

The crab spider–pitcher plant relationship is a nutritional mutualism that is dependent on prey-resource quality

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Abstract

1. Nutritional mutualisms are one of the three major categories of mutualisms and involve the provision of limiting nutrients (resources) to one species by another. It was recently shown in laboratory experiments that two species of pitcher-dwelling crab spiders (Thomisidae), *Thomisus nepenthophilus* and *Misumenops nepenthicola*, increased capture rates of flesh flies (Sarcophagidae) for their host, *Nepenthes gracilis*. The spiders ambushed pitcher-visiting flesh flies and dropped their carcasses into pitchers after consuming them. The consumption of shared prey-resources by crab spiders and pitcher plants presents the possibility of parasitism between them. However, ecologically generalizable mechanisms that predict the context-dependent outcomes of such mutualisms are not known.
2. The effectiveness framework (mutualism effectiveness = quality × quantity) is useful for examining the total effect of mutualisms, but its quality component can be difficult to define. We identify the crab spider–pitcher plant interaction as a type of resource conversion mutualism and propose that the quality component in such interactions is the amount of the underlying resource contained in each unit of resource processed. We then used the crab spider–pitcher plant interaction to test the hypothesis that resource conversion mutualisms are more beneficial to the nutrient recipient when operating through high-quality resources (i.e., large prey, in this interaction).
3. We sampled the prey and inquilines of 107 *N. gracilis* upper pitches in situ and analysed the differences between pitchers that were inhabited or uninhabited by crab spiders, and the differences between nutritional contents of prey that were consumed by crab spiders or not.
4. Pitchers inhabited by *T. nepenthophilus* contained higher numbers of several prey taxa, many of which were flying insects. Consumption by *T. nepenthophilus* reduced the nutrient contents in all prey examined. Overall, *T. nepenthophilus*-assisted prey capture is likely to result in a net nutrient gain for *N. gracilis* that is proportional to the size of prey consumed by *T. nepenthophilus*.
5. Our results suggest that resource conversion mutualisms are more likely to operate through high-quality resources, since the nutrient-processing species necessarily reduces the quality of the resource it processes while increasing its availability to the nutrient recipient species.

KEYWORDS

facilitation, *Henriksenia labuanica*, *Misumenops nepenthicola*, *Nepenthes gracilis*, Nutritional mutualism, resource quality, substitutable resources, *Thomisus nepenthophilus*

1 | INTRODUCTION

Nutritional mutualisms are one of the three major categories of mutualisms, in which a species provides one or more limiting nutrients (resources) to another species in exchange for another limiting nutrient, or indirect benefits such as protection and/or domicile (Bronstein, 2015). Many cases of nutritional mutualisms have been described in *Nepenthes* pitcher plants, carnivorous plants that grow in nutrient-poor soils and supplement their nutrient requirements through prey caught using pitfall-type traps in their leaves. Dipteran larvae inhabit the fluids of almost all known *Nepenthes* species (Beaver, 1979; Clarke & Kitching, 1993; Mogi & Yong, 1992) and have been shown to increase the nutrient sequestration rate and yield in *Nepenthes gracilis* (Lam, Chong, Anand, & Tan, 2017). The tendril-inhabiting predatory ant, *Colobopsis schmitzi* (previously *Camponotus schmitzi*), has been shown to increase prey capture in its host, *Nepenthes bicalcarata*, by attacking escaping prey on pitcher walls (Bazile, Moran, Le Moguédec, Marshall, & Gaume, 2012; Bonhomme et al., 2010), while *N. hemsleyana* provides the insectivorous bat, *Kerivoula hardwickii* with pitcher-roosts, and is in turn fed by its nitrogen-rich faeces (Grafe, Schöner, Kerth, Junaidi, & Schöner, 2011; Schöner et al., 2017).

Nutritional mutualisms may operate through the mutual trade of essential, non-substitutable resources (de Mazancourt & Schwartz, 2010; Schwartz & Hoeksema, 1998), a subcategory we term as resource trade mutualisms, or through the conversion of substitutable resources from one, inaccessible resource state to another, more accessible one, a subcategory we term as resource conversion mutualisms. Two resources are essential with respect to each other when growth or reproduction of a species is impossible in the absence of either, but when two resources are substitutable with respect to each other, growth or reproduction can be sustained in the absence of one as long as the other is present in sufficient quantities (Tilman, 1980). Competition between partners in resource trade mutualisms is minimal because each species in such a mutualism is limited by the essential resource that its partner has in excess and supplies it with (de Mazancourt & Schwartz, 2010; Schwartz & Hoeksema, 1998). For example, autotrophic *Symbiodinium* algae and heterotrophic corals form stable mutualisms through specialization and trade on categorically different resource types. However, theoretical studies (de Mazancourt & Schwartz, 2010; Schwartz & Hoeksema, 1998) show that mechanisms sustaining resource trade mutualisms are wholly dependent upon the essential (non-substitutable) nature of the resources being traded, and thus cannot be extended to resource conversion mutualisms, which operate through substitutable resources. An example of a resource conversion mutualism is the bat (*K. hardwickii*)-pitcher plant (*N. hemsleyana*) interaction. Both *N. hemsleyana*

and *K. hardwickii* consume insect prey, but *K. hardwickii* converts its insect prey into nitrogenous waste which it deposits in *N. hemsleyana* pitchers, in which it often roosts (Schöner et al., 2017). The consumption of overlapping resources by both partners in such mutualisms presents the possibility of parasitism (Anderson & Midgley, 2007), since both species essentially utilize one limiting, underlying resource.

The *Nepenthes*-associated nutritional mutualisms described previously fall into the subcategory of resource conversion mutualisms, since their mutualists facilitate the conversion of nitrogen from poorly accessible (e.g., complex insect protein or infrequently caught arthropods) to more easily accessible forms (e.g., ammonium or faeces). Ecologically generalizable mechanisms that predict the context-dependent outcomes of resource conversion mutualisms have not been identified to date. But clearly delineating the subcategories of nutritional mutualisms based on their underlying mechanisms can pave the way for formulating mechanism-informed predictions that are likely to be generalizable across all such interactions. We hereafter refer to the two subcategories simply as resource trade and resource conversion mutualisms, and focus on the latter subcategory in this study.

