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Competition and Intraguild Predation Between Beetles, *Pterostichus stygicus* (Coleoptera: Carabidae) and Centipedes, *Scolopocryptops sexspinosus* (Scolopemdomorpha: Scolopocryptopidae)

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Competition and Intraguild Predation Between Beetles, *Pterostichus stygicus* (Coleoptera: Carabidae) and Centipedes, *Scolopocryptops sexspinosus* (Scolopendromorpha: Scolopocryptopidae)

Michele E. Julian, Cari-Ann M. Hickerson, and Carl D. Anthony

Abstract

Studying interactions between distantly related species is necessary to understand the complexity of food webs. Generalist predator interactions, such as intraguild predation (IGP) and competition, can alleviate predation pressure and weaken top-down control that predators have on lower trophic levels. Centipedes (Chilopoda) and carabid beetles (Coleoptera) are common deciduous forest floor generalist predators that may interact by competing for resources beneath rocks and logs on the forest floor, especially during dry periods when prey become confined to such microhabitats. We used laboratory and field studies to determine whether the carabid beetle, *Pterostichus stygicus* (Say), and the centipede, *Scolopocryptops sexspinosus* (Say) co-occur under artificial cover. Additionally, a laboratory mesocosm experiment was used to examine competitive interactions in intra- and interspecific trials. There was significant negative co-occurrence of beetles and centipedes beneath cover objects in the field and laboratory. Pairings of *S. sexspinosus* and *P. stygicus* within mesocosms resulted in high mortality of *P. stygicus*, and reciprocal but asymmetric IGP. Centipedes maintained weight within solitary, intra- and interspecific mesocosm treatments, however, beetles lost mass in all treatments. *Scolopocryptops sexspinosus* responded more favorably to intra- and interspecific competition than did *P. stygicus*. Analysis of the leaf litter mesofauna indicated that these predators consumed similar prey in laboratory mesocosms. Our results suggest that species with very different trophic morphology have the potential to compete for shared microhabitat and prey.

Key words: cannibalism, aggression, co-occurrence, temperate deciduous forest, mesocosm

Competition for resources among species is thought to be ecologically important and can influence community structure and stability (Niemelä 1993, Levine et al. 2017, but see Lövei and Sunderland 1996). At the community level, interspecific competition can lead to coexistence via niche partitioning, competitive exclusion, or local extinction of the inferior competitor (Schoener 1974, Jenkins et al. 2019). Although there is empirical evidence of strong competitive interactions between phylogenetically distinct species, many studies have focused on testing the competition-relatedness hypothesis (Darwin and Wallace 1858) which predicts that niche space overlap, and therefore competition, should be greatest between closely related species because of morphological and functional similarity (i.e., niche conservatism). It is critical, however, to recognize that closely related species with similar morphology can differ in their functional traits (Resetarits and Chalcraft 2007), and that distantly

related taxa may have similar function despite morphological differences (Brown and Davidson 1977, Gerhold et al. 2015). Phenotypic traits need not be similar between species for there to be strong competition for shared resources (Gall et al. 2003, Wilcox et al. 2018). A newly proposed alternative to the competition-relatedness hypothesis proposes that researchers focus on a broad range of taxonomic relatedness (Wilcox et al. 2018). This model assumes that closely related taxa will have high niche similarity and similar competitive abilities due to high phenotypic and functional overlap, but that distantly related taxa can also have high niche overlap due to shared functional traits. Distantly related taxa, however, may have even larger effects on competitors because, despite utilizing similar resources, they may differ in other key morphological, physiological and/or behavioral traits. Any of these traits may place them at a competitive advantage.

