

## RESEARCH ARTICLE

# Experimental reduction of plant abundance changes interaction frequency of a tri-trophic micro-food web: contrasting responses of generalists and specialists

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## Abstract

1. Species abundance is vulnerable to climate change and anthropogenic impact. Although numerous studies have examined the food web response to species loss, their response (e.g. in network topology and interaction frequency) to changes in species abundance has received little attention.
2. We experimentally reduced the abundance (by c. 60%) of one host plant species (*Saussurea nigrescens*) in a tri-trophic micro-food web consisting of two common Asteraceae species (*S. nigrescens* and *Anaphalis flavescens*), their pre-dispersal seed predators (tephritid flies) and the parasitoid wasps that feed on these seed predators.
3. The neutral process hypothesis posits that network topology and interaction frequency are determined by the relative abundances of the participating species. Accordingly, we hypothesized that interaction frequency (indicated by the rate of flies infesting plants and of parasitoid wasps parasitizing flies) would decrease with decreasing abundance of host plant abundance.
4. Consistent with the neutral process hypothesis, abundance reduction significantly decreased the rate of generalist flies infesting the manipulated plant host species, but increased the rate on unmanipulated plant species. In contrast, abundance reduction significantly increased the rate of specialist flies infesting the manipulated species, but it had no demonstrable effect on the specialists on the unmanipulated plant host.
5. Moreover, abundance reduction significantly increased the rate of parasitoid wasps (as a species group) parasitizing flies in the manipulated species, but decreased the rate of the unmanipulated species. These results were not attributable to neutral processes, but can be explained by adaptive foraging theory. In addition, experimental manipulation did not shift the qualitative presence-absence of the linkages in the micro-food web, and the change in the abundance of both fly and wasp species was smaller than the abundance changes of the manipulated plant species.
6. *Synthesis.* Our results indicate that both neutral processes and/or adaptive foraging likely contributed to food web stability in responses to changes in species

abundance. Because species abundance is vulnerable to abiotic and biotic environmental changes, we suggest more research should be conducted to understand how food webs respond to climate change and anthropogenic disturbance.

#### KEYWORDS

adaptive foraging, food web stability, interaction frequency, neutral process, trophic cascade

## 1 | INTRODUCTION

Understanding how biological communities and ecosystems maintain stability in response to perturbations has been a long-standing, central concern for ecologists (Pascual & Dunne, 2006; Pimm et al., 1991), particularly regarding food-web stability, which is more relevant than ever in the context of global environmental change (Brook, Sodhi, & Ng, 2003; McCann, 2000). Numerous empirical and theoretical studies (e.g. Dobson et al., 2006; Saavedra et al., 2008) have addressed the mechanisms underlying food web responses to species loss in the face of climate change and anthropogenic disturbances (e.g. pollution and habitat destruction) that have driven widespread species extinctions locally or globally (e.g. Brook et al., 2003). However, little is known about how food web structures (reflected by their topology and interaction frequencies) respond to changes in species abundance (however, see Barbosa, Fernandes, Lewis, & Morris, 2017), although such changes are much more common than species extinction in nature.

Indeed, species abundance has been proposed to be a crucial factor affecting both the interaction frequencies and topology of ecological networks. The neutral process hypothesis (NPH), which is an extension of the neutral theory of biodiversity for a single trophic community (Hubbell, 2001), posits that individuals interact randomly, independent of their traits in ecological networks (Krishna, Guimarães, Jordano, & Bascompte, 2008). It predicts that the probability of forming a trophic linkage (Dupont, Hansen, & Olesen, 2003; Krishna et al., 2008), as well as the frequency of trophic interactions (Vázquez et al., 2007; Xi, Mu, Peng, Eisenhauer, & Sun, 2016), increases with an increasing abundance of the participating species. The NPH has gained empirical support in both mutualistic (Vázquez et al., 2007) and antagonistic networks (Canard et al., 2014; Tylianakis, Tschardtke, & Lewis, 2007; Vázquez, Poulin, Krasnov, & Shenbrot, 2005). According to the NPH, a large abundance reduction in a resource species should induce a large decrease in the interaction frequency between the resource species and its consumer species regardless of whether the consumer species is a specialist or generalist. The prediction of the NPH regarding the interaction frequency between resource species and generalist consumers has gained support from empirical evidence. For example, generalist consumers often shift their prey from the abundance-reduced resource species to other more abundant resource species (Brose, Williams, & Martinez, 2003; Kondoh, 2003; Uchida, Drossel,