Recently, Lim, Lam, and Tan (2018) showed that two obligate pitcher-dwelling crab spider (Thomisidae) species, *Thomisus nepenthophilus* and *Misumenops nepenthicola* (Figure 1a,b), increased flesh fly (Sarcophagidae) capture rates of their host, *N. gracilis*, in laboratory experiments (*Misumenops nepenthicola* is also known as *Henriksenia labuanica* (Striffler & Rembold, 2009), although this name has not been accepted in the World Spider Catalog [<http://www.wsc.nmbe.ch/>]). The spiders ambushed flesh flies as these visited pitchers to feed, and dropped their carcasses into pitcher fluids after consuming them. However, crab spider consumption of flesh flies resulted in a lower total nitrogen gain by pitchers, per flesh fly trapped. Lim et al. (2018) showed that the total benefit received by pitcher plants from such an interaction with crab spiders was likely to be dependent on environmental prey-resource levels, being positive (mutualistic) in environments where prey is scarce, and negative (parasitic), where prey is abundant.

The natural history of *T. nepenthophilus* and *M. nepenthicola* is poorly studied in general, although earlier works have established that both are obligate pitcher inhabitants which are completely dependent upon *N. gracilis* for all stages of their life cycle, even constructing their nests within pitchers (Figure 1a,b; Clarke, 2001). Both crab spiders dive into pitcher fluids and hide themselves among prey carcasses when threatened (Clarke, 2001; Pocock, 1898). This behaviour is believed to be a defensive adaptation against predatory birds or wasps (Pocock, 1898). Aside from the study of Lim et al. (2018) which showed that both crab spider species attack flesh flies

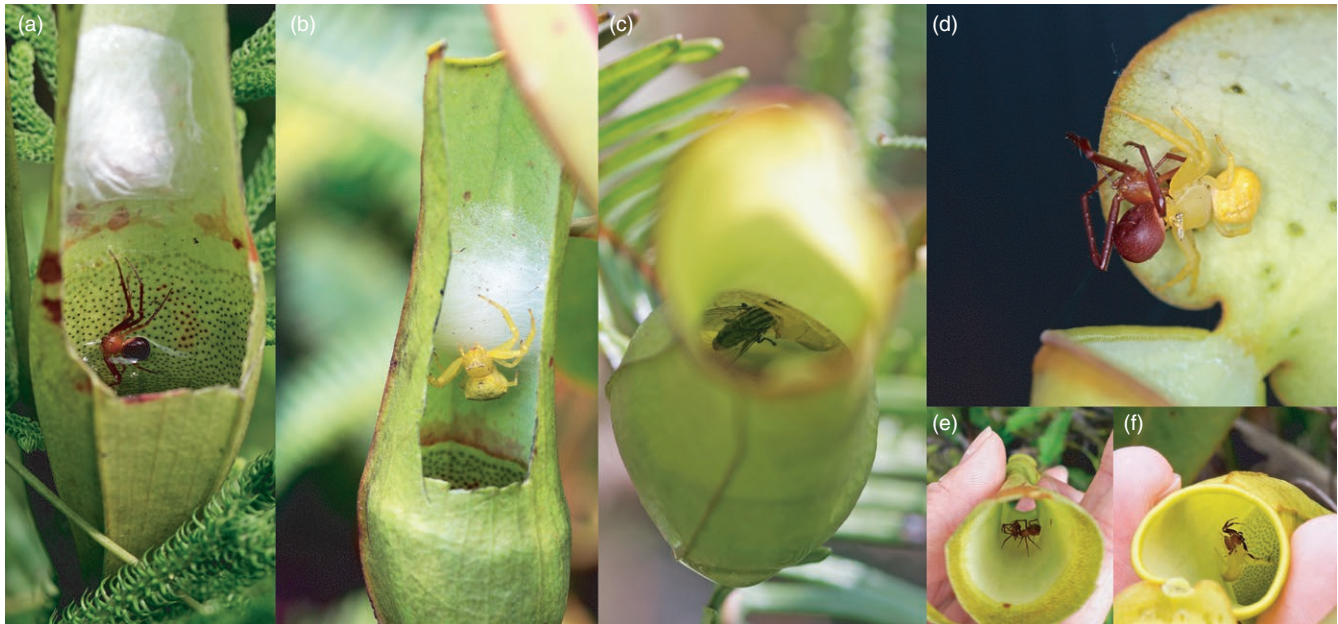


FIGURE 1 Adult female (a) *Misumenops nepenthicola* and (b) *Thomisus nepenthophilus* with egg sacs, in dissected *Nepenthes gracilis* pitchers in situ; (c) *T. nepenthophilus* with flesh fly (Sarcophagidae) prey in situ; (d) *T. nepenthophilus* consuming *M. nepenthicola* during a laboratory experiment; (e) *M. nepenthicola* cannibalizing a smaller *M. nepenthicola* individual in situ (view from the bottom of a pitcher dissected transversely at its base); (f) *T. nepenthophilus* female cannibalizing a male *T. nepenthophilus* in situ (view from above, with pitcher lid pulled back)

(Sarcophagidae) at pitcher peristomes, little is known about the foraging habits of *T. nepenthophilus*, but those of *M. nepenthicola* are better documented. *M. nepenthicola* is known to prey on both the larvae and emerging adults of specialist dipterans that inhabit pitchers (known as inquilines) (Chua & Lim, 2012; Clarke, 2001), has been observed attacking pitcher visitors (Clarke, 2001; Pocock, 1898) and has been filmed consuming recently drowned pitcher prey (an *Oecophylla smaragdina* ant worker; Planet Earth Episode 8: “Jungles” (2006), British Broadcasting Corporation). Reiskind (1978) also observed *M. nepenthicola* attacking struggling insect prey from the surface of pitcher fluids in *N. rafflesiana* and interpreted this to be a form of kleptoparasitism. However, struggling prey sometimes succeed in escaping pitchers, and the action of attacking struggling prey could also contribute to higher prey retention frequencies in pitchers (Bonhomme et al., 2010).

Nepenthes pitcher plants trap diverse arthropod prey taxa (Di Giusto, Grosbois, Fargeas, Marshall, & Gaume, 2008). These prey represent substitutable resources because they are interchangeable (substitutable) sources of nitrogen, a limiting resource in *Nepenthes* habitats (Adam, 1997; Moran, 1996; Moran & Moran, 1998). Prey species also differ greatly in resource quality, with larger prey containing higher quantities of nitrogen per prey individual than smaller ones. However, Lim et al. (2018) did not examine the effects of the crab spider presence on the in situ capture rates of flesh flies or the many other prey taxa of *N. gracilis*, and the possible relationship this had with prey-resource quality. Furthermore, the effects of crab spiders on in situ pitcher inquiline communities have never been examined.

