dimensional space, presumably related to functional traits (Eklöf et al. 2013). Phylogeny

is used as a proxy of similarity in trait values between related groups of species (Webb et al.

2002) and accordingly indicates an evolutionary based conservatism in interactions of close

relatives (Bersier & Kehrli 2008). This aspect could be particularly important for traits that are hard to measure, such as chemical defence of prey (Eisner, Eisner & Siegler 2005) or digestive enzymes of predators (Feyereisen 1999).

Although mixing both traits and phylogeny could be efficient to predict ecological interactions (Morales-Castilla et al. 2015), food web models including them are descriptive only (Rezende et al. 2009; Rohr et al. 2010; Rafferty & Ives 2013; Krasnov et al. 2016). The few existing predictive models are still based uniquely on trait-matching (Gravel et al. 2013; Rohr et al. 2016). The trait-matching approach takes into account the probability of interactions between the traits of the consumer and the traits of the resource (Rohr & Bascompte 2014; Gravel, Albouy & Thuiller 2016a). An example of trait-matching would be the matching of pollinator tongue length with flower traits such as corolla tube depth (Ibanez 2012). Similarly, traits of marine mammal predators such as swimming speed and muscle lipid content can be matched to prey traits such as lipid and caloric content (Spitz, Ridoux & Brind'Amour 2014).

The trait-matching approach has been extended through the matching-centrality formalism, which considers simultaneously the matching and the centrality components of a network and has the added advantage of being able to predict unobserved, but existing links between rare or newly co-occurring species (Rohr et al. 2016). The matching component quantifies the compatibility between the foraging traits of the consumer and the vulnerability traits of the resource. The centrality component determines the specificity/ generality of a species; in other words, species sharing similar traits are expected to realize a similar number of interactions (Rohr & Bascompte 2014). Each species (consumer and resource) is characterized by a set of matching traits and centrality traits; these could be evaluated as

latent variables or directly using measured traits (e.g. body size, tongue length, nectar holder depth). The phylogenetic position of a species in a community could be used as an intermediate since it is essentially a latent variable aimed to represent unmeasured functional traits (Cadotte et al. 2009). It provides an elegant solution to circumvent problems related to the measurement of some traits, but the drawback is that one does not acquire insight into possible mechanisms as when measuring true functional traits.

In the specific case of predator/ prey interactions in terrestrial environments, the use of trait-matches to predict interactions has been limited to the size ratio of predator and prey through the matching-centrality formalism (Gravel et al. 2013). Other known important traits of predators such as biting force (Wheater & Evans 1989; Christiansen & Wroe 2007) and handling ability (Brodie & Formanowicz 1983; Cunha & Planas 1999) have yet to be matched to relevant prey traits. For instance, the cuticular toughness of prey can act as an armor protecting them from weaker predators (Broeckhoven, Diedericks & Mouton 2015). Such matching could create a shift in the predator/ prey size ratio relationship such that the predator could interact with larger soft prey and smaller hard prey (Enders 1975). Including these traits could help to refine trait-matching models, but so far, neither their descriptive nor they predictive ability were quantified for any system.

Our objective was to develop a predictive model to infer predator/ prey interactions using ground beetles (Coleoptera: Carabidae) as model organisms. We used functional traits as the main predictors of interactions, based on the matching-centrality formalism, and we complemented our analysis with phylogenetic information to represent traits that were not documented or that were hard to measure. Our working hypothesis was that both traits and phylogeny would explain most of the observed feeding interactions. Our predictions were

that i) the most important ground beetle traits would be body size, mandibular gape and biting force (Evans & Forsythe 1985; Wheater & Evans 1989; Cohen et al. 1993) combined respectively to the prey traits body size, body width and cuticular toughness, and ii) ground beetles belonging to the same clade would be more likely to share prey than distantly related ones. We tested these predictions with a feeding experiment to determine prey with which different species of ground beetles did or did not successfully interact. Then, we predicted the feeding interactions of ground beetles based on the matching-centrality formalism.

Material and methods

Collection of specimens

Ground beetles and their prey were collected at several sites and in various habitat types in southern Quebec, Canada, to maximize phylogenetic and morphological diversity. Overall, we collected specimens of 20 species of ground beetles representing 13 genera, nine tribes and four sub-families (Table 1 and S1 in Supporting Information) and a total of 115 prey species of arthropods (woodlice, millipedes, caterpillars, spiders, etc), earthworms, mollusks and land planarians (Table S2). These included all life stages from eggs to dead specimens. Prey were identified to the lowest taxonomic level we were able to reach, or were classified as morphospecies (hereafter referred to as species), when species level identification was impossible. We kept at least one specimen of each species in 70 % alcohol when possible (i.e. when we had more than one specimen on hand) to measure traits that could not be assessed on live specimens. Likewise, all ground beetle predators were preserved in 70 % alcohol.

Feeding experiment

We conducted a total of 475 pairwise feeding experiments in the laboratory in a regulated environment at 24°C, 70 % humidity and a day/ night cycle of 16/ 8 hours. Given the major effort to collect organisms (e.g. once or twice a week for two months), identify them and keep them alive prior to the experiment, pairwise tests were generally not replicated, and not every possible interaction was tested. Nonetheless, interactions were chosen to maximize the variation in traits and phylogenetic diversity of prey for each ground beetle species (Appendix S2). Ground beetles were kept separately in plastic containers of $11 \times 11 \times 4.5$ cm lined with a moistened filter paper at the bottom. Filter paper was moistened daily and changed twice a week.

Ground beetles were starved for 24 h prior to the feeding experiment, after which they were provided with one prey at a time. Prey consumption was recorded after 24 and 48 h. A realized interaction was noted if the prey was killed and consumed at least partially. An unrealized interaction was recorded if the ground beetle did not kill the prey after 48 h. On two occasions, the ground beetle successfully killed the prey, but did not consume it; the interaction was considered as unrealized.