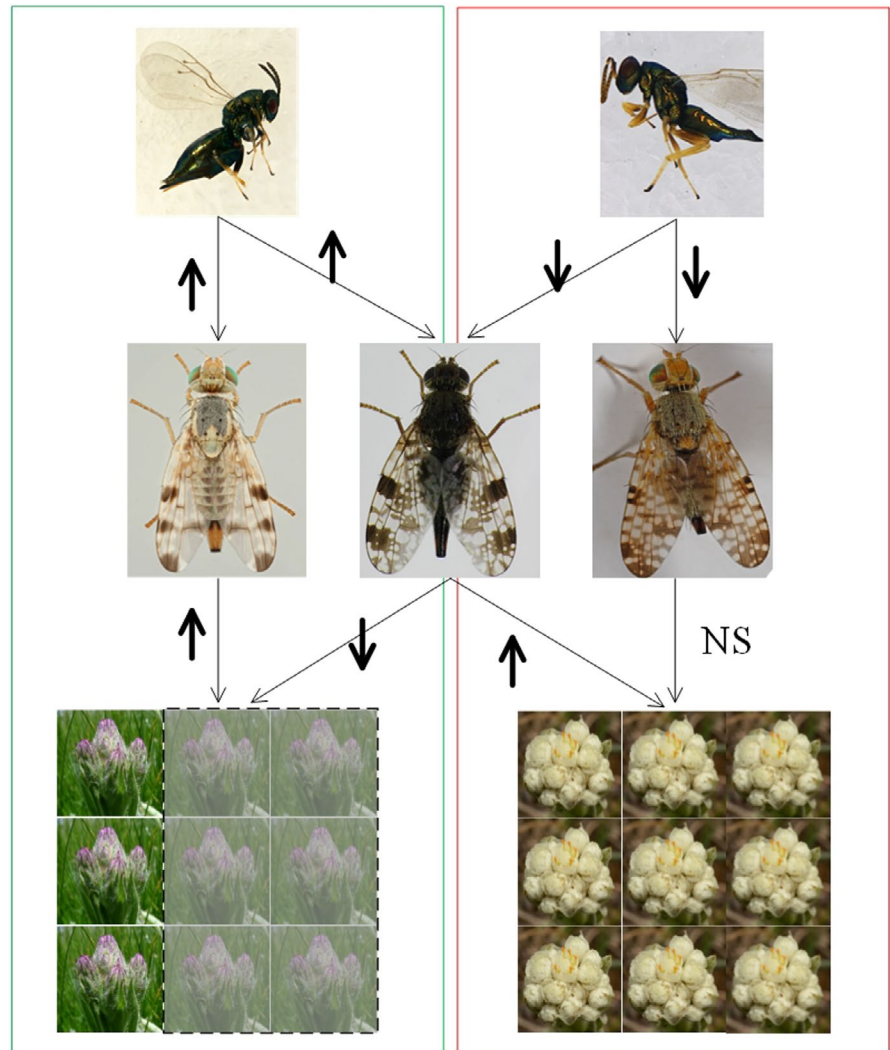
& Brose, 2007), with a decreased interaction frequency (i.e. the proportion of resource or host species being consumed or parasitized, Berlow et al., 2004) with the abundance-reduced species but an increased frequency with the other species.

However, specialist consumers, which cannot select another species when their resource species are depleted, do not necessarily decrease their interaction frequency with decreasing abundance of resource species. It has been reported that specialist consumers may maintain their foraging success at a low resource abundance level by virtue of their greater ability to search and handle food resources relative to generalists. For example, specialist parasitoids are highly adapted to finding and exploiting their hosts (Godfray, 1994); specialist bumblebees are often endowed with high nectar-locating skills (Lavery & Plowright, 1988). In particular, specialist parasitoids may increase their interaction frequency with host species even if the abundance of their host species is reduced (e.g. Barbosa et al., 2017; Tylianakis et al., 2007). Since specialists constitute a majority of species in ecological networks (Vázquez et al., 2005), examining the difference in the responses to species abundance change between generalists and specialists may better understand the contribution of species abundance to network structure and interaction frequency (Lewis & Gripenberg, 2008).

In a multi-trophic food web, the change of species abundance at low trophic level may propagate to affect the frequency of trophic interactions between species at intermediate and high levels as suggested by “bottom-up” regulations of communities, in which plants may mediate herbivore-predator-parasitoid interactions primarily through directly influencing the abundance of herbivores (Price et al., 1980). For example, plant population dynamics often changes the interaction frequency between host and parasitoids (reflected by the rate of parasitoids parasitizing herbivorous insects; e.g. Barbosa et al., 2017; Sheehan & Shelton, 1989). According to NPH, a reduction in plant species abundance may decrease the interaction frequency between parasitoids and herbivorous insect hosts by decreasing the herbivorous insect abundance as a result of decreased interaction frequency between the plant and herbivorous insect. Nevertheless, parasitoids are often host species-specific with a pronounced efficiency of locating their hosts (Godfray, 1994), and therefore the rate of parasitoids parasitizing herbivorous insects may increase with decreasing host abundance.