Mutualisms are often context dependent (Bronstein 1994). The effectiveness framework (mutualism effectiveness = quality × quantity) of Schupp, Jordano, and Gómez (2017) is useful for examining context dependency, but its quality component can be difficult to define. As with Lim et al. (2018), we propose that the quality component in such interactions is the amount of the underlying resource contained in each unit of resource processed, and aim to use the crab spider–pitcher plant interaction to examine the outcomes of this mutualism when operating through different, substitutable, resources (prey taxa). The quantity component should be understood as the unit in which this resource is consumed, and is thus the number of prey individuals trapped by pitchers in this case. Because there is likely to be a limit to the amount of nutrients a crab spider can extract from a large prey item in a single prey capture event, we hypothesize that the crab spider–pitcher plant interaction would be more beneficial towards *N. gracilis* when it operates through high-quality resources.

The specific objectives of the study are to (a) determine how the presence of *T. nepenthophilus* and *M. nepenthicola* alters the prey and inquiline compositions of the *N. gracilis* pitchers that they inhabit, and (b) determine how crab spider-assisted prey capture alters the quality (nutritional content) of different prey types. We first conducted field surveys to examine the in situ prey and inquiline compositions of *N. gracilis* pitchers that were inhabited by crab spiders or not (control). We then analysed the nutrient contents of high- and low-quality prey species using in vitro digestion experiments. Finally, we fitted these nutrient values into an in situ prey capture model to determine whether crab spider assistance in the capture of high- or

low-quality resources resulted in net benefit for their pitcher plant hosts.

2 | MATERIALS AND METHODS

2.1 | In situ observation—field surveys

Nepenthes gracilis pitchers were sampled at two locations on the equatorial, aseasonal Singapore Island where stable, reproducing populations of both pitcher plants and crab spiders had been observed. These locations were Sembawang Avenue (1°26′30.9″N 103°49′14.1″E) and Area A (this location cannot be disclosed for security reasons).

A paired-sampling method was used to compare the prey contents of 107 *N. gracilis* upper pitchers that were either inhabited by adult, female *T. nepenthophilus* ($n = 30$), adult, female *M. nepenthicola* ($n = 28$), or in which no spiders were found (hereafter referred to as control pitchers; $n = 49$). Transects (10–20 m long), spaced at least 10 m apart were laid haphazardly at each site. All pitchers encountered along these transects were checked for the presence of crab spiders. When a crab spider was encountered, environmental covariates (Supporting Information Table S1) of the pitcher in which it was encountered were recorded. These environmental covariates reflect variations in pitcher microhabitats and can alter the prey composition of *N. gracilis* pitchers (W. N. Lam, pers. obs.). They were thus included in the models to account for environmental effects on prey numbers.

To prevent the introduction of bias in the selection of sampled pitchers, stringent criteria were used to select control pitchers. After a crab spider-inhabited pitcher was found, adjacent *N. gracilis* shoots produced by the same plant were identified within a 1-m radius of that pitcher, and an uninhabited pitcher of the same age was selected from these as a control pitcher. If several candidate control pitchers were present, the one that was most similar to the focal pitcher in other environmental covariates (Supporting Information Table S1) was selected. These environmental covariates were generally independent of each other (Supporting Information Figure S1). Pitchers were not sampled at all if no pitchers met the criteria for selection as the paired control, if all possible control pitchers were also inhabited by the same species of spider, or if the only eligible control pitcher was more than 1 m from the pitcher inhabited by the crab spider. Pitchers inhabited by juvenile spiders or adult male spiders, both of which are significantly smaller than the adult females, were also rejected because of the difficulty of parameterizing spider gender or size in models. In addition to preventing experimenter bias, this procedure eliminates the effects of intraspecific variation in pitcher prey-trapping efficiencies, controls for local variations in prey abundances and minimizes differences in prey capture caused by pitcher microhabitat variations. As a result of these controls, differences in the environmental covariate values between crab spider-inhabited and control pitchers were negligible (Supporting Information Figure S2).

Additionally, only the first, second or third sequential pitchers were sampled. The first sequential pitcher is the pitcher borne on the youngest pitcher-bearing leaf of a given stem. As pitchers are produced sequentially on leaves that emerge from the apex of growing stems, the first sequential pitcher is in most cases the youngest pitcher on a given stem. We limited our samples to first–third sequential pitchers for two main reasons. Firstly, it is often difficult to identify the highly degraded prey contents of the older pitchers. Secondly, our sampling methodology cannot differentiate between pitchers that were previously inhabited by crab spiders but later abandoned and pitchers that had never been inhabited by crab spiders before, since crab spider presence can only be reliably determined by its presence at the time of observation. Because prey assemblages of pitchers reflect the cumulative prey input over the life span of pitchers, sampling older pitchers would have increased the probability of encountering such false negatives in the data (i.e., pitchers whose prey spectra accumulated through crab spider prey capture, but were wrongly classified as uninhabited pitchers because they had been abandoned by the time of sampling). We thus chose to use only younger (first–third sequential) pitchers to keep the probability of such false negatives low.

All metazoan inquilines and prey content from sampled pitchers were collected and brought back to the laboratory for sorting and analysis. Prey carcasses and inquilines were counted and identified to as low a taxonomic level as possible with the help of experts or guides (Choo, Koh, & Ng, 1997; Marshall, 2012).

2.2 | In situ observation—prey/inquiline categorization and data analysis

Rare prey taxa which occurred in less than three samples were either grouped with closely related taxa or excluded from the analysis (Supporting Information Table S2). The total numbers of prey or inquiline individuals in each of these taxa were then modelled against crab spider presence and other environmental covariates (Supporting Information Table S1) using a Bayesian multivariate model, as implemented in the hierarchical modelling of species communities (HMSC) framework (Ovaskainen et al., 2017). HMSC was developed as a type of joint species distribution model, which predicts the compositions of whole communities using individual species distribution models which are integrated through a latent variable model (Ovaskainen et al., 2017). HMSC utilizes Bayesian Markov chain Monte Carlo (MCMC) methods for the estimation of parameter values. Multivariate models were first developed as alternatives to distance-based multivariate tools (Warton, Wright, & Wang, 2012), but have since gained acceptance as a modern statistical tool for community ecology (Warton, Foster, De, Stoklosa, & Dunstan, 2015b; Warton et al., 2015a), and especially so in species distribution modelling (Thorson et al., 2016). Multivariate models have also been used to model prey assemblages in *Nepenthes* pitchers (Lam et al., 2018).

A Poisson error structure (log link function) was used for the multivariate model. Model fixed effects were the environmental covariates measured for each sampled pitcher (Supporting Information Table S1), as well as the presence of *T. nepenthophilus* or *M. nepenthicola* in pitchers. All continuous variables among the environmental covariates were transformed where necessary to ensure normal errors, and standardized (centred on zero and scaled to standard deviation units) before the modelling process. Pitcher pair, transect and site were also included as nested random effects (Supporting Information Table S1) to account for local variations in prey abundances (site and transect) and the paired nature of the samples (pair). Finally, the model also utilized latent variables to model the biotic interactions and/or joint responses of prey/inquiline taxa to unparameterized environmental variables.

