

Individual differences in predators but not producers mediate the magnitude of a trophic cascade

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Abstract Top-down community dynamics are commonly mediated by the foraging mode of the dominant predator. However, functional intraspecific variation in foraging mode may also mediate these interactions, particularly if the magnitude of intraspecific variation mimics or exceeds that of interspecific variation. Here, we simultaneously assess the role of intraspecific variation in predator activity level and plant constitutive defenses in mediating the presence and magnitude of a trophic cascade. In experimental mesocosms, we constructed tri-trophic ecological modules containing eight herbivores (two cabbage loopers, two beet armyworms, two darkling beetles, and two banded crickets) and lettuce plants of one of three cultivars which vary in their constitutive latex defense. In a portion of the mesocosms, we added individual cursorial spiders which vary consistently in their activity level (i.e., foraging mode). We then measured herbivore mortality and average plant leaf damage via herbivory after 1 week. The presence of a spider alone did not reduce plant damage, yet communities containing more active spiders had up to a 50 % reduction in plant damage compared with communities with more sedentary spiders. Notably, spider activity level did not influence herbivore mortality; thus, the decrease in plant damage associated with predatory activity appears to be the outcome of indirect non-consumptive

effects. Increases in constitutive plant latex content did not decrease herbivory, possibly because the cabbage looper uses a countermeasure called “leaf trenching.” Together, these data reveal that the effects of functional intraspecific variation on a trophic cascade can be dramatic and varied, depending on the trophic level under consideration.

Keywords Constitutive defense · Individual variation · Non-consumptive effects · Tri-trophic interaction · Trophic cascade

Introduction

Ecologists have garnered strong evidence for the value of biodiversity in promoting community stability and ecosystem services (MacArthur 1955; Johnson et al. 1996; Tilman 1996). Studies in agroecosystems, in particular, have shown that species-rich assemblages of natural enemies can stabilize pest communities and reduce crop loss (Cardinale et al. 2003). However, much of the functional diversity represented by animal communities is due to intraspecific variation, where individuals of the same species exhibit consistent individual differences in key functional traits, such as behavior (Sih et al. 2012) or body size (Brose 2010; Boukal 2014). Consequently, research that focuses on interspecific variation alone and maximizing species richness per se risks inadvertently ignoring vital aspects of functional diversity that occurs intraspecifically. This discrepancy critically diminishes our understanding of the nature of predator–prey interactions that are central to the structure and stability of communities (Ings et al. 2009; Bolnick et al. 2011; Kalinkat 2014).

Studies on inter-individual variation in predator body size metrics have illuminated the power of intraspecific

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variation in predicting ecosystem processes. For example, reduced variation in predator body size classes can reduce the attack rate on prey of different sizes and thus cause marked shifts in prey community composition (Wahlström et al. 2000). Although body metrics such as gape size can place upper limits on the size classes of prey available to a predator, we reason that predator foraging is inherently a combination of *behavioral* and *morphological* traits. Unfortunately, consistent inter-individual behavioral variation is more cryptic and often harder to quantify than morphological traits, and body size alone often fails to explain important aspects of trophic interactions (Ingram et al. 2011; Rall et al. 2011; Rudolf et al. 2014).

Huey and Pianka (1981) first argued that the effects of predators on prey communities would differ based on the predator's foraging behavior, where active predators should consume inactive prey and sedentary predators should consume active prey (i.e., “the locomotor-crossover hypothesis” Huey and Pianka 1981). Their study, however, focused on interspecific variation in foraging mode and did not consider whether intraspecific variation could similarly generate differences in the strength of predator–prey interactions. Indeed, many predators exhibit marked and significant intraspecific variation in foraging mode and we now know that these intraspecific differences can similarly alter the strength and nature of interactions across broad predator–prey systems (e.g., sea star–snail: Pruitt et al. 2012; spider–cricket: DiRienzo et al. 2013; Sweeney et al. 2013; crab–mussel: Toscano and Griffen 2014).