One way that individuals reduce the effects of competition is through direct predation of guild members. Intraguild predation (IGP) is common in food webs and has the potential to add significant complexity to interactions among species within communities (Polis 1991, Wang et al. 2019). IGP occurs when potential competitors also engage in predator–prey interactions. IGP can be categorized as symmetrical (looping; Polis et al. 1989), in which species A and B are mutual predators of one another, or asymmetrical in which species A always preys on species B. Research investigating how IGP affects trophic cascades in food webs is important because it shows how interactions among guild members can potentially alter the strength of the indirect effects at lower trophic positions (Holt and Polis 1997). More specifically, studies have suggested that IGP can play a role in weakening top-down effects in some systems (Finke and Denno 2002, 2003; Halaj and Wise 2002). Additionally, environmental factors such as the degree of habitat complexity can alter the outcome of IGP. For example, Finke and Denno (2002) found evidence in the laboratory and field that IGP can affect herbivore density in a terrestrial arthropod system differently depending on the structural complexity of the microhabitat. In simple habitats, IGP between spiders and mirids relaxed predation on herbivorous leafhoppers, but in complex habitats, the two predators were collectively able to suppress herbivores because mirids were able to find refuge from spiders.

Deciduous forest floor communities are complex and contain a diversity of generalist predators (Polis 1991, Rosenheim et al. 1999, Hickerson et al. 2012) which have the potential to interact within shared microhabitat beneath cover objects such as rotting logs and rocks. Such naturally occurring cover objects retain moisture and house invertebrates and some small vertebrates as the surrounding leaf litter environment dries. Therefore, moist microhabitats and prey can become limited resources during periods between precipitation events (Dillion and Dillion 1961, Jaeger 1981, Lewis 1981). It is during the dry periods that interactions among generalist forest floor predators are expected to be most intense because they are restricted from openly foraging in the leaf litter. Two groups of predators, centipedes (Chilopoda), and carabid beetles (Coleoptera) have large biomasses within forest floor communities (Lewis 1981, Loreau 1984), and are ecologically similar because they are thought to share prey and microhabitat. However, these predators bring disparate traits to the competitive stage. For example, unlike carabid beetles, centipedes are venomous. Carabid beetles have good vision, but many centipede species are blind. It is these types of traits that might place one taxon at a competitive advantage. Additionally, studying the interactions between ecologically similar deciduous forest floor predators may prove helpful in determining interaction strengths within these systems.

We examined the potential for competitive interactions and IGP between two common forest floor predators [the centipede, *Scolopocryptops sexspinosus* (Say) and the carabid beetle, *Pterostichus stygicus* (Say)]. To observe spatial distributions of these invertebrates, we examined the degree to which these two taxa co-occur in the microhabitat beneath artificial cover objects in both the field, and in simple arenas in the laboratory. Additionally, we conducted a laboratory mesocosm experiment in which we indirectly assessed competitive dominance in two ways. First, we measured changes in mass of individuals in intra- and interspecific pairs over time, and we recorded instances of IGP and cannibalism. Second, we assessed the degree of diet overlap by comparing the natural prey remaining in the intraspecific beetle and centipede mesocosms at the end of the experimental period. We hypothesized that *S. sexspinosus* and *P. stygicus* would be negatively associated under cover objects in the field and laboratory. Our prediction was based on data reported from a predator removal study conducted by Hickerson et al.

(2012) who found that the removal of centipedes from beneath artificial cover objects (ACOs) in the field had a strong positive effect on carabid beetle abundance (Fig. 1). Next, we hypothesized that competition might be an important interaction between *S. sexspinosus* and *P. stygicus* in mesocosms containing natural prey, and it would be reflected in mass losses over time as resources become depleted but not experimentally replenished.

Materials and Methods

Co-occurrence Beneath Cover in the Field and Laboratory

To assess the degree of co-occurrence of carabid beetles and *S. sexspinosus* in the field, we collected data April 2004–December 2007 at the Cuyahoga Valley National Park (CVNP), Summit County, OH (41°13'46.62"N, 81°31'7.77"W). The presence of *S. sexspinosus*, and carabid beetles were recorded from beneath 72 ceramic ACOs (30.5 × 30.5 cm) spaced at least 1 m apart on a north facing forested hillside (see Hickerson et al. 2012, 2017 for a detailed description of the site). We visited the site between 0800 and 1800 hours every other week (2004–2005) or weekly (2006–2007) during the active season of our focal species (53 sampling dates, April through November or early December each year). We assessed the presence of centipedes and beetles by carefully lifting each ACO and noting which taxa were present. Since the field data were collected as part of an unrelated study, we did not know the species identity of the carabid beetles used in this portion of our project. We later were able to determine that *P. stygicus* was not only the most common species of carabid beetle at our field site but also had the most similar surface activity pattern to *S. sexspinosus* and so we used this species in subsequent laboratory experiments.

