Received: 13 July 2022 | Accepted: 9 February 2023

DOI: 10.1111/1365-2656.13905

Journal of Animal Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Arthropod food webs predicted from body size ratios are improved by incorporating prey defensive properties

Ruben Van De Walle[1,2] | **Garben Logghe**[1,3] | **Nina Haas**[1] | **François Massol**[2] | **Martijn L. Vandegehuchte**[1,4] | **Dries Bonte**[1]

[1]Department of Biology, Terrestrial Ecology Unit, Ghent University, Ghent, Belgium

[2]Univ. Lille, CNRS, Inserm, CHU Lille, Institut Pasteur de Lille, U1019—UMR 9017—CIIL—Center for Infection and Immunity of Lille, Lille, France

[3]Research Institute for Nature and Forest (INBO), Brussels, Belgium

[4]Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway

Correspondence
Ruben Van De Walle
Email: ruben.vandewalle@hotmail.com

Funding information
Bijzonder Onderzoeksfonds, Grant/Award Number: BOF/24J/2021/066; Centre National de la Recherche Scientifique; Fonds Wetenschappelijk Onderzoek, Grant/Award Number: 1130223N; Interreg 2 Seas; University of Lille

Handling Editor: Nate J. Sanders

Abstract

1. Trophic interactions are often deduced from body size differences, assuming that predators prefer prey smaller than themselves because larger prey are more difficult to subdue. This has mainly been confirmed in aquatic ecosystems, but rarely in terrestrial ecosystems, especially in arthropods.
2. Our goal was to validate whether body size ratios can predict trophic interactions in a terrestrial, plant-associated arthropod community and whether predator hunting strategy and prey taxonomy could explain additional variation.
3. We conducted feeding trials with arthropods from marram grass in coastal dunes to test whether two individuals, of the same or different species, would predate each other. From the trial results, we constructed one of the most complete, empirically derived food webs for terrestrial arthropods associated with a single plant species. We contrasted this empirical food web with a theoretical web based on body size ratios, activity period, microhabitat, and expert knowledge.
4. In our feeding trials, predator–prey interactions were indeed largely size-based. Moreover, the theoretical and empirically based food webs converged well for both predator and prey species. However, predator hunting strategy, and especially prey taxonomy improved predictions of predation. Well-defended taxa, such as hard-bodied beetles, were less frequently consumed than expected based on their body size. For instance, a beetle of average size (measuring 4 mm) is 38% less vulnerable than another average arthropod with the same length.
5. Body size ratios predict trophic interactions among plant-associated arthropods fairly well. However, traits such as hunting strategy and anti-predator defences can explain why certain trophic interactions do not adhere to size-based rules. Feeding trials can generate insights into multiple traits underlying real-life trophic interactions among arthropods.

KEYWORDS
feeding trials, hunting strategy, insects, invertebrate community, marram grass dunes, trophic interactions

Ruben Van De Walle and Garben Logghe share first authorship.

1 | INTRODUCTION

Biodiversity is in a worldwide crisis, with unprecedented declines in the species richness of many taxa (Ceballos et al., 2015). An understudied aspect of this biodiversity crisis is the loss of species interactions (Fortuna et al., 2013). These interactions even disappear at faster rates compared to species loss (Valiente-Banuet et al., 2015) and therefore contribute substantially to the degradation of ecosystem functions and services (Griffiths et al., 2016; Keyes et al., 2021). Not only mutualistic interactions, such as pollination and facilitation (Montoya et al., 2012; Traveset et al., 2018), but also trophic interactions, such as herbivory and predation, can have important effects on ecosystem functioning (Lavorel et al., 2013; Schmitz, 2008). To realistically gauge the effect of disappearing trophic interactions, a precise quantification and understanding of food web structure is necessary (Novak et al., 2011). This is, however, challenging for smaller and less studied organisms such as invertebrates, even though they often attain high numbers and diversity in natural systems (Gongalsky, 2021; Traugott et al., 2013).

Body size is generally used to identify potential trophic interactions, with the assumption that predators usually feed on prey that are (slightly) smaller than themselves (Gravel et al., 2013). Body size further constrains the potential diet of a species between a lower and upper limit (Cohen et al., 1993; Hirt et al., 2020). On the one hand, prey that are much larger than the predator will be very difficult to handle and subdue, with pack-hunting and host–parasite systems as notable exceptions (Hirt et al., 2020; Kalinkat et al., 2013). Very small prey items, on the other hand, would not yield sufficient energy to compensate for the invested effort, except if harvesting can be done efficiently (Naisbit et al., 2012). However, ratios between predator and prey body sizes can vary greatly between and within taxonomic entities (Brose et al., 2006; Naisbit et al., 2011).

Empirical evidence on predator–prey size ratios is growing fast. Nevertheless, data is still scarce for terrestrial invertebrates (Gongalsky, 2021; Traugott et al., 2013) despite mentionable efforts (Brose et al., 2008; Eitzinger et al., 2018; Miller-ter Kuile et al., 2022). Furthermore, a positive relationship between body size and trophic level is usually very clear in both marine and freshwater environments (Boukal, 2014; Sholto-Douglas et al., 1991), but less pronounced in terrestrial ecosystems (Brose et al., 2006; Potapov et al., 2019). The difference is due to inherent dissimilarities between aquatic and terrestrial ecosystems: first, the range of body sizes of the main terrestrial and aquatic primary producers (vascular plants vs. unicellular algae respectively) is different (Brose et al., 2006; Perkins et al., 2019; Potapov et al., 2019; Shurin et al., 2005); second, many terrestrial invertebrate predators have developed strategies to handle larger prey species by use of toxins or suctorial mouth parts (Brose et al., 2006). Thus, whereas some small terrestrial herbivores consume large plants (e.g. most aphids and caterpillars) and some small terrestrial predators can attack relatively large prey (e.g. small spiders killing large insects), most aquatic prey are fed upon by larger predators, in turn fed on by even larger predators and so on (Potapov et al., 2019).

Apart from body size differences, hunting strategy is another factor influencing the likelihood of predator–prey interactions (Brose et al., 2019; Miller et al., 2014; Potapov et al., 2022). Ambush predators use the element of surprise to hunt prey that happen to pass by (Hirt et al., 2020; Kersch-Becker et al., 2018; Nentwig & Wissel, 1986). Ambush predators are incentivized to attack a larger range of prey species since their overall encounter rates are lower than those of active predators, as the former stay stationary for longer periods of time (invertebrates and ectotherm vertebrates) or occupy a smaller territory (endotherm vertebrates; Hirt et al., 2020; Strand & Obrycki, 1996). Active predators, however, confront their prey head-on, a strategy that is more successful with a larger body size (Hirt et al., 2020; Nentwig & Wissel, 1986).

The outcome of a predation event is not only influenced by the predator, but also by the prey species. Prey use different mechanisms to try to escape predation, ranging from evasive behaviour (e.g. leaf- and grasshoppers, gazelles) to the development of defensive properties such as camouflage (e.g. owls, stick insects), hard body armour (e.g. beetles, turtles) or chemical defences (e.g. dart frogs, shield bugs; Jeschke et al., 2008; Peschel et al., 2006). There is considerably more selective pressure to specialize towards particular prey species than there is to develop specific defensive traits against particular predator species, because it is more necessary to avoid overlap of resources than it is to avoid sharing natural enemies (Rossberg et al., 2006). As a consequence, defence mechanisms seem to be largely uniform across each arthropod taxonomic group (Witz, 1990). Some studies even suggest that prey phylogeny is more important than body size when determining predator–prey interactions (Naisbit et al., 2012).

Food webs are important tools to study ecosystem functioning (Montoya et al., 2006; Thébault et al., 2007). Despite some notable exceptions (e.g. McLaughlin et al., 2010), empirical studies on terrestrial arthropod food webs are mostly restricted to one-on-one interactions (e.g. among specific pest species and their main predators) or highly simplified food webs from agricultural systems or extreme environments (e.g. Curtsdotter et al., 2019; Digel et al., 2014; Sint et al., 2019). Size-based predictions of predator–prey interactions from soil food webs were shown to provide useful insights into the realized food web structure, but their accuracy can be optimized by including species traits (Potapov, 2022). Furthermore, validation of the assumed interactions between species is still needed for such soil food webs (Potapov, 2022; Potapov et al., 2022).