Nonetheless, to our knowledge there are no studies that have evaluated whether these individual differences can extend to mediate tri-trophic interactions. Thus, the effects that predators have on herbivores could depend on the foraging mode of individual predators and this, in turn, could mediate damage to host plants (e.g., producers). This is, however, a top-down view of trophic dynamics. In contrast, individual differences in plant chemical defenses may similarly ricochet up to impact tri-trophic interactions and thus mediate or ablate the impact of apex predators.

To truly understand the effects of individual variation on community-wide phenomena, studies must move beyond single-species or species-pair approaches to consider how individual variation in multiple, interacting trophic levels changes community-level outcomes. This is because functional variation in one trophic level could conceivably accentuate or negate the consequences of intraspecific variation in another interacting trophic level. Here, we simultaneously consider the effects of individual variation in functional traits of both a predator and a producer in mediating tri-trophic dynamics. Previous studies have explored the consequences of intraspecific variation in producers (Hughes and Stachowicz 2004; Crutsinger et al.

2006), herbivores (Griffen et al. 2012), or predators alone (Pruitt et al. 2012; Sweeney et al. 2013; Toscano and Griffen 2014). In this study we build on this framework in an attempt to explore how individual variation in multiple trophic levels unites to mediate the behavior of a simple community.

Here, we use individual wolf spiders as the sole predator in mesocosms containing an assemblage of herbivores (cabbage loopers, beet armyworms, darkling beetles, and banded crickets) feeding on lettuce plants to test the trophic consequences of spider intraspecific behavioral variation (Wise 1995). We use these mesocosms to address the following question: How does intraspecific variation in predator activity level and plant constitutive defenses influence herbivore communities and plant damage? Specifically, we hypothesize the following:

1. Individual variation in predator activity levels will mediate trophic linkages in a tri-trophic system. In particular, communities containing more active spiders should have decreased herbivory rates, based on previous work demonstrating that active predators generally have higher encounter rates with prey (Scharf et al. 2006; Avgar et al. 2008; Sweeney et al. 2013).
2. Consistent with the locomotor-crossover hypothesis (Huey and Pianka 1981; Pruitt et al. 2012), active spiders should encounter and consume sedentary herbivores (loopers and beetworms) while less active/sedentary spiders should encounter and consume more active herbivores (beetles and crickets).
3. Variation in host plant chemical defenses will ricochet up food chains to mediate the top-down impact of predators. In particular, communities containing plants with more chemical defenses will have decreased herbivory rates, increased herbivore mortality, and decreased mass gain by predators.

Materials and methods

Study organisms

Wolf spiders, *Trochosa ruricola*, were collected in old-fields and farmlands across three populations in western Pennsylvania (Butler, PA, Zelienople, PA, and Pymatuning Laboratory of Ecology). These spiders were maintained individually in the laboratory, fed a weekly diet of three two-week-old domestic crickets, and provided ad libitum water. To normalize their hunger level, we fed spiders ad libitum once weekly (fed them one cricket every 5 min until they rejected two consecutive crickets) for their first 3 weeks in the laboratory.

Four herbivore species (cabbage loopers, *Trichoplusia ni*; beet armyworms, *Spodoptera exigua*; darkling beetles, *Tenebrio molitor*; and banded crickets, *Gryllobates sigillatus*) were obtained from commercial vendors (Benzon Research, Carlisle PA; Ghann's Cricket Farm, Augusta GA). The armyworms and loopers were maintained in an environmental chamber with an ad libitum artificial diet for 1 week prior to behavioral assays. Crickets and beetles were maintained separately in the laboratory under natural light conditions and fed an ad libitum diet of romaine lettuce and chick feed (Kalmbach Feeds, Upper Sandusky, OH).