Functional traits

Ground beetle and matched prey traits were selected to represent hypothesized limitations in their potential interactions (Table 2). These limitations included 1) predator/ prey size ratio (measured as body length) which is a commonly used proxy for physical limitation of interactions (Cohen et al. 1993); 2) predator biting force (estimated from allometries with head and mandibular size (Wheater & Evans 1989)) that was to match prey cuticular toughness (Wheater & Evans 1989; Broeckhoven et al. 2015); 3) predator mandibular gape,

which is related to handling ability and was to match prey body width (Evans & Forsythe 1985); and 4) predator eye size that was to match the speed of movement of prey (Bauer & Kredler 1993). We also included four predator traits associated to mandibular characteristics hypothesized to relate to prey handling (Evans & Forsythe 1985; Acorn & Ball 1991), but that were difficult to match to any prey traits. These were mandibular length, length of liquid absorption section, length of cutting section (terebra) and length of apical tooth. Body length instead of body mass was selected for practical reasons: it was impossible for us to weigh prey before offering them to predators, and metrics to estimate body mass were not available for many of our prey types. All measurements of ground beetle traits were made on alcohol-preserved specimens under a dissection microscope with a graduated eyepiece. Body length and width of prey were measured when possible on living specimens. Cuticular toughness of prey was measured on dead specimens with a Pesola® pressure set (Medio-Line) to which we added an entomological pin of 0.45 mm of diameter. All traits, except for cuticular toughness, were measured on every individual ground beetle and prey specimen. Cuticular toughness was measured on one to six specimens per species (depending on availability); a mean trait value per species was used for model construction. Further detail on the methodology used to measure traits can be found in Appendix S2.

Phylogeny

The phylogenetic distance matrices of prey and ground beetle species were based on taxonomic level. For each of the 15 taxonomic levels (species to super-phylum), the distance was incremented by one so that it characterized only the topology of the tree. For morphospecies, the distance was assigned as the next taxonomic level; e.g. all Noctuidae sp. were considered as belonging to different sub-families. Principal coordinates analyses (PCoA) were performed on both ground beetle and prey distance matrices to determine the

position of each species in the phylogenetic space. The PCoA were performed on a δ

transformed phylogenetic distance matrix to reduce the importance of superior taxonomic

levels on the species scores permitting a finer resolution between lower taxa (orders, families,

genera) (Pagel 1997). We selected the δ value for each group giving the best goodness-of-fit

of the model with the hypothesized trait-matches predator size/ prey size, predator biting

force/ prey cuticular toughness and predator mandibular gape/ prey body width; it was set to

three for ground beetles and six for prey. The phylogenetic score of all eggs, pupa and dead

specimens of a particular prey species was set to the same value corresponding to 50 points

over the previous stage group on both axes. By so doing, it was possible to correctly

distinguish interactions of ground beetles with inactive stages of prey from interactions with

active stages.

Statistical analysis

We recorded for each tested pair of species (i, j) if they interacted or not (noted L_{ij}). Realized

interactions were coded as $L_{ij} = 1$ and unrealized interactions $L_{ij} = 0$. When development

stages of a same species were highly different, they were included as two different species

(e.g. immobile stages vs. mobile stages, larva and adult of holometabolous insects), each with

their own trait values. Overall, the matrix included 151 prey types. We added 88 realized

interactions reported in Larochelle and Larivière (2003); only interactions we could confirm

from cited references were included (Table 1). For these 88 cases (representing 13 prey

species), prey were attributed trait values of equivalent measured specimens. No unrealized

interactions were included from the literature as these have been rarely documented. We also

added 74 forbidden interactions (Morales-Castilla et al. 2015) between the smallest predators

and larger prey, such as between the ground beetle *Elaphropus anceps* (LeConte) (size = 2.1

mm) and the millipede *Narceus americanus* (de Beauvois) (size = 70 mm).

Matching-centrality formalism

Interactions were analyzed following the matching-centrality formalism (Rohr et al. 2016). Each species was represented by a "matching" and a "centrality" component. The "matching" component represented the combined effect of predator (f_j) and prey (v_i) traits; i.e. how the traits interact. The "centrality" component represented the direct effect of the traits alone for predator and prey, i.e. accounts for their respective specificity/ generality relative to the number of associated prey or predators. The probability of interaction $P(L_{ij} = 1)$ based on a general linear model (GLM) follows a log-linear model of the form (Rohr et al. 2016):

$$\text{logit}(P(L_{ij} = 1)) = -\lambda(v_i - f_j)^2 + \delta_i v_i + \delta_2 f_j \tag{1}$$

where λ, δ_1 and δ_2 are parameters describing the importance of the "matching" $(v_i - f_j)^2$ and of the "centrality" of prey (v_i^*) and predators (f_i^*). Ecologically, the v term represents the vulnerability of the prey, while the f term represents the foraging ability of the predator (Rohr & Bascompte 2014). Rohr et al. (2016) evaluated latent traits and related them after to observed traits, while here we considered them directly. We tested four hypothesized trait-matches that included predator body length/ prey body length, predator biting force/ prey cuticular toughness, predator mandibular gape/ prey body width and predator eye size/ prey speed of movement. For unmatched predator traits (Table 2), only the centrality was accounted for. We also considered the phylogenetic position of a species (as determined by PCoA scores along the first two axes), which is equivalent to a latent trait representing the conservatism of interactions resulting from evolutionary processes (Bersier & Kehrli 2008; Morales-Castilla et al. 2015).