In general, food webs can be constructed by compiling fundamental trophic niches, which include all pairwise trophic interactions that a species can potentially establish with other species (Torres-Campos et al., 2020). These niches can be inferred from literature or ratios between putative prey and predator body sizes (e.g. Hines et al., 2019). Not all potential interactions are, however, necessarily realized in a given food web (Torres-Campos et al., 2020). Predator and prey species can for instance be separated in space or time (e.g. through differences in seasonal activity, microhabitat choice or behaviour) or potential prey can have defensive properties that deter predators from attacking (Ruxton et al., 2004; Torres-Campos et al., 2020). Additionally, smaller juveniles might eat smaller individuals and even species that are no prey for larger adults (Cuff et al., 2021). Since average adult body size is often used for the construction of food webs, interactions by juveniles or exceptionally large or small individuals are usually ignored (Gongalsky, 2021). Realized food webs can thus be more complex than those based on adult size, which begs the question to what extent a purely size-based approach is adequate to construct food webs in terrestrial ecosystems (Petchey et al., 2008). Food webs can be based on realized interactions through isotope studies, field observations or gut content analyses (mostly through DNA metabarcoding; e.g. Jacob et al., 2011; Miller-ter Kuile et al., 2022). However, these methods have some shortcomings, the most important one being the inability to distinguish predating and scavenging when gut content is used as a proxy for realized interactions (Kamenova et al., 2017; Miller-ter Kuile et al., 2022).

In order to reconstruct a natural but practically tractable food web, we focused on the arthropod community associated with a keystone plant species of coastal sand dunes: marram grass (*Calamagrostis arenaria*). This grass is an engineering species of coastal foredunes where harsh conditions, such as salt spray, strong winds and extreme absolute temperatures, restrict the number of species that are capable of surviving in this unique ecosystem (McLachlan, 1991). Nevertheless, species communities in marram grass dunes are much more diverse and complex than those in most agricultural systems, making this ecosystem appropriate for studying the reliability of size-based food web construction (Moore, 1994).

The aim of this study is to assess whether the arthropod food web in marram grass dunes can be accurately predicted through the assessment of body size ratios. This was done by constructing two food webs representing the trophic interactions in marram grass dunes. A theoretical food web was constructed based on body size ratios, expert knowledge and literature data on microhabitat, phenology and trophic interactions. The second food web was derived from experimental feeding trials with arthropod pairs in small vials. We hypothesise that the theoretical food web based on body size ratios is able to predict trophic interactions, but would be improved by incorporating species traits like prey defences and predator hunting strategy.

2 | MATERIALS AND METHODS

2.1 | Construction of the theoretical food web

To construct the arthropod food web of marram grass dunes, we used data from coastal dune areas along the Channel and the North Sea, covering the North of France, Belgium, the Netherlands and the United Kingdom (Appendix S1). Arthropods were sampled by sweep-netting and manually searching the base of 638 marram grass tussocks during the summers of 2017–2019. In total, more than 15,000 specimens were caught and identified, using a stereomicroscope. The overarching food web was constructed by pooling the data of all sites and countries. Interactions between two species were based on the species' feeding ecology, body size differences between predator and prey, microhabitat (i.e. whether the species reside primarily among the marram grass leaves or on the ground at the base of the tussock), seasonal activity periods (all collected from literature; see Appendix S2 for a full overview of the used literature) and expert knowledge. This method has been used before (e.g. Hines et al., 2019). We refer to the resulting network as the theoretical food web.

2.2 | Construction of the empirical food web

This study did not require ethical approval or a permission for fieldwork.

2.2.1 | Collection of arthropods

During the summer of 2019, 718 arthropod individuals belonging to 155 different species were collected in several marram grass dune areas along the Belgian coast: 93 individuals were caught in De Panne (51.0949° N, 2.5635° E; 27/07), 107 in Wenduine (51.2972° N, 3.0717° E; 03/08), 270 in Blankenberge (51.3205° N, 3.1446° E; 06/07, 15/07, 10/08 and 24/08) and 248 in Oostduinkerke (51.1368° N, 2.6997° E; 03/07, 17/08 and 31/08). All arthropods were caught in marram grass tussocks (*Calamagrostis arenaria*) by hand or aspirator. After sampling, all arthropods were deprived of food for at least 24 h to create a baseline, except for aphids (Sternorrhyncha), leafhoppers (Auchenorrhyncha) and true bugs (Heteroptera), which were provided with small pieces of marram grass to avoid mortality. Water was presented to all individuals in the form of a small ball of wet paper.

2.2.2 | Pairwise feeding trials

Feeding trials were used to test pairwise interactions between and within species. These trials were conducted in 60 mL vials that were closed off with mesh to allow free air flow. The bottom of each arena was covered in sand originating from coastal dunes to simulate a slightly more natural environment. Neither marram grass, nor any other form of structure was added to exclude any influence these could have on the interaction. Water was provided on a daily basis. Each trial consisted of two randomly chosen individuals interacting with each other. These could also be individuals from the same species but with different sizes, in order to test for cannibalism. Additionally, the pairs of interacting individuals could be any combination of herbivores, omnivores and carnivores. However, two strict herbivores were never paired. Testing of two predators (either omnivores or carnivores) was included to study intra-guild predation. At later stages of the experiment, some specific interactions were tested in order to maximize the number of tested potential links.

After introducing the arthropods to the vial, it was stored in a shady area at room temperature and left alone. The outcome of the trials was checked and recorded daily with minimal interference. Trials were terminated when at least one of the two interacting individuals had died; that is, there was no fixed time limit for the trials. In case two known carnivores (e.g. two spiders, either belonging to the same or two different species) did not consume each other, the same trial was counted twice: once with individual one as predator and individual two as prey and vice versa. The dead arthropod was stored in 70% ethanol for later identification, whereas the surviving individual, after being deprived of food for at least 1 day, could be reused for subsequent trials. At the end of the series of experiments, all tested arthropods were identified with a stereomicroscope to the most detailed taxonomic resolution according to morphology and/or life stage. This resulted in 617 specimens identified to species level, 63 to genus level and 38 to family level. The food web that resulted from pooling the pairwise trophic interactions will be referred to as the experimental food web.

2.2.3 | Determining body size

Since it was not possible to determine the dry weight of individuals, we used body length as an alternative measure for body size (Ganihar, 1997; Martin et al., 2014; Moretti et al., 2017). Before the start of each trial, a digital photograph of every individual was taken with a camera mounted on a stereomicroscope and used to measure its body length using ImageJ version 1.52a (Schneider et al., 2012). Body length was measured from cephalon to abdomen, excluding appendages such as antennae, chelicerae, legs or wings. The body length across all tested species and individuals ranged from 1.6 to 12.3 mm (Appendix S4).

2.3 | Statistical analyses

2.3.1 | Data preparation

Predators were categorized as active or ambush hunter. A separate third category for web-building spiders was included because the use of a web possibly enables spiders to catch larger prey (Enders, 1975; Nentwig & Wissel, 1986) and spiders appeared as outliers in size-based automated food web construction attempts (Bohan et al., 2011). However, since almost all web-building spiders did not construct a web during the feeding trials, this category served more as a correction for the absence of a web; that is, we expect lower prey size for web-building spiders in the context of standardized experiments in which web-building was not possible. Since closely related species are known to have similar defence mechanisms, order-level taxonomy of the prey was used as a proxy for defensive traits. Because of large differences in defence mechanism within the order of the Hemiptera, suborders Sternorrhyncha (reproduce rapidly to survive), Heteroptera (chemical defence mechanisms) and Auchenorrhyncha (escape predation by rapid movement) were used instead.

Data from 42 feeding trials were omitted, because predation could not be reliably determined:for example it seemed likely that the “predator” was scavenging or an individual escaped. After removing these data points, the dataset consisted of 586 trials, of which 170 ended in predation and 416 did not.

2.3.2 | Testing pairwise interactions in the lab

To test the link between predation success, predator/prey body size ratio, hunting strategy of the predator (ambush, active, web-building) and prey taxonomy, we used generalized linear mixed models with a logit link function and binomial distribution. The outcome of the feeding trial, that is, success (1) or failure (0), was used as response variable, while the log-transformed length of the prey (included for the purpose of correction) and the log-transformed predator/prey size ratio together with categorical variables for hunting strategy and prey taxonomy were used as explanatory variables. Orders that included fewer than 15 tested individuals (Blattodea, Collembola, Dermaptera, Diptera, Hymenoptera, Isopoda, Myriapoda, Neuroptera, Opiliones, Orthoptera, Trombidiformes and Sternorrhyncha), were grouped together into a single category due to convergence issues. This artificial group was then used as a baseline for the comparison with the other included groups (Araneae, Auchenorrhyncha, Coleoptera, Heteroptera, Pseudoscorpionida and Psocoptera). The importance of hunting strategy and prey taxonomy for predator–prey interactions was determined by modelling them as fixed effects, with or without an interaction with the predator–prey body size ratio. According to model selection based on the corrected Akaike information criterion (AICc), several models could be considered to best describe the data (Appendix S3). The model with the lowest AICc was used because model averaging does not allow post-hoc comparison for prey taxonomy and hunting strategy.