We used three cultivars of Romaine lettuce, *Lactuca sativa*, which vary in a constitutive latex defense (Valmaine has high latex, and Tall Guzmaine and Parris White have low latex; Huang et al. 2003; Sethi et al. 2008). Seeds of each cultivar were kept overnight in petri dishes lined with wet filter paper. Germinated seeds were transplanted into seedling trays with a commercial soil mix (MetroMix 220) and allowed to grow for 2 weeks in a greenhouse. Plants with seven to eight fully expanded leaves were then transplanted to plastic pots, watered daily, and fertilized weekly (Peters 20-20-20, N-P-K, W.R. Grace, Fogelsville, PA) until the onset of experimentation.

Activity assays

We measured the activity level of individual spiders ($n = 25$) once daily for four consecutive days. Each spider was placed in the center of a plastic container (12.5 cm \times 13 cm \times 3.5 cm) atop a 2-cm grid, given a 30-s acclimation period, and then, we counted the number of times the spider moved from one square to another in a 5-min period. Herbivore activity assays were performed similarly but atop a 5-mm grid (due to their smaller body sizes). We did not perform multiple testing on individual herbivores, but instead measured multiple individuals from each species to obtain mean activity values for each species ($n = 30$ armyworms; $n = 37$ crickets, $n = 30$ loopers, $n = 37$ beetles).

Spider foraging aggressiveness

We measured the foraging aggressiveness of adult wolf spiders following the protocol of the "satiation threshold" (Pruitt and Krauel 2010; Pruitt 2010) for other wolf spiders. Foraging aggressiveness was assessed 1 day after a routine weekly feeding by offering spiders with size-matched domestic crickets every 5 min until two consecutive prey items were rejected (i.e., detected visually or mechanically, but not attacked). The rejected prey items were removed, and the spiders were allowed 24 h to finish feeding on the prey items they attacked. The following morning, we

counted the number of cricket carcasses in the container that showed no evidence of feeding. Thus, we suggest that these crickets were attacked after the spider was satiated and that this number is a measure of the spiders foraging aggressiveness, rather than their hunger level.

Experimental design

In each of 41 30 cm \times 30 cm \times 30 cm mesocosms, we placed four *L. sativa* plants, each with seven to eight fully expanded leaves. Each mesocosm contained plants of only one cultivar ($n = 14$ Parris White, $n = 14$ Tall Guzmaine, $n = 13$ Valmaine). We then placed two individuals from each of four different lettuce herbivore species (cabbage loopers, beet armyworms, darkling beetles, and banded crickets) in every mesocosm, and an individual adult wolf spider in the "spider present" mesocosms ($n = 24$). The remaining 17 mesocosms did not contain a spider. This allowed us to ascertain whether any differences in herbivory were due to predator traits, or simply their presence/absence. Although we are unsure if the activity level of the spiders is preserved from our assays to the mesocosms which contained more topographical complexity (e.g., Savino and Stein 1982; Uetz 1991; Rickers and Scheu 2005), previous studies on consistent predator traits in one context have shown to carry over to multi-species mesocosms (e.g., Pruitt et al. 2012; McGhee et al. 2013; Sweeney et al. 2013). The mesocosms had two cloth screens to promote air flow, while the remaining sides were sheer plastic to allow light penetration (Bioquip 1450 BCV; Fig. 1a). We maintained the mesocosms in the laboratory under natural light cycles (approximately 10.5 h light/13.5 h dark) for 1 week.

At the end of the week, we approximated herbivory (i.e., leaf area loss) on each plant by visually estimating leaf loss for each leaf on a 1–10 scale (Fig. 2b, c). This method is qualitative in nature and may lack the accuracy and precision of other, more quantitative methods (e.g., O'Neal et al. 2002; Bakr 2005). Thus, to minimize the subjective nature of our herbivory measurements, the same two observers estimated leaf loss for each plant independently, and then, the average of these two scores was used. Further, the leaf damage and herbivore mortality data were scored blindly. We also counted the number of living herbivores in each mesocosm and measured the mass of each spider before and after the duration of the experiment.