General Additive Models (GAM)

We used general additive models (GAM) which permit a higher flexibility than general linear models (GLM) (Wood 2006) to fit the matching-centrality formalism. GAMs are based on a smooth function determining the number of inflexion points in the curve of the model for each term. High smoothing can, however, force the curve to over-fit observed data such that missing data highly influence the shape of the curve and can make it ecologically meaningless (Wood 2006, p. 128). To prevent this problem, we tested separately each trait-match to find the lowest smoothing limit from which a smooth curve representing the hypothetical relationship was obtained (Appendix S3).

We fitted the phylogenetic model as an interaction between the scores of the two PCoA axes of ground beetles and prey. This model thus explains the probability of a species to interact with another based only on its position in phylogenetic space. The new equation for the matching-centrality formalism, based on a GAM and including the phylogenetic component, is given as:

$$E\big(P(L_{ij}=1)\big) = s_1\big(PCoA1_{fi}, PCoA1_{vi}\big) + s_1(PCoA1_{fi}, PCoA2_{vi}) + s_1\big(PCoA2_{fi}, PCoA1_{vi}\big) + s_1\big(PCoA2_{fi}, PCoA2_{vi}\big) - \lambda\big(s_2(v_i - f_i)^2\big) + \delta_1 s_3(v_i) + \delta_2 s_4(f_i) \qquad (2)$$

where s_x are smooth functions and $PCoAx_{fi}$ and $PCoAx_{vi}$ are respectively PCoA scores for predators and prey on axis x.

Goodness-of-fit

We wanted to determine the predictive ability of predator/ prey interactions of each trait-match, unmatched trait and the phylogenetic term, but also to determine which model had the best fit. The goodness-of-fit was defined based on four metrics: accuracy, sensitivity, specificity and true skill statistic (TSS) (Allouche, Tsoar & Kadmon 2006). Accuracy is the

percentage of well-predicted realized and unrealized interactions; sensitivity is the percentage of well-predicted realized interactions and specificity is the percentage of well predicted unrealized interactions. All three measures have a value between 0 (absence of good prediction) and 1 (perfectly predicted). TSS represents correct predictions in relation to incorrect predictions and varies between -1 (incorrectly predicted) and 1 (perfectly predicted). The goodness-of-fit was computed for all possible combinations of the four trait-matches, four unmatched traits and the phylogenetic term (representing a total of 511 possible combinations of the nine terms - Table S4).

For many prey species, we observed a wide range of trait values reflecting intraspecific variation. Given that predator/ prey interactions would be influenced by this variability, the probability of interaction was calculated for all potential combinations of prey trait values considering a step of 0.5 mm for length and width, and a step of 2 g mm^{-2} for cuticular toughness. No variation was allowed for speed of movement. Predicted realized interactions between a ground beetle and a prey species were determined in two steps. First, the predicted probability of interaction needed to be ≥ 0.5 for at least one combination of the trait value of the prey. Second, the model needed to predict at least 25 % of realized interactions. This approach allowed us to eliminate cases where the ground beetle was predicted to interact only with individuals of the species with extreme trait values.

Null model

We tested the statistical significance by comparing the predictive ability of the models with two null models. The first null model hypothesized that interactions were distributed independently of traits, phylogeny or species. This scenario was computed by randomizing the interactions in the observed matrix between predators and prey. The second null model

hypothesized that the level of specialization (number of interactions observed) was species-specific for ground beetles, but that traits and phylogeny were not involved. In this scenario, interactions of the observed matrix were randomized only between prey, so that each ground beetle species always had the same number of realized and unrealized interactions. Ten thousand iterations were run for both null models. We calculated accuracy, sensitivity, specificity and TSS for each randomized matrix. Significance of each aspect of the tested models (accuracy, sensitivity, specificity and TSS) was determined by calculating standardized effect size (SES) with the formula SES = $(I_{obs} - I_{sim})/\sigma_{sim}$ where I_{obs} is the observed value, and I_{sim} and σ_{sim} are respectively the mean and the standard deviation of the null model. The SES was calculated for both null models after verifying normality, and the mean value was used to test the significance (Veech 2012). We accepted that a SES>1.96 (P<0.05) indicated a better goodness-of-fit than the null models (Veech 2012).

The over-fitting of the phylogenetic term by the GAM could not be evaluated visually as for the trait-matches. Thus, we created a null model assuming a random phylogenetic relationship between ground beetles and prey species. In a first step, the phylogenetic scores of ground beetles and prey species were randomized. Then, we calculated the TSS of a model based on equation 2 including only the randomized phylogenetic term. We varied the degree of smoothing (s_1) from 10 to 30 with a step of two. These operations were performed with 500 iterations for each degree of smoothing. We kept the upper degree of smoothing for which the mean TSS was within the range of the null models, i.e. the higher smoothing value for which a randomized phylogeny did not predict more interactions than chance alone. The degree of smoothing was fixed at 24. All smoothing was done using the "Thin Plate Regression Splines (TPRS) with shrinkage" approach (Wood 2006). The gamma term was set to 1.4 to prevent over-fitting (Kim & Gu 2004). All models were computed as a binomial regression using the function 'gam' in the R package 'mgcv' (Wood 2015).

Results

Between 4 and 71 observations were made for each ground beetle species with on average 23 per species (Table 1). Realized interactions were observed in 54 % of the feeding tests for the 17 ground beetle species with $\geq$ 10 observations. Only four species had < 50 % of realized interactions with offered prey, including *Myas cyanescens* Dejean that did not interact with any of the 14 offered prey species. *Pterostichus caudicalis* Say was the species with the highest percentage (86 %) of realized interactions (12 interactions over 14 observations).