Although theoretical predictions are well established for the response of trophic interaction frequency to species abundance

**FIGURE 1** Schematic diagram of the study system including two major plant species, their pre-dispersal seed predators (tephritid flies), and the wasps that parasitize the flies. The upward and downward arrows respectively denote the positive and negative responses of interaction frequency as a hypothetical consequence of the abundance reduction of one plant species (indicated by the shaded portion of the left hand plant species). “NS” denotes a non-significant effect of plant abundance reduction on the interaction frequency. Parasitoid wasps are plant species-specific, that is, they can parasitize the larval flies living on one of but not both of *Saussurea nigrescens* and *Anaphalis flavescens* plants (as indicated by green and red rectangles, respectively)



change, empirical testing is extremely rare. The potential difference in the response between generalists and specialists has not been examined particularly for multi-trophic food webs. Importantly, the difference cannot be detected without the aid of experimental studies. For example, the high abundance of one common prey may mask the ability of generalist predators to prey on rare species; rare prey species would be consumed only when the abundant prey species is depleted or lost (Pimm et al., 1991). Unfortunately, controlled field experiments have rarely been conducted to determine food web responses to changes in species abundance in part because manipulating species abundance at a large spatial scale for a community-wide multi-trophic food web is exceedingly challenging. Nevertheless, the experimental exploration of “micro-food webs” (i.e. small subsets of a complex food web) has provided important insights into the mechanisms structuring the networks (Brosi, Niezgod, & Briggs, 2017; Junker, Höcherl, & Blüthgen, 2010; Kaiser-Bunbury, Muff, Memmott, Müller, & Cafilich, 2010).

Here, we experimentally reduced the abundance of one plant species by c. 60% in a micro-food web in an alpine meadow that includes two host Asteraceae species, pre-dispersal seed predators (tephritid flies), and the parasitoid wasps of the seed predators

(Figure 1). We examined the effect of species abundance reduction on food web topology and the interaction frequency between plant and their seed predators, and between the seed predators and their parasitoid wasps. The primary objective of this study is to determine how specialist and generalist consumers respond to species abundance change in a tri-trophic food web.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

This study was conducted in Hongyuan County (32°48'N, 102°33'E), Sichuan Province, China, in the eastern part of Qinghai-Tibetan Plateau. The altitude is about 3,500 m and the climate is characterized by long-cold winters and short-cool summers. The annual mean temperature is 0.9°C and the annual mean precipitation is 744 mm, most of which occurs during May to August. Detailed information about the climatic conditions of the study area can be found in Zhao, Yang, Xi, Zhang, and Sun (2014).

The vegetation is characterized by alpine meadows with 90% plant coverage. The meadows are grazed by domestic yaks (*Bos*

*grunniensare*) in the warm season (Mid-June to late September; summer pasture) and in the cold season (October to early June; winter pasture), respectively. Our experiment was conducted in the winter pastures that are free from grazing in summer. Forbs, such as *Saussurea nigrescens*, *Anaphalis flavescens* and *Potentilla anserine* predominate and account for >70% of the total plant biomass (Wu, Duffy, Reich, & Sun, 2011).