We used the methodology of Anthony et al. (2007) to assess the ability of *S. sexspinosus* and *P. stygicus* to displace one another in a structurally simple environment. We constructed arenas with low (dry portion of the arena), intermediate (dampened filter paper covering a portion of the arena floor), and high-quality

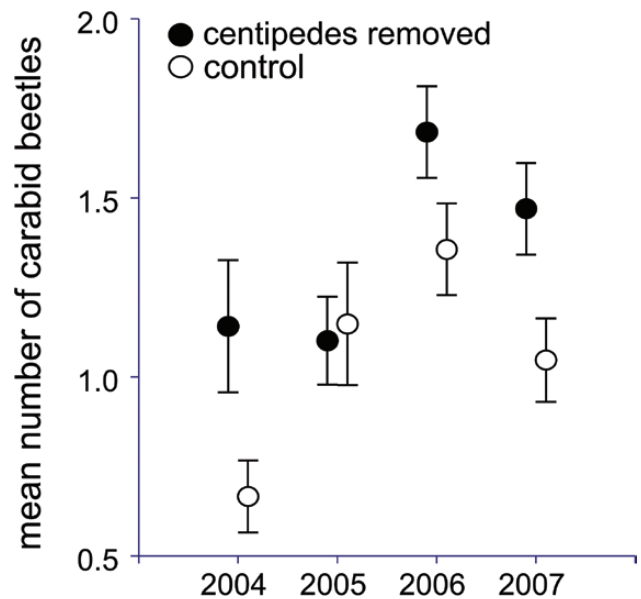


Fig. 1. Mean number of carabid beetles quantified per year from beneath artificial cover objects in centipede removal compared to control plots. Data were collected in the Cuyahoga Valley National Park over a 4-yr period that included 53 sampling dates.

microhabitats (dampened filter paper and space beneath artificial cover; Fig. 2). Arenas were kept at $18 \pm 2^\circ\text{C}$, 12:12 (L:D) h photoperiod and were covered with white paper which was lifted during data collection. We placed either a single centipede, a single beetle, or one individual of each species into arenas, and after 24 h, the locations of individuals in nine interspecific pairs were compared to locations of nine solitary individuals of each species. In the absence of interference, individuals are expected to gain access to high-quality habitat (Anthony et al. 2007). In interspecific trials, we predicted that, if competition were occurring for high-quality space, competitively dominant individuals would gain access to the highest quality microhabitat in laboratory arenas.

Competition in Laboratory Mesocosms

We collected 53 *P. stygicus* (adults) and 53 *S. sexspinosus* (≥ 35 mm in length) from 1 June 2011 to 17 July 2011 from the CVNP. Prior to the start of the experiment, individuals were weighed, measured (mean mass for *S. sexspinosus* = 0.218 ± 0.067 g, *P. stygicus* = 0.132 ± 0.015 g; mean length for *S. sexspinosus* = 41.89 ± 3.95 mm, *P. stygicus* = 16.23 ± 0.36 mm), and then housed in separate circular Pyrex glass (Greencastle, PA) 473 ml containers in 50 g of leaf litter collected from the same site. The leaf litter was mixed thoroughly to ensure that naturally occurring mesofauna (prey items) were distributed throughout. We removed predatory macroinvertebrates and vertebrates (spiders, salamanders, etc.) from the leaf litter by hand. The mesocosms were kept on a 12:12 (L:D) h photoperiod and were held at $18 \pm 2^\circ\text{C}$. Leaf litter was kept moist by spraying spring water into each container once a week, or as needed.