The best overall model had an accuracy of 83.4 %, a TSS of 0.65 and included three trait-matches (predator size/ prey size, predator biting force/ prey cuticular toughness and predator eye size/ prey speed), two unmatched predator traits (length of the mandible and length of cutting section) and the phylogenetic term (Appendix S4). All four aspects of the goodness of fit (accuracy, sensitivity, specificity and TSS) were significantly higher than both null models (SES>3.9, *P*<0.001). The 'best parsimonious' model was predator size/ prey size + predator biting force/ prey cuticular toughness + phylogeny, with an accuracy of 81.4 % and a TSS of 0.61. This model also had significantly higher scores for the four aspects of the goodness of fit than for both null models (SES>3.7, *P*< 0.001) (Table 3). Adding the trait-match predator mandibular gape/ prey body width slightly increased the accuracy to 82.5 % and TSS to 0.63.

The best single trait-match model was predator biting force/ prey cuticular toughness (accuracy = 71.5 % (SES=3.17, *P*<0.001); TSS = 0.37 (SES=2.92, *P*=0.002)), followed by predator mandibular gape/ prey body width (accuracy = 67.5 % (SES= 2.44, *P*= 0.007); TSS = 0.26 (SES= 1.94, *P*> 0.05)) and predator size/ prey size (accuracy = 66.4 % (SES= 2.24, *P*= 0.013); TSS = 0.23 (SES= 1.67, *P*> 0.05)) (Table 3). The model with predator biting force/

prey cuticular toughness had a significantly higher accuracy, sensitivity and TSS than null models, but not specificity. The model predicted an increased probability of realized interactions between strong predators and hardened prey, but we found an abrupt threshold response around a cuticular toughness of 40 g mm^{-2}, following which no realized interactions were predicted (Figure S8A).

Adding phylogenetic information increased the accuracy and the TSS of all models (Appendix S4). It also had a strong positive impact on the specificity increasing it on average for all models by 24 %. For individual trait-matches and unmatched traits, the specificity increased by 29 % on average with the added phylogenetic term. When taken alone, phylogenetic information (accuracy = 74 % (SES=3.61, P<0.001); TSS = 0.46 (SES=3.72, P<0.001)) had a better goodness of fit than any single trait-match model (Table 3).

Discussion

We found that the matching-centrality formalism accurately predicted predatory interactions of ground beetles (Table 3). The combination of the phylogenetic term with trait-matches predator biting force/ prey cuticular toughness and predator/ prey size ratio captured most of the variation of predator/ prey interactions observed in our experiments. This success demonstrated that combining these three terms could increase our ability to infer trophic interactions among arthropod and soil invertebrates better than considering predator/ prey size ratio alone. While predator/ prey size ratio is of common use, biting force has rarely been considered when studying interactions of arthropods (but see Ibanez et al. 2013; Deraison et al. 2015 for herbivorous arthropod examples). It is, however, commonly used with vertebrates (e.g. Wroe, McHenry & Thomason 2005; Christiansen & Wroe 2007). The resistance of arthropod ecologists to use it is possibly due to the difficulty to measure the

force of arthropod bites, but this could be circumvented by the use of allometries as used with extinct vertebrates (Wroe et al. 2005). Our study shows that these allometries are reliable, at least as a comparative tool, and can be used to successfully predict interactions between arthropods. Contrary to our expectation, predator biting force/ prey cuticular toughness had an overall better goodness of fit than predator/ prey size ratio (Table 3).

Phylogeny

No model accurately predicted unrealized interactions without the inclusion of phylogenetic information. While all the models with TSS higher than the null models predicted at least 80 % of realized interactions, none predicted more than 58 % of unrealized interactions (i.e. equal to the null models). This difference demonstrates that realized interactions were easier to predict than unrealized interactions based on trait-matching only. The lack of replication for many interactions in the feeding experiment may have artificially increased the number of unrealized interactions, making them harder to predict. Furthermore, it is highly probable that unrealized interactions could be better predicted by including traits that reflect prey defence strategies, such as mucus secretion by slugs (Pakarinen 1994), fast jumping ability of springtails (Bauer & Kredler 1993) and deterrent chemical compounds (Eisner et al. 2005). However, chemical and other specialized defence strategies can be hard to quantify and thus to include in a trait-matching model. As these traits are generally shared with close relatives (Eisner et al. 2005), phylogenetic information can be useful to assess several aspects of predator/ prey interactions that cannot be accounted for easily with available trait data (Morales-Castilla et al. 2015).

Phylogeny in itself captures much of the variation explained by the traits (Table 3), which could suggest that using phylogeny alone would be more parsimonious. However, phylogeny is relevant only for species (or maybe genera) included in the present experiment, and does not bring any information on the mechanisms involved in prey selection. In contrast, the information gathered through trait matching is generalizable to other arthropods and useful to understand food web structure (Morales-Castilla et al. 2015; Gravel et al. 2016a). Also, a phylogenetic analysis could miss relevant variation among close relatives. For example, it was shown that in tiger beetles (Carabidae: Cicindelinae), body size and length of the mandibles were unrelated to their phylogenetic position (Barraclough, Hogan & Vogler 1999). We see phylogeny as a useful tool helping to circumvent problems caused by the collection of important, but hard to measure, traits.

Trait-matching

The trait-match biting force of predator/ cuticular toughness of the resource was the best predictor with ground beetles, but we expect it to be generalizable to other predators (Verwaijen, Van Damme & Herrel 2002), granivores (Abbott, Abbott & Grant 1975; Lundgren & Rosentrater 2007), herbivores (Ibanez et al. 2013) and potentially detritivores (David 2014). It provides a common currency, more generalizable than body size (Bartomeus et al. 2016) and thus, has potential to describe interactions of omnivorous species. Contrary to our original hypothesis, the trait-match mandibular gape of the predator/ body width of the prey did not bring significantly more information to the trait-matches biting force of predator/ cuticular toughness, predator/ prey size ratio and the phylogenetic term. However, this trait-match is expected to be more important for predators that swallow their resources as a whole (Bremigan & Stein 1994), which were absent from our dataset. Similarly, the matching of the eye size of the predator and the movement speed of prey was hypothesized to be

important to predict predation of ground beetles on springtails that often co-occur in the leaf litter layer (Bauer & Kredler 1993). However, this trait-match was also a poor predictor, possibly explained by the inclusion of only one truly big-eyed predator (*Notiophilus aeneus* (Herbst)). Despite that, it is of interest that *N. aeneus* was the sole species to successfully consume springtails in our experiment.