The model was run for 100,000 iterations with a burn-in of 10,000 and a thinning rate of 50. Flat priors were used, as the analysis was primarily exploratory in nature and we had no prior expectations of parameter values. MCMC chains were visually inspected to ascertain convergence; 95% credible intervals were obtained from the 2.5th and 97.5th percentiles of the posterior sample of each fixed effect coefficient.

2.3 | Comparison of nutritional benefit

We wanted to know the difference in nitrogen obtained by pitchers from prey of different size classes, as well as to determine whether in situ crab spider-assisted prey capture rates were high enough to offset the nutrient losses sustained in crab spider-consumed prey. The nutritional contents of prey taxa of differing sizes were thus compared in this section.

We first selected five prey taxa whose capture rates were significantly higher in pitchers inhabited by *T. nepenthophilus* (Figure 2). These were Culicidae (mosquitoes), Phoridae (scuttle flies), Sarcophagidae (flesh flies), miscellaneous Hemiptera (i.e., large-bodied true bugs from the families Alydidae and Rhyparochromidae, sometimes known as “seed bugs”) and Blattodea (cockroaches; most of which are likely to be *Blattella germanica*). We then obtained seven to 12 live individuals of representative species from each of these five taxa from field sites—these were *Tripteroides tenax* (Culicidae), *Endonepenthia schuitemakeri* (Phoridae), Sarcophagidae species (Sarcophagidae), *Riptortus cf. linearis* (miscellaneous Hemiptera) and *Blattella germanica* (Blattodea). Details of how each of these prey species was

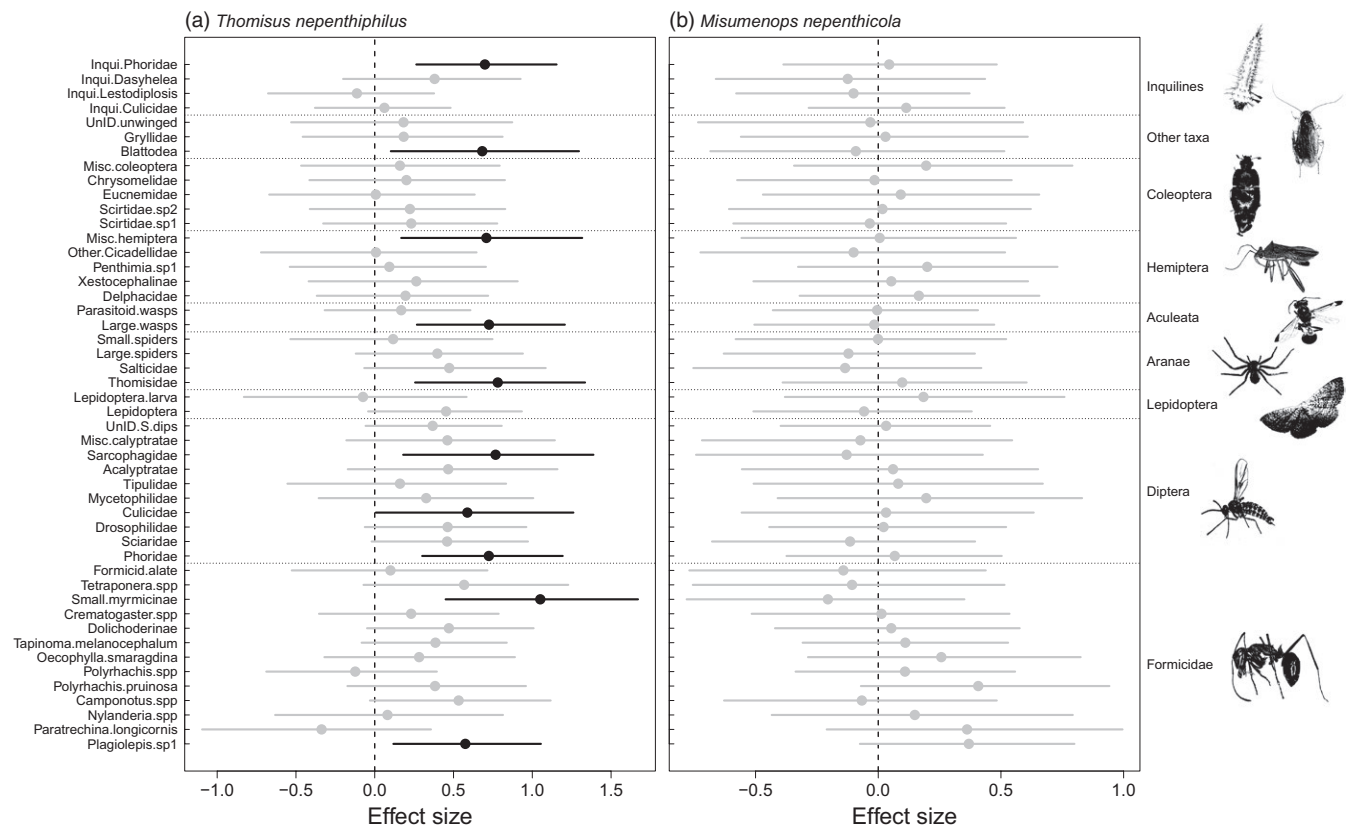


FIGURE 2 Effect size estimates (posterior means; points) from the multivariate model, with their 95% credible intervals (horizontal lines about the points), for each prey or inquiline taxon (y-axis) in (a) *Thomisus nepenthophilus*- and (b) *Misumenops nepenthicola*-inhabited pitchers. Effect size is the difference in log-transformed prey/inquiline intercept estimates between control pitchers and crab spider-inhabited ones. Effects whose 95% credible intervals do not intercept with zero are coloured black, while those which do are coloured grey, for clarity. The prefix “Inqui” in the y-axis labels identifies the inquiline taxa (i.e., the living, aquatic larvae of specialized dipterans inhabiting the pitchers)—all other taxa are prey taxa; labels on the right side of the figure are the higher level taxonomic groups into which prey/inquiline taxa may be categorized; see Supporting Information Table S2 for more information on prey and inquiline identification and classification

obtained are described in the Supplementary methods in the online supplementary information.