Experimental mesocosms consisted of rectangular $22.86 \times 33.02 \times 5.08$ cm Pyrex glass baking dishes. Each mesocosm received 110 g of leaf litter with naturally occurring prey. To ensure animals could not escape from the mesocosms, aluminum foil was pressed around the top of the mesocosm and heavy-duty plastic wrap was wrapped around the mesocosm twice. After punching small holes through all layers of plastic and aluminum foil, rubber bands were

stretched around the circumference of the mesocosm to hold the cover in place. Forty-five mesocosms were assigned to three treatments categories: interspecific (one *P. stygicus* paired with one *S. sexspinosus*; $n = 15$), intraspecific *P. stygicus* (two individuals paired together; $n = 15$) and intraspecific *S. sexspinosus* (two individuals paired together; $n = 15$). Eight individuals of each species were also kept individually in similarly constructed mesocosms to assess any mass changes in the absence of the other predator ($n = 8$ *P. stygicus* and $n = 8$ *S. sexspinosus*). Size asymmetries in pairings were minimized to reduce the fighting advantage of a larger animal by randomly pairing animals within size classes. In order to distinguish between individual *P. stygicus* in intraspecific mesocosms, we clipped two tarsal segments and claw from the middle leg on the left side of one beetle, and repeated the procedure on the right side of the other beetle. In *S. sexspinosus* pairings, we clipped the third to last leg on the left side of one centipede and again repeated the procedure on the right side of the other centipede. Mesocosms were searched weekly for 9 wk to assess mortality and mass change. Each week, individuals were removed and weighed (g) to an accuracy of three decimal places before being returned to their mesocosm. Evidence of IGP included finding the exoskeleton fragments of the other predator in the mesocosm and substantial weight gain of the surviving individual.

Mesocosm Leaf Litter Invertebrates

We used Berlese funnels (60W bulbs for 48 h, 70% EtOH) to extract invertebrate prey from leaf litter used in mesocosms. Invertebrates were counted and identified to order, and in some cases, family. Invertebrate prey from 15 litter samples were immediately extracted to determine baseline prey availability. An additional 15 mesocosms without adult beetles or centipedes were created to examine how prey availability changed over the 9-wk experimental period (post-experimental controls). We estimated the diets of centipedes and beetles in intraspecific mesocosms by comparing remaining invertebrates to those in post-experimental control mesocosms with neither predator, a method used by Walton and Steckler (2005) to indirectly measure diet.

Statistical Analyses

Co-occurrence Beneath Cover in the Field and Laboratory

A Spearman Rank correlation was used to analyze co-occurrence under cover objects in the field (Hickerson et al. 2018). This approach was used to determine whether carabid beetles and *S. sexspinosus* had negative spatial associations under cover objects in the field. Cover objects that did not have either predator beneath them during the study were removed from the analysis. To be conservative, individual ACOs were examined for temporal co-occurrence within 4 wk of an individual occupying a tile. For example, if *S. sexspinosus* occupied an ACO during 1 wk and within 4 wk, a ground beetle was found under the same ACO, we defined such a scenario as a co-occurrence. This method over-estimates the frequency of co-occurrence between groups because an ACO occupied by a carabid beetle on one collecting date and by a centipede on another is considered a shared cover object in the analysis. This approach, therefore, makes finding a significant negative correlation more difficult. Correlations (two-tailed) of carabid beetles and centipedes were run on each year separately: 19 June 2004 to 30 September 2004 ($n = 51$), 20 June 2005 to 1 October 2005 ($n = 84$), 17 May 2006 to 28 June 2006 ($n = 49$) and 9 July 2007 to 28 September 2007 ($n = 37$). In our laboratory arenas, we used a Fisher exact test (two-tailed) to compare