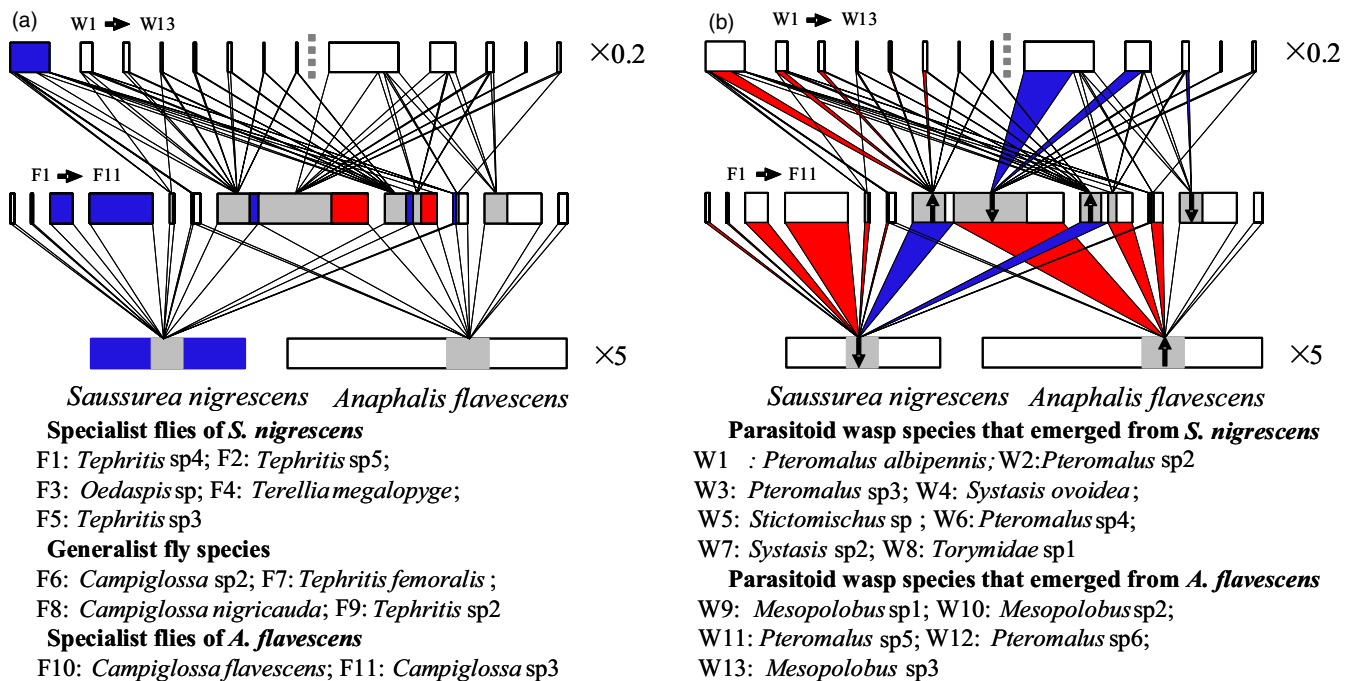
## 2.2 | Study system

The study system consisted of two Asteraceae species (*S. nigrescens* and *A. flavescens*), their pre-dispersal seed predators (tephritid flies) and the wasps that parasitize the flies (Figure 1). *S. nigrescens* and *A. flavescens* are the major host species for tephritid flies in the study site. They both flower from June to August, with c. 2 months overlap in flowering time (Xi, Eisenhauer, & Sun, 2015). *S. nigrescens* produces fewer but larger capitula per plant than *A. flavescens* and therefore provide more seed resources for insect growth (Xi, Yang, Yang, Segoli, & Sun, 2017).

Tephritid flies are the most diverse species group of pre-dispersal seed predators, accounting for >90% seed loss in Asteraceae species (Zhang, Yang, Xi, Niklas, & Sun, 2018). Female

tephritid flies oviposit on plant capitula before flowering, and fly larvae then grow up within the capitula consuming developing seeds. Moreover, some endoparasitoid wasps (Hymenoptera: Pteromalidae) may attack the fly larvae within the capitula. Female parasitoid wasps lay eggs into the bodies of developing fly larvae, and the parasitoid wasp larvae obtain nutrients from the host fly larvae. The parasitized fly larvae are not killed until they finish pupation, when the parasitoid wasps pupate within the larvae, from which they eventually emerge.

Previous field investigations revealed a total of 11 tephritid fly species and 13 wasp species from *S. nigrescens* and *A. flavescens* in the study meadow. Of the 11 tephritid flies, four species are regarded as generalists because they infest the capitula of both *S. nigrescens* and *A. flavescens*. However, five species are regarded as specialists to *S. nigrescens* and two specialists to *A. flavescens* because they were found to infest one plant species only. In addition, 13 wasp species are found to parasitize six of the 11 tephritid fly species (Figure 2). Importantly, all the parasitoid species are plant species-specific, that is, they can parasitize larval flies living on one but not both of *S. nigrescens* and *A. flavescens*, presumably because of the large variation in the capitulum size and nutrient content available between these two plant species (Xi et al., 2017).