Half (randomly selected) of the individuals of these representative prey species were offered to *T. nepenthophilus* as done in Lim et al. (2018). The other half were killed by freezing at -20°C . Carcasses were then digested in vitro in 1 ml (for *T. tenax* and *E. schuitemakeri*) or 3 ml (for *R. cf. linearis*, *B. germanica* and Sarcophagidae) of filtered *N. gracilis* pitcher fluids for 14 days to determine the amount of nitrogen that pitchers may extract from them. Soluble protein and ammonium in fluids were then measured using the Bradford assay (Hammond & Kruger, 1988) and a salicylate assay as described in Lam et al. (2017), respectively. Different volumes of fluids (1 ml or 3 ml) were used to keep fluid protein and ammonium concentrations within detectable ranges. *T. nepenthophilus* also defecated in their containers (15 ml Cellstar[®] centrifuge tubes) after consuming prey. Their faeces were dissolved in 500 μL of water and tested for uric acid using a colorimetric uric acid assay (BioVision Inc., Milpitas, CA, USA). Total pitcher-available nitrogen was calculated by summing up the nitrogen content of soluble protein, ammonia and (for *T. nepenthophilus*-consumed prey) uric acid. All procedures used in this section were directly comparable to those of Lim et al. (2018), and data of flesh fly nutrient contents are the same as those in Lim et al. (2018).

The approximate nitrogen gain of pitchers under in situ conditions was estimated for each representative prey species for *T. nepenthophilus*-inhabited and control (uninhabited) pitchers. This was done in accordance with the effectiveness framework of Schupp et al. (2017), which states that the effectiveness of a mutualistic interaction is equal to the product of its quality and quantity components. Thus, the net nitrogen gained by pitchers from the interaction with *T. nepenthophilus* (effectiveness of the mutualism, which we denote N_{net}) for each prey taxon can be expressed thus:

$$N_{\text{net}} = N_{\text{mut}} - N_{\text{cont}} = (C_{\text{mut}} \times \text{PAN}_{\text{mut}}) - (C_{\text{cont}} \times \text{PAN}_{\text{cont}}) \quad (1)$$

In this equation, N is the total nitrogen gained by a pitcher that is inhabited by crab spiders (N_{mut}) or uninhabited (N_{cont}). C is the prey capture rate of pitchers (the “quantity component”) which are inhabited (C_{mut}) or uninhabited (C_{cont}) by crab spiders. Estimates of C_{mut} and C_{cont} were obtained from the multivariate model-predicted prey capture rates of *T. nepenthophilus*-inhabited and control pitchers, respectively. PAN is the total pitcher-available nitrogen per prey individual which has been consumed by crab spiders (PAN_{mut}) or killed by freezing (PAN_{cont}). The net nitrogen benefit of *T. nepenthophilus* (N_{net}) was calculated individually for each of the five prey taxa on which the in vitro nutrient analysis had been performed. We hypothesized that N_{net} would be higher in larger prey taxa.

The fresh weight of each prey taxon was also obtained by weighing prey specimens (five each for *R. cf. linearis* and *B. germanica*, 10 each for Sarcophagidae, *T. tenax* and *E. schuitemakeri*) which had been killed by freezing on a MS304TS analytic balance (Mettler Toledo™; Greifensee, Switzerland).

All statistical analyses and mathematical calculations were performed in R ver 3.4.0 (R Core Team, 2017).

3 | RESULTS

3.1 | In situ observation

We identified 69 prey taxa and five inquiline species from surveys of the contents of 107 *N. gracilis* upper pitchers, with ants (Formicidae) being the most numerically abundant prey group (Supporting Information Table S2). In the multivariate prey capture model, the presence of crab spiders (both *T. nepenthophilus* and *M. nepenthicola*) accounted for an average of 14% of the explained variance, while the environmental covariates collectively accounted for 58% of the explained variance, and the random effects, for 28% (Supporting Information Figures S3,S4).

The presence of *T. nepenthophilus* was positively correlated with many prey and inquiline taxa (posterior mean of the *T. nepenthophilus* coefficient was positive in 44 of the 48 prey or inquiline taxa), but this effect was strongly positive (95% credible intervals did not intercept zero) only in one inquiline, namely larval inquiline Phoridae (Diptera), and nine prey taxa, namely small Myrmicinae (inclusive of *Meranoplus malaysianus*, *Tetramorium* sp., *Monomorium* sp. and *Pheidole* sp.; Formicidae), *Plagiolepis* sp. (Formicidae), large wasps (various unidentified families from Hymenoptera), Culicidae (Diptera), Phoridae (Diptera), Sarcophagidae (Diptera), miscellaneous Hemiptera (Alydidae and Rhyparochromidae) and Blattodea (most of which are likely to be *Blattella germanica*) (Figure 2a). For the non-formicid prey taxa among these, the model predicted that pitchers inhabited by *T. nepenthophilus* trap approximately twice as many prey individuals as control pitchers (Figure 3; Table 1a), in the terminology of Equation 1, this means that C_{mut} was approximately double C_{cont} in the prey taxa for which a strong *T. nepenthophilus* effect was observed. However, the presence of *M. nepenthicola* in pitchers was not strongly correlated with the abundances of any of the prey or inquiline taxa (posterior mean of the *M. nepenthicola* coefficient was positive in only 28 of the 48 prey or inquiline taxa, and 95% credible intervals intercepted zero in all of these; Figure 2b).

3.2 | Comparison of nutritional benefit

Pitcher available nitrogen varied greatly across the five prey species examined, with the larger ones generally yielding larger total amounts of nitrogen (Figure 4; Table 1b). *T. nepenthophilus*-consumed prey yielded lower total pitcher available nitrogen (PAN_{mut} values of Equation 1) than prey which had been killed by freezing (i.e., the controls; PAN_{cont}) in the five prey species examined (Figure 4; Table 1b). This corresponded to a 22.8%–67.3% loss in nitrogen (Table 1b).

The calculated net nutritional benefit (N_{net} in Equation 1) provided by *T. nepenthophilus* to pitchers was found to be slightly negative in the smallest prey taxon (Culicidae, which was represented by *T. tenax* in the nutritional analysis), but positive in all other prey taxa (Table 1c). This nutritional benefit was also positively correlated with log-transformed prey biomass (Figure 5).