The model used to analyse the data from the feeding trials was:

$$\begin{aligned}&\text{success} \sim \log(\text{Length prey}) + \log(\text{Length predator}/\text{Length prey})\\&+\text{Hunting strategy} + \text{Prey taxonomy} + \log(\text{Length predator}/\text{Length prey})\\&\times \text{Hunting strategy}.\end{aligned}$$

Post-hoc tests with Tukey adjustments were used to compare different levels of the fixed effects. Individual ‘prey ID’ was used as a random variable to correct for re-using some prey individuals in different trials. ‘Predator ID’ was included as a random variable in the initial models but excluded from final models because it explained almost no variation.

2.3.3 | Comparing the empirical and theoretical food webs

Some species were not represented in both food webs, since the theoretical food web was based on biodiversity data and the experimental food web depended on the sampled species. The exclusion of these species resulted in the two final food webs containing the same 85 species (Figure 1; see Appendix S4 for the full species list). The number of interactions in the subset theoretical food web was much higher than in the empirical food web (726 vs. 143 interactions) because not all possible interactions could be tested in the experimental trials. Therefore, only interactions that were tested in the feeding trials were selected and compared between both food webs (Figure 1). The interactions were classified into four categories of agreement, with the first and second digit indicating whether or not the interaction was observed in the theoretical or the empirical food web respectively: (1-1) interactions that did or (0-0) did not occur in both food webs, (0-1) interactions that were only observed during the feeding trials or (1-0) interactions only described in the theoretical food web. These categories were linked to the taxonomy of the prey and predator species separately via the construction of mosaic plots. The mosaic plot helps visualize the observed and expected interactions more clearly. The relative frequency of the prey taxonomic groups within each category of agreement between the two food webs are represented by the size of the boxes. We use 0-0 and 1-1 to represent the theoretical and experimental food web agreeing on the absence or presence of an interaction, respectively. 0-1 represents a link that is not present in the theoretical food web but happened during the experimental trials, while 1-0 means the opposite. Over- or under-representation of a taxon in one of the categories is determined by the size of standardized residuals (Meyer et al., 2006) and is indicated by the colouring of the boxes: blue indicates over-representation while red indicates under-representation. The statistical significance of the residuals is eventually indicated by the shading (legend of Figure 5).

Since we were interested in the presence or absence of interactions between different species, the length of the arthropods was not needed in this analysis, which allowed us to include 12 extra lab trials (for which we could not reliably determine the size of one of the tested individuals due to wrong scale bars on the photographs), resulting in a dataset with 598 tested interactions.

R version 4.0.4 (R Core Team, 2021) was used to perform all data analyses. Generalized linear mixed models (glmm) were fitted with 'lme4' (Bates et al., 2015) and 'lmerTest' (Kuznetsova et al., 2017). The 'anova' function was used to perform likelihood ratio tests between nested models. The 'emmeans' function, with Tukey adjustment of p-values, from 'emmeans' package (Lenth, 2022) was used to assess and test parameter differences between categories of hunting strategies and taxonomic groups. The 'emtrends' function from the same package was used to test differences in the effect of predator–prey body size ratio between different hunting strategies. Network metrics were calculated using the 'igraph' package (Csardi & Nepusz, 2006). Mosaic plots were made with the 'mosaicplot' function of the R base package 'graphics' (R Core Team, 2021). Gephi software (Bastian et al., 2009) was used for network visualization.

3 | RESULTS

3.1 | Pairwise interactions

On average, the body size ratio between (potential) predator and prey was larger for successful predation events compared to trials where predation did not happen (Figure 2). The probability of successful predation depended on the ratio of predator to prey size

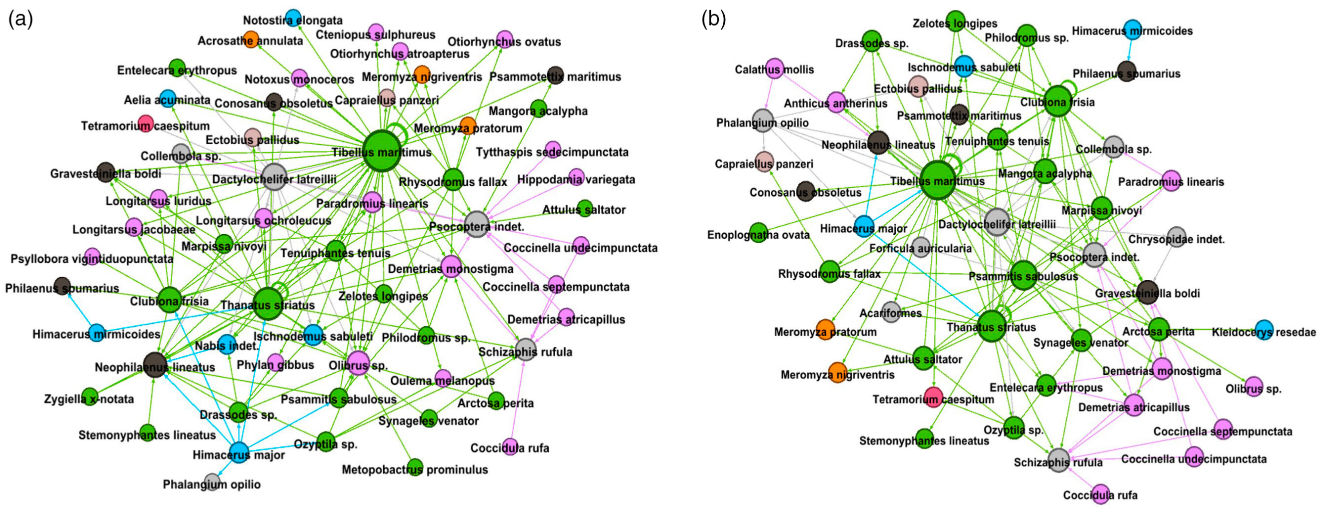

FIGURE 1 (a) The theoretical food web and (b) the empirical food web. Node colours indicate the species' taxonomic group: beetles (purple), spiders (green), true bugs (blue), leaf hoppers (black), flies (orange), ants (pink), cockroaches (beige) and others (grey). Interaction arrows point from predator to prey and the colour indicates predator taxonomic group.

(Likelyhood Ratio Test [LRT], $\chi^2_1 = 10.27$, $p = 0.001$), but was generally lower when the prey was larger (LRT, $\chi^2_1 = 9.43$, $p = 0.002$). Overall, the results indicated that individual predators prefer to consume prey that are ca. 20% shorter than themselves (Figure 3).

The probability of predation was further influenced by predator hunting strategy (LRT, $\chi^2_2 = 13.43$, $p < 0.001$) and prey taxonomy (LRT, $\chi^2_6 = 110.3$, $p < 0.001$), while the interaction between predator hunting strategy and body size ratio did not significantly increase the goodness-of-fit (LRT, $\chi^2_2 = 4.37$, $p = 0.113$). Active (z ratio = 3.182, $p = 0.004$) and ambush hunters (z ratio = 2.932, $p = 0.009$) engaged more into predation compared to web-building spiders; however, no difference was found between the first two hunting strategies (z ratio = 0.420, $p = 0.907$). Nonetheless, differences between active and ambush hunting strategy were found when only spider data was used for the analysis (Appendix S6). Post-hoc comparisons among taxonomic groups showed that barklice (Psocoptera), leafhoppers (Auchenorrhyncha) and spiders (Araneae) are most likely to be preyed upon when tested during the feeding trials, while beetles (Coleoptera) and pseudoscorpions (Pseudoscorpionida) are least likely to be consumed (Figure 4; Appendix S5).

3.2 | Food web comparison

The theoretical (based on body size ratios and expert knowledge) and experimental food webs (based on the feeding trials) agreed on most interactions (436/598 or 72.9%; 370 interactions were absent and 66 were present in both food webs), although there were still some discrepancies between the two (81 interactions that were present only in the theoretical and 81 interactions only in the empirical food web).