**FIGURE 2** Quantitative tri-trophic networks showing the response of species abundance (a) and interaction frequencies (b) to species abundance reduction. The triangles indicate the interaction frequency and the bars indicate the species abundance. The gray part of the bars at the plant and fly trophic levels denotes the number of capitula been infested by flies or the number flies been parasitized by parasitoid wasps. Upward and downward arrows within the bars indicate a significant increase and decrease respectively in the overall rate of plants being infested by tephritid fly species group or the overall rate of specific fly species being parasitized by parasitoid species group. Red and blue bars indicate a significant increase and decrease respectively in species abundance (a). Red and blue triangles indicate a significant increase and decrease respectively in the infestation rate of specific fly species on each plant species and the parasitism rate of parasitoid species on specific fly species as induced by the reduction of *Saussurea nigrescens* abundance (b, see Tables S2–S3 for detailed results). Scales in the wasps and plants were 5 and 0.2 times respectively than that for fly species due to the lower number of wasps and higher number of plant capitula

## 2.3 | Abundance–reduction experiment

A random-block experimental design was employed because the study site is floristically and faunistically heterogeneous. We randomly selected five blocks over 5 km × 5 km with a similar physical environment and plant composition (Appendix Table S1). Within each block, we set up two 100 m-diameter circular plots. The plots were a minimum of 500 m apart, and the blocks were a minimum of 1 km apart. A pre-experimental survey showed that the natural abundance of *S. nigrescens* and *A. flavescens* was indistinguishable between control and treatment plots within each block ( $Z = 0.31$ ,  $p = .75$  for *S. nigrescens* and  $Z = 0.14$ ,  $p = .89$  for *A. flavescens* respectively, Generalized linear mixed model with Poisson error structure). In each block, the abundance of *S. nigrescens* was artificially reduced in one plot (designated hereafter as the abundance-reduced plot), but not in the other plot (designated hereafter as the control plot).

The experiments were initiated on 1st July, when most *S. nigrescens* plants started to bud and tephritid flies had not started to oviposit. Because there is a variation in flowering phenology among *S. nigrescens* individuals, abundance reduction was conducted three times in the early (1st July), middle (14th July) and late (24th July) flowering season of the species. We randomly cut off all of the capitula of >26,000 *S. nigrescens* plants in each of the abundance–reduction plots, resulting in an approximately 60% reduction in the abundance of *S. nigrescens* compared to the control plots for each block (see Appendix Table S1). In addition, we counted the capitula of the plants of all other Asteraceae species (which are potential hosts for tephritid flies) in all of the plots. The total capitulum number of the other Asteraceae species was approximately 3,000 capitula in each plot, which amounted to less than 3% of total number of *S. nigrescens* and *A. flavescens* capitula.

We harvested >12,000 *S. nigrescens* capitula and >21,000 *A. flavescens* capitula within each plot in the end of August, when most of the tephritid fly larvae within capitula might have finished their pupation and were about to emerge. These capitula were brought into the laboratory and opened individually to determine whether they were infested with tephritid flies. When present, fly pupae were individually transferred to 10 ml glass tubes, and the larvae were cultivated with artificial food consisting of wheat bran, corn flour, cane sugars and yeast powder. Over 85% of the pupae and larvae successfully developed into adults, which emerged as flies devoid of being parasitized by wasps, or as wasps that had parasitized fly larvae. Emergent flies, emergent wasps (and associated residual puparium) and undeveloped dead larvae were individually placed in 1.5 ml plastic tubes and stored in a –20°C refrigerator for subsequent species identification.

Mature flies and wasps were identified by morphological traits including nervure pattern and antenna hairs. DNA barcoding was used to identify the species of both dead fly maggots and puparia. The DNA from dead maggots and puparia were extracted and their cytochrome c oxidase subunit I (Col) was amplified and sequenced. Each sequence was subsequently compared with a reference bank composed of all of the emergent adult flies from all of the Asteraceae

in the study area. Detailed barcoding procedures are provided by Xi et al. (2017).

## 2.4 | Data analysis

Micro-food web topology was characterized by species richness and the qualitative presence/absence of interaction linkages. Interaction frequency was characterized by the rate of flies infesting plant capitula and by the rate of parasitoid wasps parasitizing flies. The infestation rate of each fly species on *S. nigrescens* and *A. flavescens* was calculated as the number of capitula infested by the specific fly species divided by the total number of collected capitula in each plant species. The parasitism rate of each wasp species on each of the fly species that grew within the capitula of each plant species was calculated as the number of parasitized flies divided by the total number of flies that infested the plant species. The overall rate of plants being infested by fly species group (including both generalists and specialists, as well as the overall rate of specific fly species being parasitized by parasitoids wasp species group (including all the wasp species), was also calculated for both manipulated and unmanipulated plant species. The species abundance of each fly and wasp species in the abundance-reduced and control plots was estimated as the product of the infestation rate and number of capitula in the studied plots (i.e. plot area × plant density × number of capitula per plant).