A novel tool to quantify predator-prey interactions

Our study brings a new tool to resolve cryptic food webs and could be generalized to a large array of organisms as all predatory interactions are determined by similar constraints; the ability to catch, handle, ingest and digest prey (Gravel et al. 2016a). Traits have been intuitively considered in the past to explain the occurrence, or the absence, of interactions but our approach now formally integrates them into a predictive model. Thus, important traits identified in one system might also prove useful to understand the interactions in another one. For example, studies on rotifers revealed similar trait-matching limitations as we observed for ground beetles: catching ability was limited by prey speed, handling by physical defence, ingestion by prey length and digestion by chemical defence (Nandini, Pérez-Chávez & Sarma 2003; Deines, Matz & Jürgens 2009).

Nevertheless, other trait combinations will undoubtedly be required to predict interactions of predators with different foraging behaviour than ground beetles. Passive predators, as web spiders, use traps adapted to behavior of prey (Schmitz 2005). In the case of flying predators, traits related to flying maneuverability of both predator and prey (e.g. wing loading) could be matched to determine their probability of interactions (Chai & Srygley 1990, Combes et al. 2013). Similarly, swimming performance could be important to determine interactions in aquatic environments (Cooper, Smith & Bence 1985, McPeek,

Schrot & Brown 1996). Beyond predator-prey interactions, for example in pollinator networks, one might consider the trait match of pollinator proboscis length/ depth of the corolla (Ibanez 2012) or to match the hairiness of different parts of the pollinator's body and the morphology of flowers (Stavert et al. 2016). The principal limitation in our capacity to extend such an approach, remains documenting more traits that restrict predator/ prey interactions, along with an extensive documentation of predatory interactions (and their absence).

Finally, our model incorporates scavenging, which allows access to high quality food acquired at a low energy cost for the predator and could be favorable to the maintenance of predator species without any cost for the species of the carrion (Wilson & Wolkovich 2011). Unfortunately, this information is frequently overlooked. Larochelle and Larivière (2003) report necrophagy observations for only 37 species of ground beetles in North America out of +2400 species. During our feeding experiment, all 14 ground beetle species (only one already identified as necrophagous (Larochelle & Larivière 2003)) that were offered a dead prey ate it at least occasionally, revealing that scavenging could be an important aspect of their feeding habits (Table 1). Molecular techniques have permitted many advances in understanding food webs, but do not easily discriminate scavenging from predation and can include errors in food web analysis (King et al. 2008). Increasing the documentation of these interactions will be important to allow their prediction in natural food webs, although ideally separate models will be used to distinguish scavenging from more classic predatory interactions given that scavenging will not influence population dynamics of prey.

Perspectives

While our model identifies the potential feeding niche of ground beetles in the laboratory, the realized niche in a truly natural environment will vary from the potential niche due to food availability, higher-order interactions and varying abiotic conditions (Poisot, Stouffer & Gravel 2015). Akin to species distribution modeling where presence-absence has to be modeled distinctively to abundance because they respond to different drivers (Boulangeat, Gravel & Thuiller 2012), potential interactions and the strength of interactions should be considered separately. The interaction of two species in a natural environment will depend on the encounter probability of the species, the matching of their traits (Bartomeus et al. 2016) and the foraging ability of the predator. The biotic context could also influence the occurrence and the realization of interactions, for instance with another predator influencing the behavior of the prey or parasites reducing its ability to escape predation. While we focus exclusively on trait-matching and phylogeny in our model, future efforts should attempt to integrate other drivers of interaction strength. While there are promising methods to account for co-occurrence (Poisot et al. 2015; Gravel et al. 2016b) and relative abundance (Poisot et al. 2015; Bartomeus et al. 2016), integrating foraging behavior may be more challenging. Integrating interaction strength is the next frontier and doing so, will require us to consider aspects such as the ability of a predator to optimize energy intake per handling time (MacArthur & Pianka 1966). It is still unclear which traits (if any) will correctly approximate energy intake and handling time, but traits such as predator/ prey body size ratio (Brose et al. 2008; Petchey et al. 2008) and biting force/ resource toughness (Verwaijen et al. 2002) could be important.

Conclusion

Species interactions influence species distributions at small and large spatial scale (Araújo & Rozenfeld 2014) which in turn have consequences for local ecological processes (Bartomeus et al. 2016). Thus, interaction networks need to be well understood to predict the consequences of species loss and species invasion caused by global change drivers. Our approach mixing traits and phylogenetic information offers a new opportunity to understand and infer accurately predatory interactions for species that are difficult to observe in the field. We demonstrate that traits such as the biting force of arthropod predators and corresponding prey cuticular toughness can help unravel their interactions. This trait-match is interesting as it is more generalizable than body size matching to infer antagonistic interactions including herbivory. The proposed approach could also be beneficial to infer other interactions such as mutualism, commensalism, etc. (Morales-Castilla et al. 2015). Adding data about species encounter probability and optimal foraging are suggested future steps to better predict food web interactions.

Author's Contribution

The ideas and the methodology were developed jointly by all three authors. Data were collected by PMB and analyzed by PMB and DG. PMB led the writing of the manuscript. All authors contributed critically to the writing.