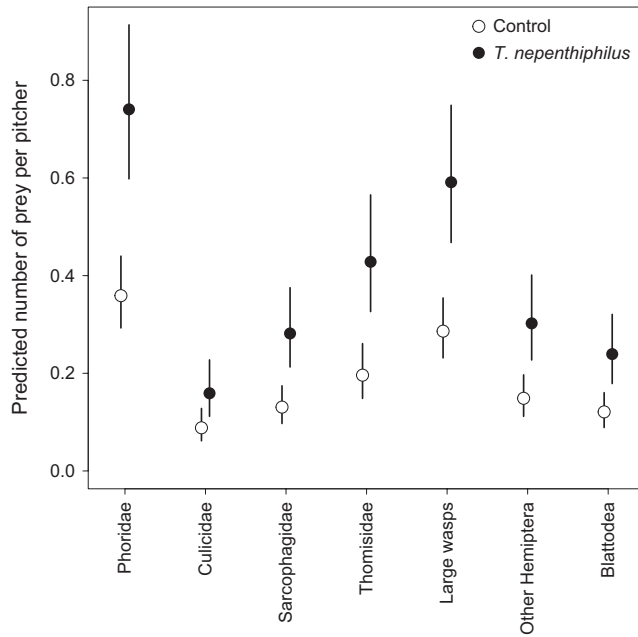


FIGURE 3 Model-predicted mean prey capture rates of control (open circles) and *Thomisus nepenthophilus*-inhabited (filled circles) pitchers for non-formicid prey taxa in which the coefficient 95% credible intervals did not overlap with zero (Figure 2). Vertical lines about the points represent standard errors of the predictions

4 | DISCUSSION

Pitcher-dwelling crab spiders have long been known to attack pitcher-visiting arthropods at the mouths of pitchers (Figure 1c), and in so doing increase the “capture rate” of such prey by pitchers (Clarke, 2001; Lim et al., 2018; Pocock, 1898). However, the potentially beneficial effects of such an interaction have not been conclusively

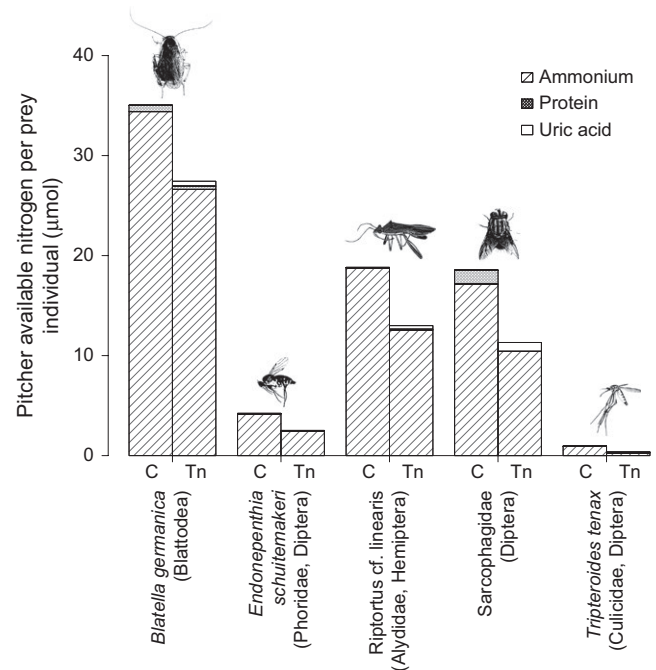


FIGURE 4 Amount of nitrogen that can be obtained from five selected prey taxa by control (C) and *Thomisus nepenthophilus*-inhabited (Tn) pitchers, as determined by in vitro digestion experiments. Total pitcher available nitrogen is the sum of inputs from three different nitrogen sources: fluid ammonium (singly hatched bars), fluid protein (doubly hatched bars) and uric acid from spider faeces (open bars); $n = 3-5$

demonstrated (in Lim et al. (2018), they were purely experimental). Using multivariate models of in situ pitcher inquiline and prey taxa, we identified several prey taxa which are caught in greater abundance in pitchers inhabited by *T. nepenthophilus* (Figures 2 and 3). Laboratory

TABLE 1 Estimated equation terms (Equation 1) for the five prey taxa examined. Prey taxa are arranged in ascending order of biomass, with the largest prey taxon (*Blattella germanica*) to the right

Equation term	<i>Tripteroides tenax</i> (Culicidae)	<i>Endonepenthia schultemakerei</i> (Phoridae)	Sarcophagidae	<i>Riptortus cf. linearis</i> (Hemiptera)	<i>Blattella germanica</i> (Blattodea)
(a) Pitcher prey capture rate (C; units: prey individuals per pitcher)					
Unassisted (C_{cont})	0.088	0.359	0.131	0.149	0.121
<i>Thomisus nepenthophilus</i> -assisted (C_{mut})	0.159	0.741	0.282	0.302	0.239
Proportion increase	1.80	2.06	2.15	2.03	1.98
(b) Pitcher-available nitrogen (PAN; units: µmol per prey individual)					
Freeze-killed prey (PAN_{cont})	4.74	21.09	55.64	75.26	175.17
<i>T. nepenthophilus</i> -consumed prey (PAN_{mut})	1.55	12.41	32.15	50.26	135.23
Proportion loss	0.673	0.411	0.422	0.324	0.228
(c) Predicted pitcher nitrogen gain (N; units: µmol)					
<i>T. nepenthophilus</i> -inhabited pitchers (N_{mut})	0.24	9.19	9.05	15.39	32.36
Uninhabited pitchers (N_{cont})	0.42	7.57	7.28	11.20	21.19
Net gain from interaction (N_{net})	-0.17	1.62	1.77	4.19	11.17

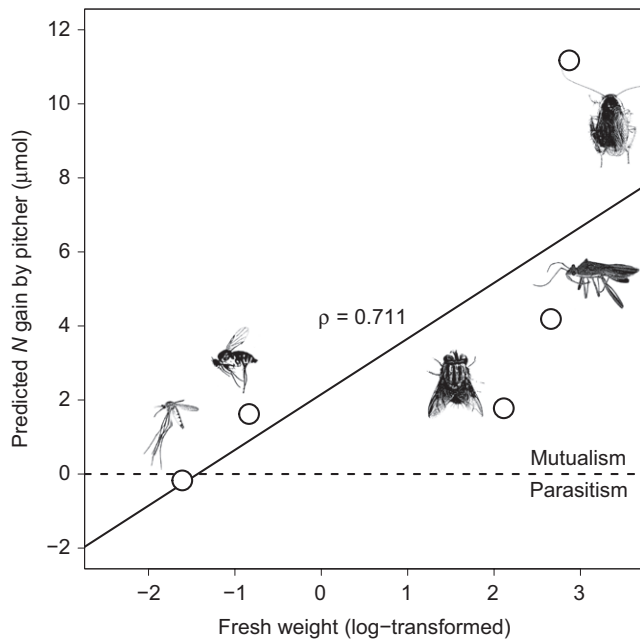


FIGURE 5 Predicted nitrogen gain (open circles) of *Nepenthes gracilis* pitchers as a result of being inhabited by *Thomisus nepenthophilus* for five prey taxa of differing fresh weights. Predicted nitrogen gain is negative (i.e., occurring within the grey region labelled "parasitism") in only one prey taxon, *Tripteroides tenax*, and is overall positively correlated with prey fresh weight (continuous black line = fitted regression line; Pearson correlation coefficient $\rho = 0.711$). The prey taxa are plotted along the x-axis of fresh weight (log-transformed) and are *T. tenax* (Culicidae, Diptera), *Endonepenthia schuitemakeri* (Phoridae, Diptera), Sarcophagidae (Diptera), *Riptortus cf. linearis* (Alydidae, Hemiptera), *Blattella germanica* (Blattodea)