Penalized quasi-likelihood generalized linear mixed models (GLMMs) with binomial errors were used to determine the effects of “Treatment” (*S. nigrescens* abundance-reduced vs. control plots), “Plant identity” (*S. nigrescens* vs. *A. flavescens*) and “Host specialization” (generalist vs. specialist tephritid flies) on the infestation rate of fly on plants and the parasitism rate of parasitoid wasps on fly species. The “Treatment”, “Plant species identity” and “Host specialization” as well as their interactions were incorporated into the model as fixed factors, and the “block” and “fly species identity” were included as random factors, with “fly species identity” nested in “host specialization” and “plot” nested in “block”. GLMMs with Poisson errors were used to determine these effects on the differences of the species abundance of each fly or wasp species between the control and manipulated plots. We also employed GLMMs with binomial errors to determine the effects of abundance reduction on the frequencies of pairwise fly–plant or wasp–fly interactions. GLMMs were performed using “*glmmPQL*” function in “*lme4*” package (Bates, Mchler, Bolker, & Walker, 2015).  $R^2$  values of the GLMM were calculated following Nakagawa and Schielzeth (2013). All data analyses were performed using R (R Core Team, 2014).

## 3 | RESULTS

Abundance manipulate did not change the food web topology, because the species richness of both fly and wasp species, as well as the qualitative presence–absence of the linkages, remained unchanged between the abundance–reduced and control plots. However,

	Infestation rate			Parasitism rate		
	Slope	Z	p	Slope	Z	p
Plant	-2.1	-14.4	<0.001	0.9	28.4	<0.001
Treatment	-0.6	-2.8	<0.001	0.9	7.3	<0.001
Specialization	-2.2	-1.8	0.12	-0.8	1.4	0.17
Plant*specialization	3.7	3.7	0.004	0.4	0.6	0.56
Plant*treatment	1.2	6.8	<0.001	-1.4	10.0	<0.001
Specialization*treatment	1.4	2.1	0.039	1.0	1.2	0.25
Plant*treatment*specialization	-1.9	-2.5	0.02	-0.4	0.6	0.58

Note: These three factors account for 77% variation in fly infestation rate and 71% variation in parasitoid parasitism rate. Bold values indicate that the factor effect was significant at  $p = 0.05$ .

abundance manipulation greatly changed the interaction frequencies among the species in both “plant-fly” and “fly-wasp” networks ( $Z = -2.8$ ,  $p < .001$  for “plant-fly” networks and  $Z = 7.3$ ,  $p < .001$  for “fly-wasp” networks; Table 1), and the abundance reduction effects varied along with the plant species and generality of fly species, as suggested by the strong interactive effects among abundance reduction, plant identity and fly host specialization on fly infestation rate on plant capitula ( $Z = 2.5$ ,  $p = .02$ , Table 1, Figure 2).

Abundance manipulation decreased the overall infestation rate of fly species group by 13% and increased the infestation rate of specialized fly species by 35%–125% on the manipulated plant species (*S. nigrescens*). In contrast, experimental manipulation had no statistically detectable effect on the infestation rate of specialized fly species on the untargeted plant species (*A. flavescens*; Table 1, Figure 2). Abundance manipulation decreased the infestation rate of generalist fly species on the manipulated plant species by 27%–47%, but increased their infestation rates on the unmanipulated plant species by 13%–88% (Table S2, Figure 2). Furthermore, the estimated abundance of each generalist fly species and two most abundant specialist flies (*Terellia megalopyge* and *Oedaspis* sp.) on *S. nigrescens* decreased by 38%–52%, whereas specialist flies on *A. flavescens* was unchanged under abundance manipulation (Table 2, Figure 2).

Abundance manipulation increased the overall rate of specific fly species being parasitized by the parasitoid wasp species group on the manipulated plant species by 2%–7%, but decreased the parasitism rate of flies on the unmanipulated plant species, as indicated by the significant interactive effects between abundance manipulation and plant species identity ( $Z = 6.8$ ,  $p < .001$ , Table 1, Figure 2). Specifically, six of eight wasp species emerging from the manipulated plant species, as well as three of five wasp species emerging from the unmanipulated plant species, showed an increase in their interaction frequencies to specific fly species (Table S3). Moreover, abundance reduction decreased the species abundance of one of the dominant wasps (W1, *Pteromalus albipennis*) that specialized on fly species in manipulated plant species by 23%, but the abundance of wasp species that emerged from the capitula of unmanipulated plant species remained unchanged (Table 2, Figure 2).