Statistical analyses

We tested for temporally consistent between-individual differences in spider activity using ANOVA to partition variance into within-individual and between-individual variance. The resulting intraclass correlation coefficient

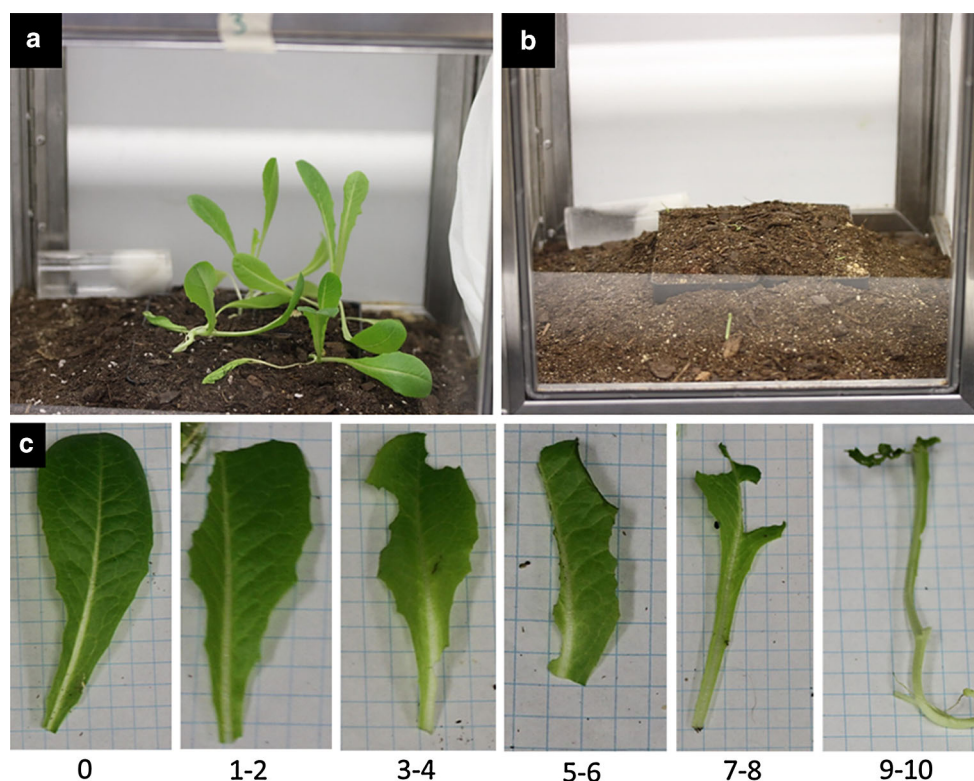


Fig. 1 **a** 30 cm × 30 cm × 30 cm mesocosm containing four *Lactuca sativa* plants (either cultivars), a simple herbivore community (two cabbage loopers, two beet armyworms, two darkling beetles, and two banded crickets), and the presence/absence of a wolf spider,

Trochosa ruricola. **b** After 1 week, some mesocosms had virtually no evidence of herbivory, while others had 100 % leaf loss. **c** An example of our leaf-damage measuring scheme, where 0 represents no damage and 10 represents total leaf loss