experiments confirmed that *T. nepenthophilus* attacks these prey species at pitcher mouths, and by consuming them reduces their overall nitrogen yield to pitchers (Figure 4). Using model-predicted prey capture rates, we showed that *T. nepenthophilus*-assisted prey capture is likely to result in a net nutrient gain for *N. gracilis* that is proportional to the size of prey consumed by *T. nepenthophilus* (Figure 5). Overall, the interaction is beneficial for *N. gracilis* when it operates through all but the smallest prey taxa (Figure 5). The *T. nepenthophilus*-*N. gracilis* interaction belongs to a subcategory of nutritional mutualisms which we term as resource conversion mutualisms, with *T. nepenthophilus* converting flying prey species which are inaccessible to *N. gracilis* into consumed prey carcasses which are deposited in its pitchers. This behaviour increases the quantities but reduces the qualities of prey-resources to the resource recipient, *N. gracilis*. Our results suggest that resource conversion mutualisms are more likely to operate through high-quality resources. That is, the resource recipient in a resource conversion mutualism is likely to receive the most net benefit when its partner processes resources containing high per unit amounts of the underlying resource. Given the prey assemblages of *N. gracilis* pitchers in the sites sampled in this study, the overall effect of *T. nepenthophilus* on *N. gracilis* is most likely to be positive.

4.1 | Crab spider-assisted prey capture in pitchers

Our findings from in situ observations corroborate the experimental results of Lim et al. (2018) and allowed the identification of several prey taxa in which the beneficial effect of *T. nepenthophilus*' feeding behaviour is manifested. In addition to strong positive effects in large wasps (various unidentified families from Hymenoptera), Culicidae (Diptera), Phoridae (Diptera), Sarcophagidae (Diptera), miscellaneous Hemiptera (Alydidae and Rhyparochromidae) and Blattodea (most of which are likely to be *Blattella germanica*), the presence of *T. nepenthophilus* also had weak positive effects on the prey capture rates of many other flying prey taxa such as moths (Lepidoptera) and fruit flies (Drosophilidae, Diptera) (Figure 2a). It must be acknowledged that, for some prey taxa which are highly susceptible to being trapped by pitchers, *T. nepenthophilus* consumption may deplete their nutrient contents without significantly increasing their capture rates. However, it is not possible to ascertain whether this indeed occurs without more meticulous observations, and we thus restrict the discussion to taxa which are trapped more successfully through *T. nepenthophilus*-assisted capture. Furthermore, the effect of juvenile and/or male *T. nepenthophilus* on prey capture rates may differ significantly from that of mature females examined in this study. Male or juvenile *T. nepenthophilus* may not increase prey capture rates as much as females, but may also have weaker negative impacts on prey nutrient value.

Many crab spider species forage on flowers, where they ambush insect pollinator species (Morse, 1981). Such a feeding habit is known to reduce the pollination rates of flowers and is understood to have a net negative effect on plants inhabited by crab spiders (Gonçalves-Souza, Omena, Souza, & Romero, 2008). Crab spider presence on flowers may deter insect pollinator visitation (Dukas & Morse, 2003; Gonçalves-Souza et al., 2008) or may increase visitation via attractive ultraviolet contrast patterns created by the spider's body on flowers (Heiling, Herberstein, & Chittka, 2003). It is unclear whether the presence of pitcher-dwelling crab spiders attracts or deters pitcher visitation by pitcher prey taxa. However, our study shows that the net effect of crab spider presence in pitchers is the increase in prey capture which is largely beneficial towards their plant hosts, unlike the case in flower crab spiders.

Because our study is correlative in nature, it is possible that increased prey capture rates in crab spider-inhabited pitchers are caused by factors other than crab spider-assisted prey capture. Flower crab spiders are known to select flowers that exhibit greater symmetry, which are similarly preferred by their bee prey (Wignall, Heiling, Cheng, & Herberstein, 2006), or inflorescences that contain the greatest number of nectar-producing flowers, which thus experience the highest insect visitation rates (Morse & Fritz, 1982). In this system, crab spiders may select pitchers that secrete larger amounts of nectar or olfactory attractants, larger pitchers or pitchers that are positioned high in the vertical strata of vegetation, so as to maximize prey capture. However, pitcher selection behaviour by crab spiders is unlikely to have significantly altered the findings of this study because of stringent controls in

the sampling procedure. These controls excluded genetic variation and age differences between pitchers, eliminated spatial variations between prey communities and accounted for possible effects of environmental variables such as the size and position of pitchers in the vertical strata of vegetation (see Supporting Information Table S1 for more information and Supporting Information Figure S4 for their effects on prey capture). As crab spiders are not found in high densities in the habitat (adult *T. nepenthophilus* occupied 13% of pitchers and *M. nepenthicola*, 10%, in a preliminary random sample of 91 *N. gracilis* pitchers [W. N. Lam, pers. obs.]), it is unlikely that they had fully occupied all “optimal” pitcher habitats, and the paired-sampling method employed in this study is thus likely to have selected appropriate control pitchers which would have been no less attractive to pitcher visitors than those inhabited by crab spiders in the study. Furthermore, earlier experimental work by Lim et al. (2018) has already demonstrated under laboratory experimental conditions that *T. nepenthophilus* significantly increase capture rates of the pitchers they inhabit. Therefore, while acknowledging that crab spider site selection may slightly bias our results towards the detection of positive effects despite all the controls already in place, we argue that any such bias would have been very small in comparison to the true effect of crab spiders on pitcher prey capture rates.

Contrary to the findings of Chua and Lim (2012), we found no evidence for inquiline predation by *M. nepenthicola* in our study. Instead, a positive correlation was found between *T. nepenthophilus* presence and inquiline phorid numbers in pitchers (Figure 2). The most possible explanation for this is that *T. nepenthophilus* often catch large prey taxa, resulting in an accumulation of such carcasses in pitchers they inhabit. Inquiline phorid species are attracted to the smell of rotting prey in pitchers, and selectively oviposit in pitchers that contain large bodied or larger quantities of prey (W. N. Lam, pers. obs.), and are thus more abundant in *T. nepenthophilus*-inhabited pitchers.