**TABLE 1** Generalized linear mixed models results showing the effects of plant species identity (plant), plant abundance manipulation (treatment) and fly host specialization (specialization) on the infestation rate of tephritid fly on host plants and the parasitism rate of parasitoid wasps on fly species

## 4 | DISCUSSION

Our investigation of the microstructure of a plant-tephritid fly-parasitoid wasp food web shows that the experimental abundance reduction of one plant species results in a series of changes in interaction frequency for both the plant–seed predator component and seed predator–parasitoid wasp component of the web. Importantly, the generalist and specialists showed contrasting responses of interaction frequency to the abundance reduction, which cannot be fully explained by the neutral process hypothesis (NPH). Our study also shows that food web topology remained unchanged despite significant changes in interaction frequency. In particular, the change magnitude in the interaction frequency and species abundance decreased with increasing trophic level.

These results indicate that the food web can maintain structural stability in response to changes in species abundance. To the best of our knowledge, this is the first experimental demonstration of multi-trophic food web flexibility in the face of a large reduction in species abundance using a micro-food web that is much more complex than those examined in previous studies (Barbosa et al., 2017; Larue, Raguso, & Junker, 2016).

Our data show that the artificial reduction in the abundance of *S. nigrescens* relative to the abundance of *A. flavescens* results in a reduced infestation rate of all of the generalist tephritid flies on manipulated plants, but increases the infestation rate on the non-manipulated plants, especially in the case of the most common tephritid fly species. These results are consistent with the predictions of the NPH that has been successful when dealing with networks between plants and pollinators, animals and pathogens and hosts and parasitoids (Kaiser-Bunbury et al., 2010; Krishna et al., 2008; Staniczenko, Lewis, Jones, & Reed-Tsochas, 2010; Verdú & Valiente-Banuet, 2011; Zhang, Hui, & Terblanche, 2011). Our results are also consistent with adaptive foraging theory (AFT), which posits that consumer species tend to maximize their energy gain per unit foraging effort by behavioural shifts in prey selection (Brose et al., 2003; Kondoh, 2003). According to AFT, reducing the abundance of the major host species in our experiment (i.e. *S. nigrescens*) is predicted to increase the time that flies used to find their host plants. Under this circumstance, an adaptive compensatory strategy

**TABLE 2** Generalized linear mixed models results showing the effects of plant reduction on the population size of each tephritid fly and parasitoid wasp species

Tephritid flies	Slope	Z	p	Parasitoid wasps	Slope	Z	p
Specialist flies on <i>Saussurea nigrescens</i>				<i>Wasps emerged from S. nigrescens</i>			
Tm	-0.56	3.5	<b>&lt;0.001</b>	W1	-0.44	<b>3.65</b>	<b>&lt;0.001</b>
Oe	-0.35	-1.9	<b>0.058</b>	W2	-0.51	1.73	0.083
T3	-0.07	-0.3	0.80	W3	-0.52	1.69	0.091
T4	-0.20	1.00	0.31	W4	-0.42	1.35	0.18
T5	-0.4	1.22	0.22	W5	-0.43	1.65	0.24
Specialist flies on <i>Anaphalis flavescens</i>				W6	-0.57	0.95	0.34
Cf	0.08	0.56	0.57	W7	-0.59	0.39	0.69
C3	0.05	0.16	0.89	W8	0.16	1.65	0.09
Generalist flies				<i>Wasps emerged from A. flavescens</i>			
Tf	-0.5	5.56	<b>&lt;0.001</b>	W9	0.13	0.66	0.51
T2	-0.49	2.14	<b>0.03</b>	W10	0.22	1.29	0.20
C2	-0.65	3.89	<b>&lt;0.001</b>	W11	0.34	0.95	0.35
Cn	-0.93	8.35	<b>&lt;0.001</b>	W12	-0.87	0.77	0.44
				W13	-0.58	1.32	0.19

Note: See Figure 2 for the full name of the fly and wasp species. Bold values indicate that the factor effect was significant at  $p = 0.05$ .

would be to shift to *A. flavescens* as the host plant species, because these plants become more abundant and thus reduce the foraging time. Importantly, such a shift from *S. nigrescens* to *A. flavescens* host plants occurred during our experiments even if *S. nigrescens* is a better host for the generalist flies in terms of food source quality and quantity compared to *A. flavescens* (see also Xi et al., 2017).