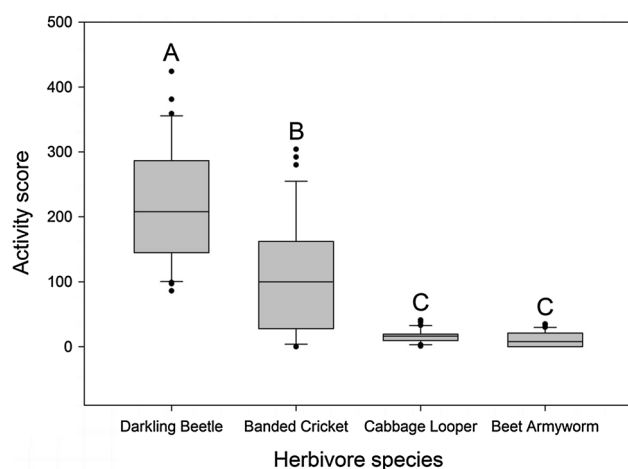


Fig. 2 Mean activity scores for the four tested herbivore species: darkling beetles, *Tenebrio molitor* ($n = 37$); banded crickets, *Grylodes sigillatus* ($n = 37$); cabbage loopers, *Trichoplusia ni* ($n = 30$); and beet armyworms, *Spodoptera exigua* ($n = 30$). The ends of the boxes denote the 25th and 75th percentiles, and error bars denote the 10th and 90th percentiles. Individual scores outside these percentiles are denoted with individual points. Boxes denoted with different letters represent significantly different values (Tukey's HSD post hoc test: $Q = 2.60$)

score was used as our estimate of repeatability (Boake 1989; Falconer and Mackay 1996). Interspecific differences in herbivore activity levels were tested using ANOVA with activity level as a dependent variable and species identity as predictor variable, since individual herbivores were not tested repeatedly. We analyzed average total leaf area loss using a Generalized Linear Model (log link function) with treatment (spider vs. no spider) and plant cultivar as independent variables and treatment × cultivar as an interaction term (Smyth 2003). We accounted for overdispersion to ensure that these data do not violate this model assumption ($\chi^2 = 16.08$, $df = 35$, $p = 0.99$; overdispersion = 0.46). To account for the absence of data on spider traits in mesocosms where spiders were absent, we excluded the “control” mesocosms from the analysis predicting average total leaf area using cultivar, spider activity (averaged across their four prior measures), spider aggressiveness, and spider prosoma width as predictor variables. Herbivore mortality was also analyzed using a Generalized Linear Model (log link function) with the same independent variables described above. None of the continuous predictors variables in our models (spider

body size, aggressiveness, and activity) were significantly correlated (all $p > 0.08$, all $r^2 < 0.20$). Post hoc analyses were performed using Tukey's HSD. All statistical analyses were performed using JMP version 10 (SAS Institute Inc., Cary, NC, USA).

Results

Trochosa ruricola wolf spiders exhibited consistent individual differences in their activity level, whose averages ranged from 5.5 to 186 ($F_{23,72} = 2.37$; $p = 0.003$, repeatability = 0.66). That is, spiders which were more active during one assay were very likely to be active during other assays, suggesting that some spiders are consistently active, while others are consistently inactive. There were also differences in the average activity level between the four herbivore species, where darkling beetles were the most active, followed by banded crickets, and the caterpillars were both relatively inactive ($F_{3,132} = 100.8$; $p < 0.0001$; Fig. 2). The presence or absence of a wolf spider in the mesocosm did not influence the amount of leaf damage over 1 week ($\chi^2 = 1.39$, $df = 1$, $p = 0.24$; Table 1). However, excluding mesocosms with spiders absent, mesocosms containing the most active spiders had more than 50 % less leaf damage than those containing more inactive spiders ($\chi^2 = 20.94$, $df = 1$, $p < 0.0001$, $r^2 = 0.12$; Fig. 3). This reduction in leaf damage was not influenced by the body size ($\chi^2 = 2.42$, $df = 1$, $p = 0.12$) or even the foraging aggressiveness ($\chi^2 = 2.72$, $df = 1$, $p = 0.10$) of the spider.