Spiders were captured by more species during the feeding trials than was expected from the theoretical food web. In contrast,

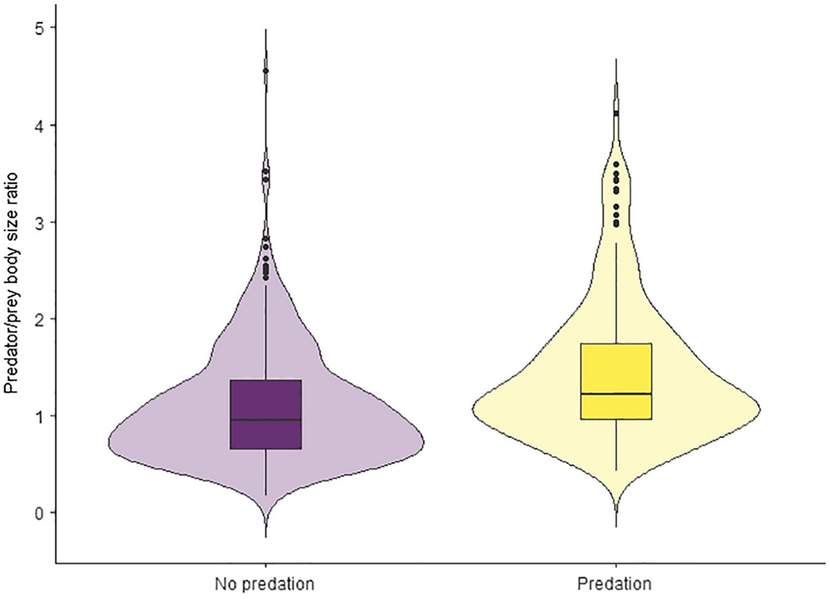

FIGURE 2 Box and violin plots represent predator–prey body size ratio in relation to the outcome of the feeding trials. Boxes represent median, 1st and 3rd quartiles. Whiskers represent 1.5 times the interquartile range.

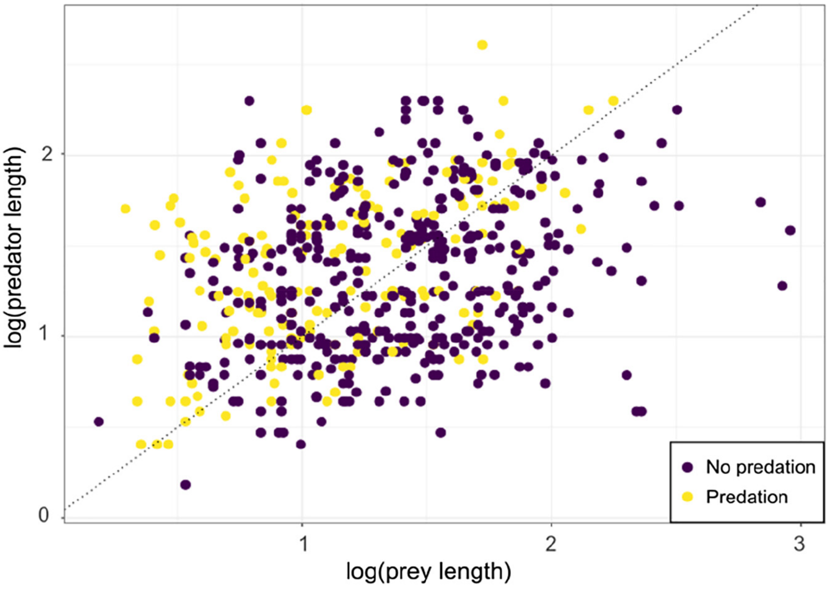

FIGURE 3 Overview of (potential) predator and (potential) prey size for all tested pairwise interactions. Colours indicate whether or not predation occurred.

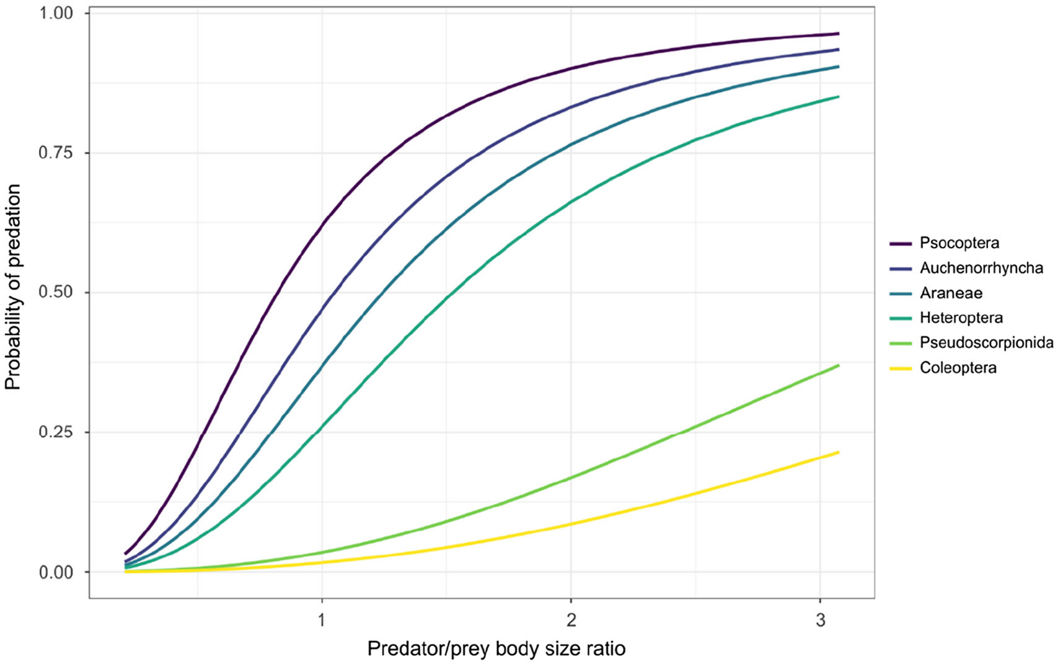

FIGURE 4 Effect of prey taxonomic group on the relationship between predation probability and predator–prey body size ratio.

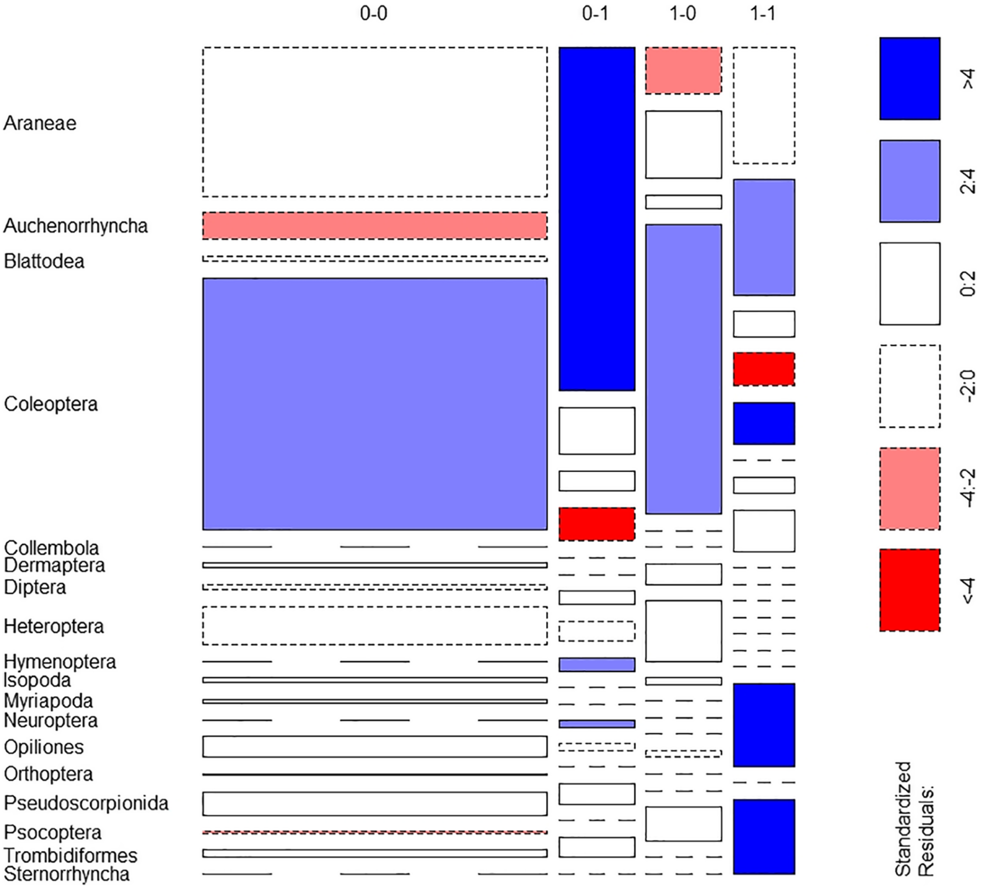

FIGURE 5 Mosaic plot representing the relative frequency of the prey taxonomic groups within each category of agreement between the two food webs. 0-0 and 1-1 represent the theoretical and experimental food web agreeing on respectively the absence or presence of an interaction respectively. 0-1 represents a link that is not present in the theoretical food web but happened during the experimental trials, while 1-0 means the opposite. The relative frequency is indicated by the area of the boxes. Blue colouration indicates over- while red indicates under-representation. Example: a blue 0-1 box indicates that the taxon is consistently more eaten during the feeding trials compared to what was expected from the theoretical food web. Shading represents the statistical significance (light colours for $\alpha = 0.05$ and dark colour for $\alpha = 0.0001$).

beetles were consumed by fewer species than expected (Figure 5). The vulnerability of leafhoppers, aphids, springtails (Collembola) and barklice were well estimated (Figure 5). Finally, Figure 5 suggests that Hymenoptera and Neuroptera were, like spiders, eaten by more species than expected. However, these results are based on 2 and 1 observation(s) respectively, so they should be interpreted with caution.