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Data Accessibility

References

Abbott, I., Abbott, L.K. & Grant, P.R. (1975) Seed selection and handling ability of four

species of Darwin's finches. *The Condor,* **77,** 332-335.

Acorn, J.H. & Ball, G.E. (1991) The mandibles of some adult ground beetles: structure,

function, and the evolution of herbivory (Coleoptera: Carabidae). *Canadian Journal*

of Zoology, **69,** 638-650.

Allesina, S. (2011) Predicting trophic relations in ecological networks: a test of the allometric

diet breadth model. *Journal of Theoretical Biology,* **279,** 161-168.

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution

models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied*

Ecology, **43,** 1223-1232.

Araújo, M.B. & Rozenfeld, A. (2014) The geographic scaling of biotic interactions.

Ecography, **37,** 406-415.

Barraclough, T.G., Hogan, J.E. & Vogler, A.P. (1999) Testing whether ecological factors

promote cladogenesis in a group of tiger beetles (Coleoptera: Cicindelidae).

Proceedings of the Royal Society of London. Series B: Biological Sciences, **266,**

1061-1067.

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,** 1894-1903.

Bauer, T. & Kredler, M. (1993) Morphology of the compound eyes as an indicator of life-style in carabid beetles. *Canadian Journal of Zoology,* **71,** 799-810.

Bersier, L.-F. & Kehrli, P. (2008) The signature of phylogenetic constraints on food-web structure. *Ecological Complexity,* **5,** 132-139.

Boulangeat, I., Gravel, D. & Thuiller, W. (2012) Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters,* **15,** 584-593.

Bremigan, M.T. & Stein, R.A. (1994) Gape-dependent larval foraging and zooplankton size: implications for fish recruitment across systems. *Canadian Journal of Fisheries and Aquatic Sciences,* **51,** 913-922.

Brodie, E.D., Jr. & Formanowicz, D.R., Jr. (1983) Prey size preference of predators: differential vulnerability of larval anurans. *Herpetologica,* **39,** 67-75.

Broeckhoven, C., Diedericks, G. & Mouton, P.l.F.N. (2015) What doesn't kill you might make you stronger: functional basis for variation in body armour. *Journal of Animal Ecology,* **84,** 1213-1221.

Brose, U., Ehnes, R.B., Rall, B.C., Vucic-Pestic, O., Berlow, E.L. & Scheu, S. (2008) Foraging theory predicts predator-prey energy fluxes. *Journal of Animal Ecology,* **77,** 1072-1078.

Brousseau, P.-M., Gravel, D. & Handa, I.T. (2017) Data from: Trait-matching and phylogeny as predictors of predator-prey interactions involving ground beetles. *Dryad Digital Repository*, https://doi:10.5061/dryad.7tn01.

Cadotte, M.W., Cavender-Bares, J., Tilman, D. & Oakley, T.H. (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *Plos One,* **4**.

Cattin, M.F., Bersier, L.F., Banasek-Richter, C., Baltensperger, R. & Gabriel, J.P. (2004) Phylogenetic constraints and adaptation explain food-web structure. *Nature,* **427,** 835-839.

Chai, P. & Srygley, R.B. (1990) Predation and the flight, morphology, and temperature of neotropical rain-forest butterflies. *American Naturalist,* **135,** 748-765.

Christiansen, P. & Wroe, S. (2007) Bite forces and evolutionary adaptations to feeding ecology in carnivores. *Ecology,* **88,** 347-358.

Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldaña, J. (1993) Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology,* **62,** 67-78.

Combes, S.A., Salcedo, M.K., Pandit, M.M. & Iwasaki, J.M. (2013) Capture success and efficiency of dragonflies pursuing different types of prey. *Integrative and Comparative Biology,* **53,** 787-798.

Cooper, S.D., Smith, D.W. & Bence, J.R. (1985) Prey selection by freshwater predators with different foraging strategies. *Canadian Journal of Fisheries and Aquatic Sciences,* **42,** 1720-1732.

Cunha, I. & Planas, M. (1999) Optimal prey size for early turbot larvae (*Scophthalmus maximus* L.) based on mouth and ingested prey size. *Aquaculture,* **175,** 103-110.

David, J.F. (2014) The role of litter-feeding macroarthropods in decomposition processes: a reappraisal of common views. *Soil Biology and Biochemistry,* **76,** 109-118.

Deines, P., Matz, C. & Jürgens, K. (2009) Toxicity of violacein-producing bacteria fed to bacterivorous freshwater plankton. *Limnology and Oceanography,* **54,** 1343-1352.

Deraison, H., Badenhausser, I., Börger, L. & Gross, N. (2015) Herbivore effect traits and their impact on plant community biomass: an experimental test using grasshoppers. *Functional Ecology,* **29,** 650-661.

Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002) Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America,* **99,** 12917-12922.

Eisner, T., Eisner, M. & Siegler, M. (2005) *Secret Weapons: Defenses of Insects, Spiders, Scorpions, and Other Many-legged Creatures*. Harvard University Press, Cambridge.

Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N.P., Dalsgaard, B., de Sassi, C., Galetti, M., Guimarães, P.R., Lomáscolo, S.B., Martín González, A.M., Pizo, M.A., Rader, R., Rodrigo, A., Tylianakis, J.M., Vázquez, D.P. & Allesina, S. (2013) The dimensionality of ecological networks. *Ecology Letters,* **16,** 577-583.

Enders, F. (1975) The influence of hunting manner on prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae, and Salticidae). *The American Naturalist,* **109,** 737-763.

Evans, M.E.G. & Forsythe, T.G. (1985) Feeding mechanisms, and their variation in form, of some adult ground-beetles (Coleoptera: Caraboidea). *Journal of Zoology,* **206,** 113-143.

Feyereisen, R. (1999) Insect P450 enzymes. *Annual Review of Entomology,* **44,** 507-533.