A similar explanation may be proposed for several ant prey taxa in which a positive correlation with crab spider presence was found (small Myrmicinae species and *Plagiolepis* sp. were strongly positively correlated with *T. nepenthophilus* presence, while *Polyrhachis pruinosa* and *Plagiolepis* sp. were weakly positively correlated with *M. nepenthicola* presence; Figure 2). Under laboratory conditions, both crab spider species could not be coerced into attacking *Polyrhachis pruinosa* (Formicinae; a large ant species) or *Dolichoderus thoracicus* (Dolichoderinae; a small- to medium-sized ant species), suggesting that crab spiders were either reluctant to attack ants unless starved, or that the correlations discovered in in situ samples may have been attributable to indirect effects such as that described for inquiline phorid larvae. Alternatively, crab spiders may avoid attacking ants directly, and instead do so only after these have fallen into pitchers and are trying to escape from fluids, as described by Reiskind (1978), and as done by predatory *C. schmitzi* ants in *N. bicalcarata* (Bonhomme et al., 2010). As such a mutualistic pathway is merely speculative, ant prey were not included in subsequent nutritional analyses.

4.2 | Interactions involving *M. nepenthicola*

Lim et al. (2018) found that *M. nepenthicola* attacked flesh flies at the peristomes of pitchers in laboratory experiments, but their positive effect on overall pitcher flesh fly capture rates was weak and statistically insignificant. *M. nepenthicola* also consumed flesh fly carcasses and reduced their total nutrient value for pitchers slightly (Lim et al., 2018). Our in situ study showed qualitatively similar findings, with *M. nepenthicola* presence having weakly positive correlations with the abundance of some prey taxa (e.g., *Penthimia* sp. [Cicadellidae, Hemiptera], caterpillars [Lepidoptera larvae], *Polyrhachis pruinosa*, *Paratrechina longicornis*, *Plagiolepis* sp. [Formicinae, Formicidae]; Figure 2b). It is possible that *M. nepenthicola* consumes drowned or drowning pitcher prey, and thus depletes prey nitrogen without increasing pitcher prey capture rates. Such a behaviour would be clearly parasitic towards pitchers. However, our findings are inconclusive in this regard, and future studies are still necessary to ascertain the true nature of the *M. nepenthicola*-*N. gracilis* interaction.

Interestingly, *T. nepenthophilus*-inhabited pitchers often contained crab spider (Thomisidae) carcasses (Figures 2a and 3), and many of these carcasses were of *M. nepenthicola* (Supporting Information Table S2), suggesting that the larger *T. nepenthophilus* regularly attacked the latter species when they encountered each other in pitchers. Such interspecific aggression has also been observed directly (Figure 1d), and cannibalism among these solitary crab spider species is also a common sight (Figure 1e,f). If interspecific habitat competition occurs, then it is possible that *M. nepenthicola* is often forced to occupy suboptimal pitchers with lower supplies of prey (e.g., smaller pitchers or those positioned lower in the undergrowth), which could have potentially made it more difficult to detect *M. nepenthicola*-assisted prey capture.

4.3 | Resource quality and the net benefit of resource conversion mutualisms

The net benefit of a mutualism is also termed as its effectiveness and is the product of quantity and quality components of the mutualism (Schupp et al., 2017). In our study system, the total nitrogen made available to pitchers (total effect; N in Equation 1) is a product of prey capture rates (quantity component; C in Equation 1) and nitrogen contents of individual prey (quality component; PAN in Equation 1). Large prey are higher in quality to both crab spiders and pitcher plants because they contain higher amounts of the limiting resource, nitrogen, per prey individual trapped (Figure 4; Table 1b). This disparity in resource quality is likely to be responsible for the difference in the predicted nitrogen benefit resulting from *T. nepenthophilus*-assisted prey capture, which was roughly correlated with the size of the prey taxa being trapped (Figure 5). This is probably because of a limit to the amount of nutrients a crab spider can extract from large prey in a single prey capture event, and/or because crab spiders may be less efficient in processing large-bodied prey (e.g., low surface area to volume ratio of large flight muscles may reduce the rate of spider proteolytic degradation), so that

small prey items are almost completely depleted of nutrients, while larger ones are dropped into pitcher fluids still containing significant amounts of undigested tissue.

Our findings about the relationship between resource quality and nutritional mutualisms may appear to contradict those of similar studies of resource facilitation. Fugère et al. (2012) found that facilitation in a stream detritus community was more pronounced when operating through “lower quality resources” (less palatable leaves which have a lower standard leaf area [SLA]). However, the discrepancy merely revolves around the definition of the term “quality.” Fugère et al. (2012) had defined low-quality resources in that detritivorous system as resources which were not easily broken down. In contrast, we have chosen to define a low-quality resource as one that contains less of the underlying resource of nitrogen in each unit of resource processed. But leaves with lower SLA contain *higher* proportions of leaf dry mass per unit area of leaf. Since Fugère et al. (2012) fixed the total leaf area of fed leaves, the lower SLA leaves actually contained higher per unit amounts of the underlying resource of leaf tissue, though much of this was not in a form that could be directly extracted by all stream detritivore species. The findings of our study and that of Fugère et al. (2012) thus agree to a large extent. Nevertheless, we argue that our definition of resource quality permits greater integration with mutualism concepts (Schupp et al., 2017), while that used by Fugère et al. (2012) may only work in detritivorous or digestive systems, and thus have narrower applicability across systems.

Furthermore, such a definition of resource quality would make explicit the substitutable nature (with respect to the resource recipient species) of resources or resource states under consideration. The resource-processing functions of upstream consumers in processing chain commensalisms (Heard 1994), of nutrient mutualists in digestive mutualisms (Anderson & Midgley, 2003), or of inquiline predators in prey capture mutualisms (Bazile et al., 2012; Schöner et al., 2017) all require that one species is better able to exploit a given resource and yet benefit its partner through a by-product of resource consumption. The unutilized by-product of this resource necessarily contains less of the underlying resource than the original resource, although enough of it remains to be of benefit to the nutrient recipient in these interactions. Such interactions are thus more likely to be beneficial to the resource recipient species when the original resource contains a higher amount of the underlying resource, as findings in this study suggest. Although intuitive, this perspective has not often been stated explicitly. We argue therefore that defining resource quality as the amount of the underlying resource contained in each unit of the resource processed would encourage both a more mechanistic and a more generalizable understanding of resource conversion mutualisms.

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AUTHORS' CONTRIBUTIONS

W.N.L. and H.T.W.T. composed the study design. W.N.L. carried out the fieldwork and data analysis. W.N.L. wrote the first manuscript draft and H.T.W.T. contributed to revisions.

DATA ACCESSIBILITY

Data are available at Figshare: <https://doi.org/10.6084/m9.figshare.7072037.v1> (Lam & Tan, 2018).

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