As predators (Figure 6), spiders and beetles again show the most remarkable results. For spiders, the theoretical and experimental food webs often disagreed (Figure 6). This means that spiders were more often able to subdue prey in the feeding trials than expected based on expert knowledge and body size ratios and conversely, some of the prey indicated for spiders in the theoretical food web were not attacked. Unlike the mismatch between the two food webs regarding beetles as prey, expectations for beetles as predators based on the theoretical food web corresponded rather well to the feeding trials (Figure 6). Finally, pseudoscorpions were less frequently able to kill their prey during the feeding trials than expected from the theoretical food web (Figure 6).

4 | DISCUSSION

Overall, the theoretical food web based on body size, activity period, microhabitat and expert knowledge converged quite well with the food web based on experimental feeding trials for both predator and prey species. Additionally, the pairwise feeding trials confirmed the general consensus that predators are typically larger than their prey (Brose et al., 2006; Cohen et al., 1993). Potential prey with a body length larger than 80% of that of the predator were in most cases not attacked.

Despite these results, several mismatches between the two food webs for some taxonomic groups were highlighted by the mosaic plots.

First, the vulnerability of certain prey taxa such as beetles (Coleoptera) and pseudoscorpions is consistently overestimated in the theoretical food web. This is likely due to their defensive traits, which deter large predators from attacking (Ruxton et al., 2004; Shinohara & Takami, 2020; Wang et al., 2018). Our feeding trials provide some indirect evidence for this hypothesis by indicating prey taxonomy as an important predictor of their outcome. While prey taxonomy is linked with a spectrum of traits, we postulate that the most relevant trait for our study is defence strategy. For instance, hard exoskeletons like those of beetles effectively lower the predation probability, even when attacked by a much larger predator (Peschel et al., 2006; Wang et al., 2018). Taxonomic groups without any particular defensive structures, such as aphids and springtails, were frequently consumed, further supporting this hypothesis. Apart from their strong exoskeleton, Coleoptera also have low protein content (Reeves et al., 2021), which could further explain why

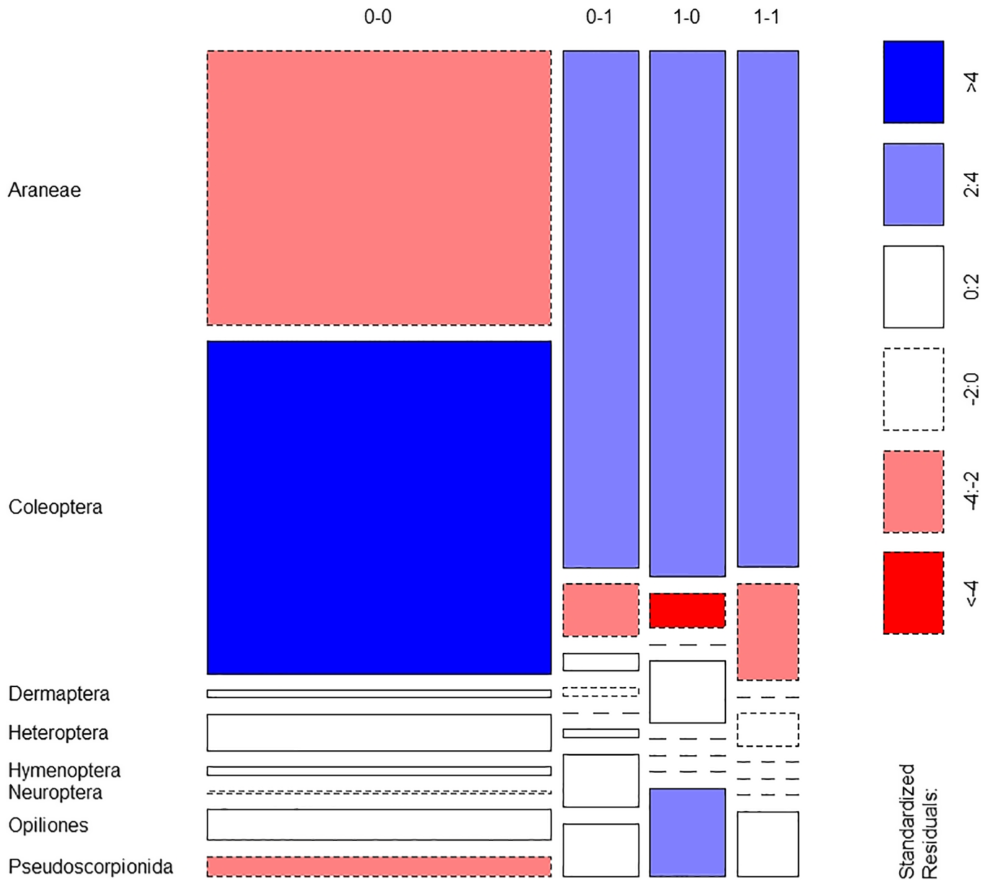

FIGURE 6 Mosaic plot representing the relative frequency of the predator taxonomic groups within each category of agreement between the two food webs. Coding and colours are as in Figure 5.

they were not predated very often. The low predation probability of pseudoscorpion prey might illustrate that, sometimes, offence is the best defence. Pseudoscorpions do not have a hard exoskeleton, but are venomous and can rapidly paralyse or even kill a potential predator (von Reumont et al., 2014). Because predators without alternative prey in our experimental setup still refused to consume these well-defended prey, their defences will likely be even more effective in nature. In case of prey species relying more on evasive behaviour, probabilities of predation were likely inflated in our trials since consistent escape was futile.

About 60% of the spider trials and 50% of the pseudoscorpion trials that were differently classified by the theoretical food web, had a beetle as prey species, which resulted in lower-than-expected predation rates (Figure 6). Since spiders are considered generalist predators, predictions for interactions between spiders and beetles were mainly based on size differences between predator and prey, but in reality, it appears difficult for spiders to kill even smaller beetles. For pseudoscorpions, however, interactions with beetles are mentioned in some studies (Del-Claro & Tizo-Pedroso, 2009; Harvey, 1986). However, Harvey (1986) mentioned beetle larvae rather than adults as prey for pseudoscorpions. In nature, beetle adults are probably mainly predated by larger vertebrate predators (O'Connor et al., 2019; Oosten, 2016; Petracci, 2002).

Second, spiders both ate more prey and were preyed upon more frequently—that is, intraguild predation was more prevalent—during the feeding trials than expected based on the theoretical food web. This may be explained by the inclusion of microhabitat, a factor known to affect spider diet (Potapov et al., 2022), in the theoretical food web. For the feeding trials, arthropod species were matched randomly. Consequently, two (spider) species living in different microhabitats could be placed together, resulting in more frequent spider-on-spider predation. Given their high protein content and relatively soft exoskeleton (Reeves et al., 2021), spiders make high risk—high reward prey for other predators. Targeting smaller spider individuals might help mitigate this risk. Our data support this, since we noticed unpredicted links in the feeding trials between predators that were substantially larger than their prey, contributing to the overall size-conditionality of predator–prey relationships. Since it is known that young spiders disperse more than adults (Humphrey, 1987), it can be expected that they encounter adult spiders inhabiting other microhabitats, that is, that these interactions, though rare, do occur in nature.