Gravel, D., Albouy, C. & Thuiller, W. (2016a) The meaning of functional trait compositions of food webs for ecosystem functioning. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **371,** 1-14.

Gravel, D., Baiser, B., Dune, J.A., Kopelke, J.-P., Martinez, N.D., Nyman, T., Poisot, T., Stouffer, D.B., Tylianakis, J.M., Wood, S.A. & Roslin, T. (2016b) Bringing Elton and

Grinnell together: a quantitative framework to represent the biogeography of ecological interaction networks. *bioRxiv*.

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,** 1083-1090.

Ibanez, S. (2012) Optimizing size thresholds in a plant–pollinator interaction web: towards a mechanistic understanding of ecological networks. *Oecologia,* **170,** 233-242.

Ibanez, S., Lavorel, S., Puijalon, S. & Moretti, M. (2013) Herbivory mediated by coupling between biomechanical traits of plants and grasshoppers. *Functional Ecology,* **27,** 479-489.

Kim, Y.-J. & Gu, C. (2004) Smoothing spline Gaussian regression: more scalable computation via efficient approximation. *Journal of the Royal Statistical Society: Series B (Statistical Methodology),* **66,** 337-356.

King, R.A., Read, D.S., Traugott, M. & Symondson, W.O.C. (2008) Molecular analysis of predation: a review of best practice for DNA-based approaches. *Molecular Ecology,* **17,** 947-963.

Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S. & Degen, A.A. (2016) Trait-based and phylogenetic associations between parasites and their hosts: a case study with small mammals and fleas in the Palearctic. *Oikos,* **125,** 29-38.

Larochelle, A. & Larivière, M.-C. (2003) *A Natural History of the Ground-Beetles (Coleoptera: Carabidae) of America north of Mexico*. Pensoft, Sofia.

Lundgren, J.G. & Rosentrater, K.A. (2007) The strength of seeds and their destruction by granivorous insects. *Arthropod-Plant Interactions,* **1,** 93-99.

MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *American Naturalist,* **100,** 603-609.

McPeek, M.A., Schrot, A.K. & Brown, J.M. (1996) Adaptation to predators in a new community: swimming performance and predator avoidance in damselflies. *Ecology,* **77,** 617-629.

Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015) Inferring biotic interactions from proxies. *Trends in Ecology & Evolution,* **30,** 347-356.

Nandini, S., Pérez-Chávez, R. & Sarma, S.S.S. (2003) The effect of prey morphology on the feeding behaviour and population growth of the predatory rotifer *Asplanchna sieboldi*: a case study using five species of *Brachionus* (Rotifera). *Freshwater Biology,* **48,** 2131-2140.

Pagel, M. (1997) Inferring evolutionary processes from phylogenies. *Zoologica Scripta,* **26,** 331-348.

Pakarinen, E. (1994) The importance of mucus as a defence against carabid beetles by the slugs *Arion fasciatus* and *Deroceras reticulatum. Journal of Molluscan Studies,* **60,** 149-155.

Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008) Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences of the United States of America,* **105,** 4191-4196.

Poisot, T., Stouffer, D.B. & Gravel, D. (2015) Beyond species: why ecological interaction networks vary through space and time. *Oikos,* **124,** 243-251.

Rafferty, N.E. & Ives, A.R. (2013) Phylogenetic trait-based analyses of ecological networks. *Ecology,* **94,** 2321-2333.

Rezende, E.L., Albert, E.M., Fortuna, M.A. & Bascompte, J. (2009) Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecology Letters,* **12,** 779-788.

Rohr, R.P. & Bascompte, J. (2014) Components of phylogenetic signal in antagonistic and mutualistic networks. *The American Naturalist,* **184,** 556-564.

Rohr, R.P., Naisbit, R.E., Mazza, C. & Bersier, L.-F. (2016) Matching–centrality decomposition and the forecasting of new links in networks. *Proceedings of the Royal Society of London B: Biological Sciences,* **283**, 20152702.

Rohr, Rudolf P., Scherer, H., Kehrli, P., Mazza, C. & Bersier, L.-F. (2010) Modeling food webs: exploring unexplained structure using latent traits. *The American Naturalist,* **176,** 170-177.

Schmitz, O.J. (2005) Behavior of predators and prey and links with population-level processes. *Ecology of predator-prey interactions* (eds P. Barbosa & I. Castellanos), pp. 256-278. Oxford University Press, Oxford.

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,** 1137-1148.

Stavert, J.R., Liñán-Cembrano, G., Beggs, J.R., Howlett, B.G., Pattemore, D.E. & Bartomeus, I. (2016) Hairiness: the missing link between pollinators and pollination. *PeerJ,* **4,** e2779.

Van der Putten, W.H., Macel, M. & Visser, M.E. (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **365,** 2025-2034.

Veech, J.A. (2012) Significance testing in ecological null models. *Theoretical Ecology,* **5,** 611-616.

Verwaijen, D., Van Damme, R. & Herrel, A. (2002) Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Functional Ecology,* **16,** 842-850.

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

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics,* **33,** 475-505.

Wheater, C.P. & Evans, M.E.G. (1989) The mandibular forces and pressures of some predacious Coleoptera. *Journal of Insect Physiology,* **35,** 815-820.

Wilson, E.E. & Wolkovich, E.M. (2011) Scavenging: how carnivores and carrion structure communities. *Trends in Ecology & Evolution,* **26,** 129-135.

Wood, S. (2006) *Generalized Additive Models: An Introduction with R.* Chapman & Hall/CRC, Boca Raton.

Wood, S. (2015) Mixed GAM Computation Vehicle with GCV/AIC/REML Smoothness Estimation. R package.

Wroe, S., McHenry, C. & Thomason, J. (2005) Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proceedings of the Royal Society of London B: Biological Sciences,* **272,** 619-625.

Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1 Species trait values

Table S1 Ground beetle trait values

Table S2 Prey trait values

Appendix S2 Additional information on methodology

Appendix S3 Smooth term of GAM models

Appendix S4 List of all models

Table 1 List of ground beetle species studied and summary of the realized (+) and unrealized (-) interactions observed in the feeding experiment, derived from the literature (only realized) (Lit.) (Larochelle & Larivière 2003), or from forbidden links (FL), and the total number of interactions included in the analysis (Total).

Subfamily	Tribe	Species	Observed interactions		Lit.	FL	Total
			+	-			
Carabinae	Carabini	*Carabus nemoralis* Müller	7	12	12	0	31
Harpalinae	Harpalini	*Anisodactylus harrisii* LeConte[†]	14	4	0	1	19
		Harpalus providens Casey[†]	5	6	11	1	23
	Perigonini	*Perigona nigriceps* (Dejean)[†]	17	10	0	16	43
	Platynini	*Agonum retractum* LeConte[†]	7	4	0	6	17
		Platynus opaculus (LeConte)[†]	6	3	0	1	10
		Platynus tenuicollis (LeConte)[†]	24	17	0	1	42
	Pterostichini	*Myas cyanescens* Dejean	0	14	1	1	16
		Pterostichus caudicalis Say	12	2	0	1	15
		Pterostichus coracinus (Newman)[†]	40	31	12	3	86
		Pterostichus diligendus (Chaudoir)[†]	17	17	11	1	46
		Pterostichus lachrymosus Newman	6	5	11	1	23
		Pterostichus mutus Say[†]	7	6	11	1	25
		Pterostichus rostratus (Newman)†	27	16	8	1	52
		Pterostichus tristis (Dejean)[†]	40	27	11	1	79
	Sphodrini	*Synuchus impunctatus* (Say)	3	1	0	1	5
Nebriinae	Nebriini	*Nebria lacustris* Casey[†]	17	16	0	1	34
	Notiophilini	*Notiophilus aeneus* (Herbst)	5	2	0	10	17
Trechinae	Bembidiini	*Bembidion chalceum* Dejean[†]	11	7	0	10	28
		Elaphropus anceps (LeConte)[†]	4	6	0	16	26
		Total	269	206	88	74	637

[†] Species for which necrophagous habits were observed during the feeding experiment.

Table 2 Traits considered in the study of ground beetle/ prey interactions based on the matching-centrality formalism.

Traits	Unit	Function
Ground beetle traits		
Body length	mm	Body length is used as a measure of body size. It is a commonly used proxy of physical and physiological constraints of interspecific interactions (Cohen et al. 1993).
Biting force	N	Related to the ability to use strong and hardened food (Wheater and Evans 1989).
Mandibular gape	mm	Determines the handling ability; i.e. the maximum size (width) of used prey (Evans and Forsythe 1985)
Eye size	mm	Related to the visual acuity and the movement speed of used prey (Bauer and Kredler 1993)
Mandible length	mm	Assumed to be related to prey handling
Terebra length (cutting edge of mandibles)	mm	Longer for strict predators; shorter for omnivores (Evans and Forsythe 1985); assumed to be related to prey handling
Length of absorption section of mandibles	mm	Longer on liquid feeders (Evans and Forsythe 1985); assumed to be related to prey handling
Length of apical tooth of mandibles	mm	Handling ability; maintains the prey in place while slicing it with the terebra (Acorn and Ball 1991); assumed to be related to prey handling
Prey traits		
Body length	mm	As for ground beetles
Cuticular toughness	g mm^{-2}	Hard cuticle acts as an armor against predators (Broeckhoven et al. 2015)
Body width	mm	Animals with thin body could be easier to handle by predators
Movement speed	Categories (0 to 5)	Fast moving prey are more difficult to catch

Table 3 Goodness of fit of two null models, of the two best models out of 511 tested models (best overall and best parsimonious) and of all used terms tested individually (four trait-matches, four unmatched traits and a phylogenetic term) to infer ground beetle/ prey interactions observed in a feeding experiment. Null model 1 is a complete randomization of the observed interaction matrix while null model 2 is a randomization of prey species only. Values for the null models represent the lower and upper limit of a 95 % confidence interval for 10,000 iterations. "Best" is the model with the highest TSS without limit of terms while "Best parsimonious" is the model with the lowest number of terms and a similar TSS to the 'best' model. Significance of each goodness-of-fit aspect was determined by calculating standardized effect sizes (SES).

Model	Accuracy	Sensitivity	Specificity	TSS
Null models				
Null 1	40 - 63	43 - 73	24 - 60	-0.24 - 0.24
Null 2	51 - 62	53 - 76	28 - 59	-0.13 - 0.29
Best models				
Best[†]	83***	87***	78***	0.65***
Best parsimonious[‡]	81***	87***	74***	0.61***
Phylogeny	74***	78**	68**	0.46***
Trait-matches (predator/ prey)				
Biting force/ cuticular toughness	71***	87***	49	0.37**
Mandibular gape/ body width	67**	89***	37	0.26
Body size/ body size	66**	92***	30	0.23
Eye size/ movement speed	60	84***	25	0.1
Unmatched predator traits				
Apical tooth	64	82**	38	0.2
Absorption	64	94***	22	0.16
Terebra	63	83***	36	0.18
Mandible	64	81**	39	0.2

*** SES > 3.09 (*P*<0.001) ** SES > 2.32 (*P*<0.01) * SES > 1.96 (*P*<0.05)

[†] Phylogeny + predator body size/ prey body size + biting force/ cuticular toughness + eye size/ speed + length of the mandible (predator) + length of the terebra (predator)

[‡] Phylogeny + predator body size/ prey body size + biting force/ cuticular toughness