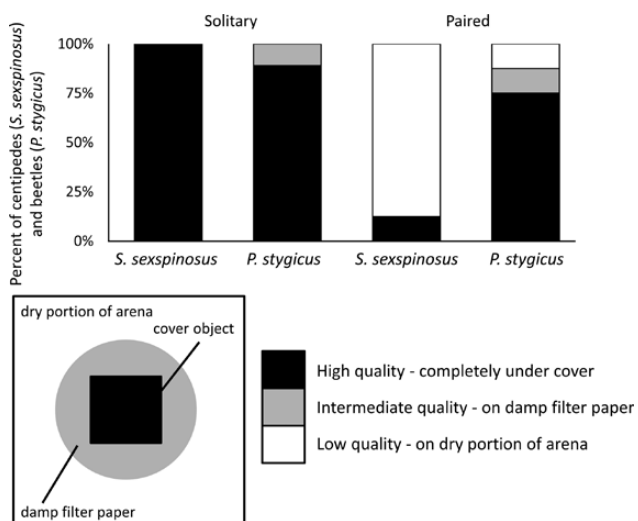


Fig. 2. Percentage of individuals of *Scolopocryptops sexspinosus* and *Pterostichus stygicus* occupying different quality microhabitats within laboratory arenas after 24 h. Pairing status (solitary or paired) is indicated above the bars. The arenas (24.5×24.5 cm) contained a cover object on damp filter paper (9.6% of arena), exposed damp filter paper (19.8% of arena), and a dry area (70.6% of arena). Both predators occupied the high-quality microhabitat beneath the cover object when alone in the arena. *P. stygicus* appears to exclude *S. sexspinosus* from high-quality microhabitat.

the number of animals found in high, intermediate, and low-quality habitat when paired alone versus when paired interspecifically.

Mass Changes in Mesocosms

As in many previous mesocosm studies, changes in mass over time were used to indirectly determine the intensity of competition (e.g., Wilbur 1987, Hickerson et al. 2005, Benard and Middlemis Maher 2011). Dominant individuals were expected to gain mass at the expense of their mesocosm mate, so we predicted that individuals would be more likely to lose mass in intraspecific trials. A Pearson's χ^2 test was used to assess if intraspecific competition was stronger than expected by chance. We divided our results into three categories: 1) those in which both individuals gained mass, 2) one gained mass/one lost mass, or 3) both lost mass. We compared our observed values to a random expectation of five mesocosms within each category. Mean changes in mass of individuals in the interspecific treatment were compared using a paired T-test (two-tailed) to determine whether one species was a superior competitor. For all mass changes, only the first 4 wk could be analyzed due to a high rate of IGP. To verify that IGP had occurred in cases in which a mesocosm mate could not be located, the mass change of predators that were suspected of eating their mesocosm mate were compared to the mass change of a random set of animals that did not lose their box mate using a Wilcoxon signed ranks test (Hickerson et al. 2005). All mass data were analyzed using SPSS for Windows, Version 16.0.

Mesocosm Leaf Litter Invertebrates

To visualize any variation in invertebrate composition among the two intraspecific treatments and post-experimental control mesocosms, nonmetric multidimensional scaling (nMDS) was used. We did not include interspecific mesocosms in this analysis because there would be no way to know which species of predator had consumed prey in those mesocosms. A one-way analysis of similarity (ANOSIM) was used to determine whether prey communities differed among the two intraspecific treatments and the control. The nMDS plots and ANOSIM are based on Bray-Curtis dissimilarity matrices. The statistical program PRIMER (v. 5) was used to create the nMDS plots and ANOSIM results.

Results

Co-occurrence Beneath Cover in the Laboratory and Field

During the 4-yr field survey, we observed 406 beetles and 75 centipedes. By allowing a 4-wk period of potential interaction, our definition of cohabitation beneath cover over-estimated co-occurrence. We observed predators under most ACOs (2004, 51.4%; 2005 62.5%; 2006, 59.8%; 2007, 54.2%), but centipedes and beetles co-occurred only 18 times. *Scolopocryptops sexspinosus* and combined species of ground beetles showed a strong, negative correlation beneath cover objects in the field each year (2004: $r_s = -0.846$, $P < 0.001$; 2005: $r_s = -0.615$, $P < 0.001$; 2006: $r_s = -0.654$, $P < 0.001$; 2007: $r_s = -0.792$, $P < 0.001$; all tests were two-tailed). These results suggest that *S. sexspinosus* and carabid beetles do not commonly reside together under cover objects in the field.

When placed in the experimental arenas in the lab, *P. stygicus* quickly located and made use of the cover objects, but *S. sexspinosus* tended to explore the arena perimeter prior to settling in any location. We observed mutual aggression and interference between the two species. In at least four trials, *P. stygicus* chased and bit *S. sexspinosus*, and we observed at least three instances in which *S. sexspinosus* bit *P. stygicus*. The two species were never found sharing ACO's at the

same time. When paired with *P. stygicus* only 12.5% of *S. sexspinosus* occupied high-quality habitat in the arena. In contrast, when housed alone, all *S. sexspinosus* occupied cover (Fig. 2, Fisher exact test, $P = 0.0004$). *Pterostichus* accessed high-quality habitat irrespective of pairing (89% when housed alone and 75% when paired with *S. sexspinosus*; Fisher exact test, $P = 0.735$).