Our feeding trials limited the natural behaviour of the species and consequently their predation success. For instance, ambush predator species are known to have more successful predation events when facing larger-bodied prey than actively hunting species (spiders, Nentwig & Wissel, 1986; Verdeny-Vilalta et al., 2015; mammals, Hirt et al., 2020). This hypothesis was supported for spiders, but not across all considered taxa. We speculate that this may be due to the absence of structural complexity within the vials resulting in decreased ambush predation success, since the predator could not really hide. The positive effect of structural complexity on predation success is known from terrestrial systems (Donadio & Buskirk, 2016; Mullin et al., 1998), but it is especially well established in aquatic systems (Flynn & Ritz, 1999; Schultz et al., 2009), where predators are even reported to switch from ambush to active hunting according to the structural complexity (Říha et al., 2021). Web-building spiders can be considered a specific type of ambush predator, using webs to tackle larger prey (Enders, 1975; Nentwig & Wissel, 1986). However, since almost all web-building spiders did not build a web during our experiment, a significantly lower chance of predating any prey species was observed for these spiders. Direct observations of insects caught in the web, or gut content DNA metabarcoding (Schrojenstein Lantman et al., 2021) offer better possibilities to study the prey species diversity of web-building spiders, but then have as disadvantage that sizes are difficult to assess after consumption.

Trophic interactions involving prey without structural defence traits were well predicted because, as discussed above, these species could not evade predation. Consuming such prey species is easy if predators are able to find the prey in a natural environment. Our results therefor imply that existing information about size, feeding behaviour, life cycle and niche differentiation can be used to generate a coarse yet useful estimate of the trophic interactions among arthropods. We demonstrated this for terrestrial arthropods in marram grass dunes, but we support the wider applicability of such theory-based food web estimates in similar habitats. Size-structured predation remains an important factor when considering intra-guild predation, and can only be quantified by direct methods such as feeding trials, because indirect methods based on molecular markers cannot correct for intraspecific variation in body size. We therefore encourage the use of this under-rated method to study intraspecific variation within traits influencing trophic interactions; because "Humans are different; why do we think arthropods are the same?" (adapted from Gongalsky, 2021).

AUTHOR CONTRIBUTIONS

Ruben Van De Walle, Garben Logghe, Nina Haas, Martijn L. Vandegehuchte and Dries Bonte designed the lab experiment. Garben Logghe, Nina Haas and Ruben Van De Walle conducted the practical work. Garben Logghe and Ruben Van De Walle wrote the first draft of the manuscript. Ruben Van De Walle and François Massol analysed the data. All authors contributed substantially to interpretation of the results and revision of the manuscript.

ACKNOWLEDGEMENTS

This research was conducted with financial support by the INTERREG 2 Seas project Endure. Ruben Van De Walle was funded by the University of Lille. Garben Logghe was funded by FWO (grantnr: 1130223N). Dries Bonte was funded by BOF (grantnr: BOF/24J/2021/066). François Massol would like to thank CNRS for general support. The authors thank everyone who has assisted with the fieldwork and/or identification of the arthropods: Paulien Vanhauwere, Laurian Van Maldegem, Gillis Sanctobin, Noëmie Van den Bon, Pieter Vantieghem, Margaux Pottiez, Arthur Van Roey, Elias Van Den Broeck, Tine Cooreman, Jurjen Logghe and the

Endure consortium. The authors thank Irene Lantman for providing the photograph used for the graphical abstract. Finally, the authors thank two anonymous reviewers for their constructive and valuable comments on the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors have declared that no competing interests exist.

DATA AVAILABILITY STATEMENT

The raw data are available via Zenodo at https://doi.org/10.5281/zenodo.7546960 (Van De Walle et al., 2023).

ORCID

Ruben Van De Walle https://orcid.org/0000-0001-5519-0153
Garben Logghe https://orcid.org/0000-0003-2000-7982
Nina Haas https://orcid.org/0000-0003-2330-6734
François Massol https://orcid.org/0000-0002-4098-955X
Martijn L. Vandegehuchte https://orcid.org/0000-0003-1283-4654
Dries Bonte https://orcid.org/0000-0002-3320-7505

REFERENCES

Bastian, M., Heymann, S., & Jacomy, M. (2009). Gephi: An open source software for exploring and manipulating networks. *International AAAI Conference on Weblogs and Social Media*, *3*, 361–362.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Bohan, D. A., Caron-Lormier, G., Muggleton, S., Raybould, A., & Tamaddoni-Nezhad, A. (2011). Automated discovery of food webs from ecological data using logic-based machine learning. *PLoS One*, *6*(12), e29028. https://doi.org/10.1371/journal.pone.0029028

Boukal, D. S. (2014). Trait- and size-based descriptions of trophic links in freshwater food webs: Current status and perspectives. *Journal of Limnology*, *73*(Suppl. 1). https://doi.org/10.4081/jlimnol.2014.826

Brose, U., Archambault, P., Barnes, A. D., Bersier, L. F., Boy, T., Canning-Clode, J., Conti, E., Dias, M., Digel, C., Dissanayake, A., Flores, A. A. V., Fussmann, K., Gauzens, B., Gray, C., Häussler, J., Hirt, M. R., Jacob, U., Jochum, M., Kéfi, S., … Iles, A. C. (2019). Predator traits determine food-web architecture across ecosystems. *Nature Ecology and Evolution*, *3*(6), 919–927. https://doi.org/10.1038/s41559-019-0899-x

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*(5), 1072–1078. https://doi.org/10.1111/j.1365-2656.2008.01408.x

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

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5), e1400253. https://doi.org/10.1126/sciadv.1400253

Cohen, J. E., Pimm, S. L., Yodzis, P., & Saldana, J. (1993). Body sizes of animal predators and animal prey in food webs. *The Journal of Animal Ecology*, *62*(1), 67. https://doi.org/10.2307/5483

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal*, *Complex Systems*, *1695*, 1–9. https://igraph.org

Cuff, J. P., Tercel, M. P. T. G., Drake, L. E., Vaughan, I. P., Bell, J. R., Orozco-terWengel, P., Müller, C. T., & Symondson, W. O. C. (2021). Density-independent prey choice, taxonomy, life history, and web characteristics determine the diet and biocontrol potential of spiders (Linyphiidae and Lycosidae) in cereal crops. *Environmental DNA*, *4*, 549–564. https://doi.org/10.1002/edn3.272

Curtsdotter, A., Banks, H. T., Banks, J. E., Jonsson, M., Jonsson, T., Laubmeier, A. N., Traugott, M., & Bommarco, R. (2019). Ecosystem function in predator–prey food webs—Confronting dynamic models with empirical data. *Journal of Animal Ecology*, *88*(2), 196–210. https://doi.org/10.1111/1365-2656.12892

Del-Claro, K., & Tizo-Pedroso, E. (2009). Ecological and evolutionary pathways of social behavior in Pseudoscorpions (Arachnida: Pseudoscorpiones). *Acta Ethologica*, *12*(1), 13–22. https://doi.org/10.1007/s10211-009-0052-y

Digel, C., Curtsdotter, A., Riede, J., Klarner, B., & Brose, U. (2014). Unravelling the complex structure of forest soil food webs: Higher omnivory and more trophic levels. *Oikos*, *123*(10), 1157–1172. https://doi.org/10.1111/oik.00865

Donadio, E., & Buskirk, S. W. (2016). Linking predation risk, ungulate antipredator responses, and patterns of vegetation in the high Andes. *Journal of Mammalogy*, *97*(3), 966–977. https://doi.org/10.1093/jmammal/gyw020

Eitzinger, B., Rall, B. C., Traugott, M., & Scheu, S. (2018). Testing the validity of functional response models using molecular gut content analysis for prey choice in soil predators. *Oikos*, *127*(7), 915–926. https://doi.org/10.1111/oik.04885

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*(970), 737–763. https://doi.org/10.1086/283040

Flynn, A. J., & Ritz, D. A. (1999). Effect of habitat complexity and predatory style on the capture success of fish feeding on aggregated prey. *Journal of the Marine Biological Association of the United Kingdom*, *79*(3), 487–494. https://doi.org/10.1017/S0025315498000617

Fortuna, M. A., Krishna, A., & Bascompte, J. (2013). Habitat loss and the disassembly of mutalistic networks. *Oikos*, *122*(6), 938–942. https://doi.org/10.1111/j.1600-0706.2012.00042.x

Ganihar, S. R. (1997). Biomass estimates of terrestrial arthropods based on body length. *Journal of Biosciences*, *22*(2), 219–224. https://doi.org/10.1007/BF02704734

Gongalsky, K. B. (2021). Soil macrofauna: Study problems and perspectives. *Soil Biology and Biochemistry*, *159*(May), 108281. https://doi.org/10.1016/j.soilbio.2021.108281

Gravel, D., Poisot, T., Albouy, C., Velez, L., & Mouillot, D. (2013). Inferring food web structure from predator-prey body size relationships. *Methods in Ecology and Evolution*, *4*(11), 1083–1090. https://doi.org/10.1111/2041-210X.12103

Griffiths, H. M., Bardgett, R. D., Louzada, J., & Barlow, J. (2016). The value of trophic interactions for ecosystem function: Dung beetle communities influence seed burial and seedling recruitment in tropical forests. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1844), 20161634. https://doi.org/10.1098/rspb.2016.1634

Harvey, M. S. (1986). *The systematics and biology of pseudoscorpions*. Australian Arachnology.