In contrast to the responses of the generalist flies to abundance reduction, the specialist flies increased their infestation rate on the abundance-reduced host species. This result is not consistent with the predictions of NPH, but it is consistent with the AFT, which predicts that true specialists require specific hosts regardless of the abundance of the host species (Rand & Tscharrntke, 2007). The fly specialist of *S. nigrescens* in our study, such as *T. megalopyge*, is typically larger in body size compared to the generalist fly species (Xi et al., 2018). Hence, they require larger amounts of nutrients and energy for their growth and development. These requirements are provided best by *S. nigrescens* compared to *A. flavescens* because of the differences in the sizes of their capitula. Similarly, the specialist fly species on *A. flavescens* did not change their infestation rates even when the relative abundance of *A. flavescens* was increased (due to the abundance reduction in *S. nigrescens*), which once again illustrates the importance of host specialization. Moreover, the shift of the generalist flies from *S. nigrescens* to *A. flavescens* did not decrease the infestation rate of the specialist species on *A. flavescens*, perhaps because this shift did not reduce host availability sufficiently to decrease the infestation rate of the specialist species, or because these specialist species are highly efficient at locating unparasitized hosts to avoid competition with generalists. Numerous studies have shown that specialist species tend to coevolve with their host species over long periods of evolutionary time and that their behavioral preferences become more correlated with their host species, e.g. a

heightened sensitivity to host plant fragrances and a reduced foraging time (Ali & Agrawal, 2012; Hassell & May, 1986). We speculate that both species abundance and host specialization (generalist vs. specialists) are important determinants of food web structure.

The abundance reduction of *S. nigrescens* further cascaded to indirectly affect the parasitism rate of flies by parasitoid wasps. Studies have demonstrated that parasitoid wasps tend to be host specialized and that they therefore are extremely efficient at locating hosts (Price & Clancy, 1986). In our study, all the wasps are plant specific. For example, the two most common generalist tephritid flies infest both plant species, but they are parasitized by different wasp species when they are in different host plant species. Accordingly, the change in the rate of parasitoid wasps parasitizing flies should be determined by the change in the abundance of the flies, that is, the parasitism rate should increase when the fly abundance was decreased by abundance manipulation and vice versa. In this study, the rate of parasitoid wasps parasitizing both generalist and specialist flies on *S. nigrescens* increased after the abundance reduction of *S. nigrescens*. Likewise, given that the abundance of *A. flavescens* was not manipulated and that the infestation rate increased in the generalist fly species but remained unchanged in specialist flies, the abundance of the generalist species increased and that of specialist species remained unchanged. It is therefore not surprising that the rate of parasitoid wasps parasitizing generalist fly species decreased and the rate of those parasitizing specialist fly species remained unaffected or decreased (resulting from host shifting of generalist wasps) on *A. flavescens*, after abundance reduction. These are consistent with the prediction of ATF but not the NPH. Similar results have been reported for the response of parasitoid wasps to changes of their host abundance (Barbosa et al., 2017; Stiling & Moon, 2005).

It is worth noting that the species richness and topology of this multi-trophic food web was unchanged by the abundance reduction despite changes in interaction frequency. Previous studies have frequently suggested that large changes in the abundance of lower trophic levels likely drive the loss of specialists at higher trophic levels. However, in our study, the magnitude of species abundance changes at the fly trophic level ( $26.7 \pm 6.0\%$ ) was much smaller than that of the plant trophic level (c. 60%). We suggest that this is because the generalist flies maintained their abundance by shifting their plant host species when their preferred plant host species decreased in abundance, whereas the specialist flies maintained their abundance by increasing their infestation rate on their plant host species. Moreover, all but one parasitoid wasp species kept their abundance unchanged by similar mechanisms. For example, the parasitism rate of the rarest wasp species (*Pteromalidae* sp4 in Figure 2) was predicted to decrease to a hardly detectable level (0.7%) according to the NPH. Yet, its parasitism rate by and large increased by 252%, and hence its abundance was not significantly affected.

Adaptive foraging (along with neutral processes) not only contributed to the stability of food web topology under a large reduction of species abundance, but also allowed the recovery of the food web examined in our study. For example, the total infestation rate of the abundance-reduced plant species *S. nigrescens* decreased after the abundance reduction, thereby releasing the plants from the pressure exerted by seed predators. Consequently, adaptive foraging may stabilize food-web dynamics by allowing resources to recover in abundance when they become rare and thereby preventing rare species from going extinct (see also Uchida & Drossel, 2007; Uchida et al., 2007). Because species abundance is very vulnerable to abiotic and biotic environmental changes, our results highlight the importance of animal adaptive foraging to understanding how food web dynamics respond to climate change and anthropogenic disturbance.

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## AUTHORS' CONTRIBUTIONS

S.S. and X.X. designed the study; X.X., Y.W., B.Z. and Y.D. performed the experiment and data analysis; S.S., X.X. and D.P.V. wrote the manuscript.

## DATA AVAILABILITY STATEMENT

Data are archived on Dryad Digital Repository: <https://doi.org/10.5061/dryad.nd57201> (Xi et al., 2019).

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