Competition in Laboratory Mesocosms

IGP, Cannibalism, and Other Mortality

Because we could not observe predation events in our mesocosms, we estimated IGP and cannibalism indirectly via presence of exoskeleton remnants and mass gain in surviving predators. Death rates were higher in mesocosms with two animals supporting the notion that mortality was due to predation. IGP occurred mutually, but instances in which *S. sexspinosus* preyed upon *P. stygicus* were more common. Predation of *P. stygicus* by *S. sexspinosus* occurred in 40% of interspecific mesocosms. Centipedes that preyed on beetles were significantly heavier the week following a predation event ($n = 6$; paired Wilcoxon signed ranks test; $P = 0.027$). Additionally, predatory *S. sexspinosus* gained a significant amount of mass when compared to non-predatory *S. sexspinosus* ($n = 6$; Mann-Whitney U test; $P = 0.037$). *Pterostichus stygicus* preyed upon *S. sexspinosus* in only two mesocosms (13.3% of mesocosms), the first instance occurred within the first week of the experiment, and the second instance was after the sixth week. Within intraspecific pairings ($n = 15$), cannibalism occurred among *S. sexspinosus* in 13% of pairings and among *P. stygicus* in 33% of the pairings. Regardless of treatment type (solitary, interspecific, or intraspecific pairings) mortality among individuals of *P. stygicus* was higher compared to mortality of *S. sexspinosus* (binomial test, $P = 0.00002$). By the end of the ninth week, 70% of *P. stygicus* in intraspecific pairings had died. Of these deaths, 10 out of 30 (33.3%) had been cannibalized by a conspecific and 13 (43.3%) died from other causes, presumably resource limitation. These individuals were found deceased, but intact. By the end of the experiment, five out of 30 (16.6%) *S. sexspinosus* from intraspecific mesocosms had been cannibalized. By the end of the 9-wk experiment, 87.5% of *P. stygicus* housed alone in mesocosms had died. These solitary beetle deaths started at week 4 and continued through the end of the experiment. Mesocosms in which *S. sexspinosus* were alone did not experience any mortality during the same time period.

Mass Changes Within Mesocosms

By the end of the fourth week of our experiment *P. stygicus* had loss mass in all treatments. There were, however, no differences in mass loss between beetles in interspecific compared to intraspecific pairings (Fig. 3A, $n = 15$; Mann-Whitney U test; $P = 0.76$). Changes in mass of centipedes in interspecific compared to intraspecific pairings also did not differ (Fig. 3B, $n = 15$; Mann-Whitney U test; $P = 0.47$). Within intraspecific pairings, both species of predators experienced mass loss, but *P. stygicus* experienced a 9.8% loss compared to 1.3% for *S. sexspinosus* (Fig. 3B and D, $n = 28$; Mann-Whitney U test; $P = 0.0002$), suggesting that intraspecific competition had a more negative effect on *P. stygicus* than on *S. sexspinosus*. In ten of 15 intraspecific centipede mesocosms one individual gained mass at the expense of its box mate, and within three mesocosms, both individuals gained mass or remained the same mass ($\chi^2 = 3.53$; $df = 1$; $P = 0.06$). In only three of 15 intraspecific *P. stygicus* mesocosms, did one individual gained mass while the other lost mass, and none of the individuals within the remaining 12 intraspecific pairings gained weight ($\chi^2 = 10.2$, $df = 1$, $P = 0.001$).

Within interspecific pairings, 40% of *S. sexspinosus* gained mass or remained the same mass during the first 4 wk of the experiment