Although herbivore mortality was greater in mesocosms containing a predator ($\chi^2 = 4.49$, $df = 1$, $p = 0.04$; Table 2), we found no evidence that spiders' activity level influenced differential predation on one herbivore over another (all $p > 0.68$). That is, herbivore death did not differ between mesocosms containing spiders of different

Table 1 The average amount of leaf damage scored for *L. sativa* plants of three different cultivars in mesocosms with a spider either present or absent

Plant cultivar	Average leaf damage	
	Mean	SE
Spider present		
Valmaine	5.96	1.16
Tall Guzmane	4.93	1.57
Parris White	5.57	1.27
Valmaine	5.81	0.6
Spider absent		
Tall Guzmane	5.5	1.81
Parris White	8.17	1.42

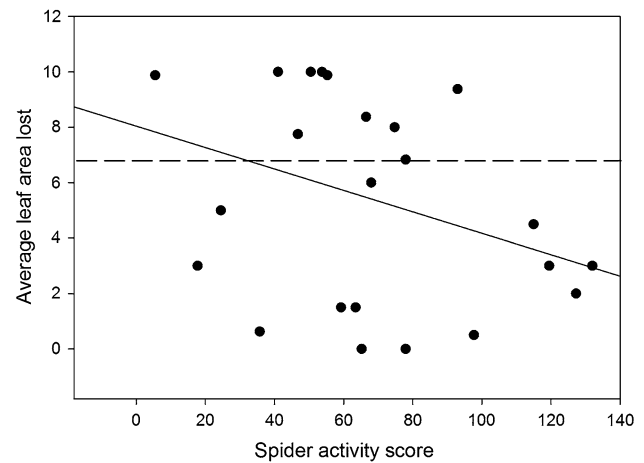


Fig. 3 Relationship between leaf damage and spider activity score, where a greater activity score corresponds to more active spiders. Only data points for mesocosms containing spiders are represented on the graph. The dotted line represents the average amount of leaf damage in mesocosms where spiders were absent

activity levels. Finally, the cultivar of lettuce and, thus, the level of constitutive latex defenses in the host plants had no influence on the amount of leaf loss ($\chi^2 = 2.69$, $df = 2$, $p = 0.26$; Table 1) or herbivore mortality ($\chi^2 = 0.91$, $df = 2$, $p = 0.63$; Table 2), regardless of whether or not a spider was present (interaction term: $\chi^2 = 1.85$, $df = 2$, $p = 0.40$).

Discussion

With this study, we simultaneously varied functional foraging traits in a predatory wolf spider alongside constitutive defenses in a producer in mesocosms containing a simple herbivore community. We found that variation in the activity of predators, but not variation in producer defenses, altered the amount of leaf area lost to herbivory. Specifically, communities containing more active spiders had plants with less leaf damage via herbivory. Astonishingly, the effect of subtle differences in predator activity levels effectively dwarfs any effect attributable to the presence or absence of a predator. Further, the resulting herbivore communities did not differ between mesocosms containing active versus inactive predators. Thus, the decrease in leaf damage associated with increased predator activity does not appear to be the consequence of direct predation per se, but rather non-consumptive indirect effects, such as fear.

Contemporary studies have revisited classic trophic ecology under the framework of predator non-consumptive effects on prey, demonstrating that predator-induced

Table 2 The number of herbivores found alive after 1 week in mesocosms containing *L. sativa* plants of three different cultivars with a spider either present or absent

Plant cultivar	Average herbivore mortality (mean \pm SE)			
	Banded cricket	Darkling beetle	Beet armyworm	Cabbage looper
Spider present				
Valmaine	1.71 \pm 0.29	1.29 \pm 0.29	1.57 \pm 0.30	1.57 \pm 0.20
Tall Guzmane	1.56 \pm 0.24	1.22 \pm 0.28	1.22 \pm 0.33	1.5 \pm 0.33
Parris White	0.88 \pm 0.23	1.5 \pm 0.19	1 \pm 0.33	1.13 \pm 0.35
Valmaine	1.67 \pm 0.33	1.33 \pm 0.33	1.33 \pm 0.42	2 \pm 0
Spider absent				
Tall Guzmane	2 \pm 0	1.6 \pm 0.4	2 \pm 0	1.6 \pm 0.4
Parris White	2 \pm 0	1.33 \pm 0.33	1.83 \pm 0.17	1.83 \pm 0.17