Hines, J., Giling, D. P., Rzanny, M., Voigt, W., Meyer, S. T., Weisser, W. W., Eisenhauer, N., & Ebeling, A. (2019). A meta food web for invertebrate species collected in a European grassland. *Ecology*, *100*, e02679. https://doi.org/10.1002/ecy.2679

Hirt, M. R., Tucker, M., Müller, T., Rosenbaum, B., & Brose, U. (2020). Rethinking trophic niches: Speed and body mass colimit prey space of mammalian predators. *Ecology and Evolution*, *10*(14), 7094–7105. https://doi.org/10.1002/ece3.6411

Humphrey, J. A. C. (1987). Fluid mechanic constraints on spider ballooning. *Oecologia*, *73*(3), 469–477. https://doi.org/10.1007/BF00385267

Jacob, U., Thierry, A., Brose, U., Arntz, W. E., Berg, S., Brey, T., Fetzer, I., Jonsson, T., Mintenbeck, K., Möllmann, C., Petchey, O. L., Riede, J. O., & Dunne, J. A. (2011). The role of body size in complex food webs. *Advances in Ecological Research*, *45*, 181–223. https://doi.org/10.1016/B978-0-12-386475-8.00005-8

Jeschke, J. M., Laforsch, C., & Tollrian, R. (2008). Animal prey defenses. *Encyclopedia of Ecology*, *1*, 189–194.

Kalinkat, G., Schneider, F. D., Digel, C., Guill, C., Rall, B. C., & Brose, U. (2013). Body masses, functional responses and predator-prey stability. *Ecology Letters*, *16*(9), 1126–1134. https://doi.org/10.1111/ele.12147

Kamenova, S., Bartley, T. J., Bohan, D. A., Boutain, J. R., Colautti, R. I., Domaizon, I., Fontaine, C., Lemainque, A., Le Viol, I., Mollot, G., Perga, M.-E., Ravigné, V., & Massol, F. (2017). Invasions toolkit: Current methods for tracking the spread and impact of invasive species. In *Advances in ecological research Vol. 56—Networks of invasion: A synthesis of concepts* (pp. 85–182). https://doi.org/10.1016/bs.aecr.2016.10.009

Kersch-Becker, M. F., Grisolia, B. B., Campos, M. J. O., & Romero, G. Q. (2018). The role of spider hunting mode on the strength of spider–plant mutualisms. *Oecologia*, *188*(1), 213–222. https://doi.org/10.1007/s00442-018-4170-y

Keyes, A. A., McLaughlin, J. P., Barner, A. K., & Dee, L. E. (2021). An ecological network approach to predict ecosystem service vulnerability to species losses. *Nature Communications*, *12*(1), 1586. https://doi.org/10.1038/s41467-021-21824-x

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13). https://doi.org/10.18637/jss.v082.i13

Lavorel, S., Storkey, J., Bardgett, R. D., de Bello, F., Berg, M. P., Le Roux, X., Moretti, M., Mulder, C., Pakeman, R. J., Díaz, S., & Harrington, R. (2013). A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science*, *24*(5), 942–948. https://doi.org/10.1111/jvs.12083

Lenth, R. V. (2022). *Emmeans: Estimated marginal means, aka least-squares means*. R package version 1.7.2 https://cran.r-project.org/package=emmeans

Martin, C. A., Proulx, R., & Magnan, P. (2014). The biogeography of insects' length-dry mass relationships. *Insect Conservation and Diversity*, *7*(5), 413–419. https://doi.org/10.1111/icad.12063

McLachlan, A. (1991). Ecology of coastal dune fauna. *Journal of Arid Environments*, *21*(2), 229–243. https://doi.org/10.1016/S0140-1963(18)30684-0

McLaughlin, Ó. B., Jonsson, T., & Emmerson, M. C. (2010). *Temporal variability in predator–prey relationships of a forest floor food web*. https://doi.org/10.1016/B978-0-12-381363-3.00004-6

Meyer, D., Zeileis, A., & Hornik, K. (2006). The Strucplot Framework: Visualizing Multi-way Contingency Tables withvcd. *Journal of Statistical Software*, *17*(3). https://doi.org/10.18637/jss.v017.i03

Miller, J. R. B., Ament, J. M., & Schmitz, O. J. (2014). Fear on the move: Predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *Journal of Animal Ecology*, *83*(1), 214–222. https://doi.org/10.1111/1365-2656.12111

Miller-ter Kuile, A., Apigo, A., Bui, A., DiFiore, B., Forbes, E. S., Lee, M., Orr, D., Preston, D. L., Behm, R., Bogar, T., Childress, J., Dirzo, R., Klope, M., Lafferty, K. D., McLaughlin, J., Morse, M., Motta, C., Park, K., Plummer, K., … Young, H. (2022). Predator–prey interactions of terrestrial invertebrates are determined by predator body size and species identity. *Ecology*, *103*, e3634. https://doi.org/10.1002/ecy.3634

Montoya, D., Rogers, L., & Memmott, J. (2012). Emerging perspectives in the restoration of biodiversity-based ecosystem services. *Trends in Ecology & Evolution*, *27*(12), 666–672. https://doi.org/10.1016/j.tree.2012.07.004

Montoya, J. M., Pimm, S. L., & Solé, R. V. (2006). Ecological networks and their fragility. *Nature*, *442*(7100), 259–264. https://doi.org/10.1038/nature04927

Moore, J. C. (1994). Impact of agricultural practices on soil food web structure: Theory and application. *Agriculture, Ecosystems and Environment*, *51*(1–2), 239–247. https://doi.org/10.1016/0167-8809(94)90047-7

Moretti, M., Dias, A. T. C., Bello, F., Altermatt, F., Chown, S. L., Azcárate, F. M., Bell, J. R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J. P., Ellers, J., & Berg, M. P. (2017). Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, *31*(3), 558–567. https://doi.org/10.1111/1365-2435.12776

Mullin, S. J., Cooper, R. J., & Gutzke, W. H. N. (1998). The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*). III. Searching for different prey types in structurally varied habitats. *Canadian Journal of Zoology*, *76*(3), 548–555. https://doi.org/10.1139/cjz-76-3-548

Naisbit, R. E., Kehrli, P., Rohr, R. P., & Bersier, L.-F. (2011). Phylogenetic signal in predator–prey body-size relationships. *Ecology*, *92*(12), 2183–2189. https://doi.org/10.1890/10-2234.1

Naisbit, R. E., Rohr, R. P., Rossberg, A. G., Kehrli, P., & Bersier, L. F. (2012). Phylogeny versus body size as determinants of food web structure. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1741), 3291–3297. https://doi.org/10.1098/rspb.2012.0327

Nentwig, W., & Wissel, C. (1986). A comparison of prey lengths among spiders. *Oecologia*, *68*(4), 595–600. https://doi.org/10.1007/BF00378777

Novak, M., Wootton, J. T., Doak, D. F., Emmerson, M., Estes, J. A., & Tinker, M. T. (2011). Predicting community responses to perturbations in the face of imperfect knowledge and network complexity. *Ecology*, *92*(4), 836–846. https://doi.org/10.1890/10-1354.1

O'Connor, J. M., Srivastava, S. K., Tindale, N. W., & Burnett, S. E. (2019). From carrion to Christmas beetles: The broad dietary niche of the red fox in a hybrid coastal ecosystem in South-Eastern Queensland. *Australian Journal of Zoology*, *67*(2), 82. https://doi.org/10.1071/ZO19059

Oosten, H. H. v. (2016). Comparative breeding biology of three insectivorous songbirds in Dutch dune grasslands. *Ardea*, *104*(3), 199–212. https://doi.org/10.5253/arde.v104i3.a2

Perkins, D. M., Perna, A., Adrian, R., Cermeño, P., Gaedke, U., Huete-Ortega, M., White, E. P., & Yvon-Durocher, G. (2019). Energetic equivalence underpins the size structure of tree and phytoplankton communities. *Nature Communications*, *10*(1), 1–8. https://doi.org/10.1038/s41467-018-08039-3

Peschel, K., Norton, R. A., Scheu, S., & Maraun, M. (2006). Do oribatid mites live in enemy-free space? Evidence from feeding experiments with the predatory mite Pergamasus septentrionalis. *Soil Biology and Biochemistry*, *38*(9), 2985–2989. https://doi.org/10.1016/j.soilbio.2006.04.035

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*(11), 4191–4196. https://doi.org/10.1073/pnas.0710672105

Petracci, P. F. (2002). Diet of sanderling in Buenos Aires Province, Argentina. *Waterbirds*, *25*(3), 366–370.