The experiment began with 2 of each herbivore species in each mesocosm

changes to prey physiology (i.e., “stress”) and behavior (i.e., “fear”) can increase the rate and magnitude of prey decline in the absence of direct predation (Brown et al. 1999; Peckarsky et al. 2008; Preisser and Bolnick 2008). Some have argued, even, that “intimidation” and trait-mediated indirect effects, where predators incite costly defensive strategies in prey (e.g., reduced feeding, investment in defenses, emigration), may be the dominant aspect of trophic interactions, effectively dwarfing consumptive effects in governing community ecology (Werner and Peacor 2003; Preisser et al. 2005; Calcagno et al. 2011). Our data are generally consistent with this argument.

In the simple ecological module that we manipulated here, we reason that active spiders may have stronger non-consumptive effects on prey compared with inactive spiders for a number of reasons. (1) Active cursorial spiders will have a greater average encounter rates with prey, though this usually depends on the movement patterns of each particular prey (Scharf et al. 2006; Avgar et al. 2008; Sweeney et al. 2013). (2) Active spiders may cause a stronger non-lethal impact on prey by causing a stronger prey response to their presence compared with inactive spiders. That is, active spiders might cause prey to become more inactive or forage less widely (Lima 1998). Scan sampling or continuous recordings of predator and herbivore activity during the course of an experiment should garner insight into this explanation. (3) Active spiders may leave larger or more apparent chemical deposit on the substrate compared with inactive spiders, whose cues have been shown to reduce herbivory in other agroecosystems (Hlivko and Rypstra 2003). These explanations are, of course, non-mutually exclusive and could be acting synergistically.

It is surprising that lettuce cultivars with more constitutive latex defenses had no influence on the amount of leaf damage via herbivory. Although previous studies have demonstrated reduced herbivory on *L. sativa* cv. Valmaine

(Huang et al. 2003), we found no observable differences between cultivars in these ecological modules. In our study, these cultivars may not have differed strongly in latex content due to genotype \times environment interactions, though we are unaware of any experiments that addressed G \times E interactions in this system. Another explanation is that the cabbage looper, *T. ni*, counteracts this constitutive defense by blocking latex flow to distal leaf areas via “leaf trenching” (Dussourd 1997; Agrawal and Konno 2009). After leaf trenching occurs, these otherwise inedible leaves can then be utilized by other herbivores in the community (Eben and Gámez-Virues 2007). We did observe leaf trenching taking place in a handful of our mesocosms, though long-term monitoring of this behavior here was impossible. This would suggest, however, that a potentially strong bottom-up effect can be diminished or even negated by the effective counter strategy of a specialist herbivore.

Past research investigating spiders’ top-down control of prey communities in tri-trophic systems have utilized diverse assemblages of spiders to reduce herbivory, regardless of individual differences in foraging traits (e.g., Riechert and Bishop 1990). Some have even specifically varied foraging mode in predators and demonstrated how trophic cascades vary based on the foraging mode of the dominant predator (Schmitz 2008). Interestingly, our data suggest that *intraspecific* variation in predators has marked effects on lower trophic levels—in some cases effectively halving the incidence of herbivory. Thus, we suggest that interested researchers should simultaneously consider both inter- and intraspecific variation and their combined effects on herbivore suppression and, in particular, focus on predators that exhibit broad intraspecific variation in key traits such as foraging mode. This will garner insights into the relative herbivore suppression efficiency of one or a few predator species with varied foraging modes versus many predator species bearing similar foraging modes (Finke and Snyder 2008). Addressing intraspecific

variation in top predators might help explain why some previous studies on the indirect effects of cursorial spiders in litter ecosystems have indicated contrasting results (e.g., Lawrence and Wise 2000, 2004). The combined efforts of these studies could usher in a new wave of predictive individual-based community ecology.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical standard Although the *L. sativa* seeds were provided by the Agricultural Research Service, USDA, we have no financial or professional relationship with this institution. All animals were handled within the animal welfare regulations of the University of Pittsburgh and United States of America.

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