Potapov, A. M. (2022). Multifunctionality of belowground food webs: Resource, size and spatial energy channels. *Biological Reviews*, *4*, 1691–1711. https://doi.org/10.1111/brv.12857

Potapov, A. M., Beaulieu, F., Birkhofer, K., Bluhm, S. L., Degtyarev, M. I., Devetter, M., Goncharov, A. A., Gongalsky, K. B., Klarner, B., Korobushkin, D. I., Liebke, D. F., Maraun, M., Mc Donnell, R. J., Pollierer, M. M., Schaefer, I., Shrubovych, J., Semenyuk, I. I., Sendra, A., Tuma, J., ... Scheu, S. (2022). Feeding habits and multifunctional classification of soil-associated consumers from protists to vertebrates. *Biological Reviews*, *97*(3), 1057–1117. https://doi.org/10.1111/brv.12832

Potapov, A. M., Brose, U., Scheu, S., & Tiunov, A. V. (2019). Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. *American Naturalist*, *194*(6), 823–839. https://doi.org/10.1086/705811

R Core Team. (2021). *R: A language and environment for statistical computing*. https://www.r-project.org/

Reeves, J. T., Fuhlendorf, S. D., Davis, C. A., & Wilder, S. M. (2021). Arthropod prey vary among orders in their nutrient and exoskeleton content. *Ecology and Evolution*, *11*(24), 17774–17785. https://doi.org/10.1002/ece3.8280

Říha, M., Gjelland, K. Ø., Děd, V., Eloranta, A. P., Rabaneda-Bueno, R., Baktoft, H., Vejřík, L., Vejříková, I., Draštík, V., Šmejkal, M., Holubová, M., Jůza, T., Rosten, C., Sajdlová, Z., Økland, F., & Peterka, J. (2021). Contrasting structural complexity differentiate hunting strategy in an ambush apex predator. *Scientific Reports*, *11*(1), 17472. https://doi.org/10.1038/s41598-021-96908-1

Rossberg, A. G., Matsuda, H., Amemiya, T., & Itoh, K. (2006). Food webs: Experts consuming families of experts. *Journal of Theoretical Biology*, *241*(3), 552–563. https://doi.org/10.1016/j.jtbi.2005.12.021

Ruxton, G. D., Sherratt, T. N., & Speed, M. P. (2004). *Avoiding attack: The evolutionary ecology of crypsis, warning signals and mimicry*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198528609.001.0001

Schmitz, O. J. (2008). Effects of predator hunting mode on grassland ecosystem function. *Science*, *319*(5865), 952–954. https://doi.org/10.1126/science.1152355

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1007/978-1-84882-087-6_9

Schrojenstein Lantman, I. M., Vesterinen, E. J., Hertzog, L. R., Martel, A., Verheyen, K., Lens, L., & Bonte, D. (2021). Body size and tree species composition determine variation in prey consumption in a forest-inhabiting generalist predator. *Ecology and Evolution*, *11*(12), 8295–8309. https://doi.org/10.1002/ece3.7659

Schultz, S., Kruschel, C., & Bakran-Petricelli, T. (2009). Influence of seagrass meadows on predator–prey habitat segregation in an Adriatic lagoon. *Marine Ecology Progress Series*, *374*, 85–99. https://doi.org/10.3354/meps07779

Shinohara, T., & Takami, Y. (2020). Functional diversity and trade-offs in divergent antipredator morphologies in herbivorous insects. *Ecology and Evolution*, *10*, 5089–5096. https://doi.org/10.1002/ece3.6262

Sholto-Douglas, A., Field, J., James, A., & van der Merwe, N. (1991). 13C/12C and 15 N/14 N isotope ratios in the southern Benguela ecosystem: Indicators of food web relationships among different size-classes of plankton and pelagic fish; differences between fish muscle and bone collagen tissues. *Marine Ecology Progress Series*, *78*, 23–31. https://doi.org/10.3354/meps078023

Shurin, J. B., Gruner, D. S., & Hillebrand, H. (2005). All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1582), 1–9. https://doi.org/10.1098/rspb.2005.3377

Sint, D., Kaufmann, R., Mayer, R., & Traugott, M. (2019). Resolving the predator first paradox: Arthropod predator food webs in pioneer sites of glacier forelands. *Molecular Ecology*, *28*(2), 336–347. https://doi.org/10.1111/mec.14839

Strand, M. R., & Obrycki, J. J. (1996). Host specificity of insect parasitoids and predators. *Bioscience*, *46*(6), 422–429. https://doi.org/10.2307/1312876

Thébault, E., Huber, V., & Loreau, M. (2007). Cascading extinctions and ecosystem functioning: Contrasting effects of diversity depending on food web structure. *Oikos*, *116*(1), 163–173. https://doi.org/10.1111/j.2006.0030-1299.15007.x

Torres-Campos, I., Magalhães, S., Moya-Laraño, J., & Montserrat, M. (2020). The return of the trophic chain: Fundamental vs. realized interactions in a simple arthropod food web. *Functional Ecology*, *34*(2), 521–533. https://doi.org/10.1111/1365-2435.13470

Traugott, M., Kamenova, S., Ruess, L., Seeber, J., & Plantegenest, M. (2013). Empirically Characterising trophic networks. In *Advances in ecological research* (Vol. *49*, 1st ed., pp. 177–224). Elsevier Ltd. https://doi.org/10.1016/B978-0-12-420002-9.00003-2

Traveset, A., Castro-Urgal, R., Rotllàn-Puig, X., & Lázaro, A. (2018). Effects of habitat loss on the plant-flower visitor network structure of a dune community. *Oikos*, *127*(1), 45–55. https://doi.org/10.1111/oik.04154

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M., & Zamora, R. (2015). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, *29*(3), 299–307. https://doi.org/10.1111/1365-2435.12356

Van De Walle, R., Logghe, G., Haas, N., Massol, F., Vandegehuchte, M. L., & Bonte, D. (2023). *Arthropod food webs predicted from body size ratios are improved by incorporating prey defensive properties* [data set on Zenodo]. https://doi.org/10.5281/zenodo.7546960

Verdeny-Vilalta, O., Fox, C. W., Wise, D. H., & Moya-Laraño, J. (2015). Foraging mode affects the evolution of egg size in generalist predators embedded in complex food webs. *Journal of Evolutionary Biology*, *28*(6), 1225–1233. https://doi.org/10.1111/jeb.12647

von Reumont, B. M., Campbell, L. I., & Jenner, R. A. (2014). Quo Vadis venomics? A roadmap to neglected venomous invertebrates. *Toxins*, *6*(12), 3488–3551. https://doi.org/10.3390/toxins6123488

Wang, L.-Y., Rajabi, H., Ghoroubi, N., Lin, C.-P., & Gorb, S. N. (2018). Biomechanical strategies underlying the robust body Armour of an aposematic weevil. *Frontiers in Physiology*, *9*, 1410. https://doi.org/10.3389/fphys.2018.01410

Witz, B. W. (1990). Antipredator mechanisms in arthropods: A twenty year literature survey. *The Florida Entomologist*, *73*(1), 71. https://doi.org/10.2307/3495331

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Sampling locations for the theoretical food web.

Appendix S2. Literature list used for theoretical food web.

Appendix S3. Model selection.

Appendix S4. Species list.

Appendix S5. Post-hoc tests.

Appendix S6. Hunting strategy with only spider data.

How to cite this article: Van De Walle, R., Logghe, G., Haas, N., Massol, F., Vandegehuchte, M. L., & Bonte, D. (2023). Arthropod food webs predicted from body size ratios are improved by incorporating prey defensive properties. *Journal of Animal Ecology*, *92*, 913–924. https://doi.org/10.1111/1365-2656.13905