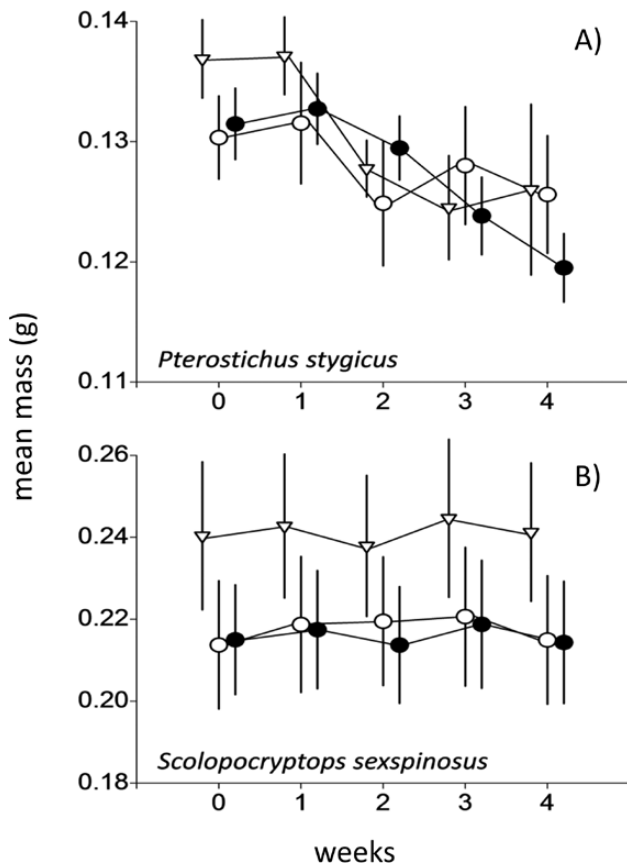


Fig. 3. Mean mass of (A) *Pterostichus stygicus*, and (B) *Scolopocryptops sexspinosus* within interspecific (open circles), intraspecific (closed circles) and solitary treatments (triangles) over the course of the first 4 wk of the experiment (mean \pm SE).

(Fig. 4A). However, when *S. sexspinosus* was paired with a conspecific, over half of the individuals lost mass (Fig. 4B). When *P. stygicus* was paired with *S. sexspinosus*, 73% lost mass (Fig. 4C), and in intraspecific pairings of *P. stygicus* 80% lost mass by the end of the fourth week (Fig. 4D). A larger proportion of *P. stygicus* lost mass when paired with *S. sexspinosus* (Fig. 4C) than *S. sexspinosus* lost when paired with *P. stygicus* (Fig. 4A), indicating that *P. stygicus* is an inferior interspecific competitor in laboratory mesocosms when compared to *S. sexspinosus*. Individuals of *P. stygicus* also suffered a much larger mass loss than *S. sexspinosus*, indicated by the distance of the points from the equal probability line in Fig. 4.

Leaf Litter Mesofauna

A total of 2,772 leaf litter invertebrates within 20 taxonomic groups were identified across the two intraspecific treatments ($n = 15$ each), the post-control mesocosms ($n = 15$), and the pre-experimental samples ($n = 15$). Overall, invertebrate abundance was lower in the predator mesocosms than the pre- and post-control mesocosms, suggesting that the predators were feeding upon the naturally occurring prey (Table 1). However, because some invertebrate groups increased in the presence of predators (e.g., Acari) and others decreased (e.g., Collembola), we did not detect a statistically significant effect on overall abundance. Invertebrate communities taken from the leaf litter of the *P. stygicus* and *S. sexspinosus* intraspecific treatments were not significantly different (ANOSIM, Global $R = 0.005$, $P = 0.351$, Fig. 5). There was a significant difference between the

pairwise comparisons of each of the two predator treatments and the post-control mesocosms (Global $R = 0.244$, $P = 0.003$ [*S. sexspinosus* vs. control]; Global $R = 0.214$, $P = 0.002$ [*P. stygicus* vs. control]), indicating that the predators significantly affected the prey community structure within mesocosms. Relative to the controls, centipedes and beetles reduced Collembola abundance by 83.6 and 82.6%, respectively and Diplopoda by 77.3 and 91.8%, respectively. These reductions relative to the controls, and other shared prey taxa (region A in Fig. 6), suggest that *S. sexspinosus* and *P. stygicus* may have dietary overlap, at least seasonally. Mite numbers were higher in both intraspecific pairings compared to the post-control mesocosms, indicating that mites, and perhaps also Pseudoscorpiones, may be avoided by both predators (region C in Fig. 6). Region B in Fig. 6 shows prey taxa that may contribute to dietary differences between these two predators.

Discussion

Despite empirical evidence supporting competition among phylogenetically divergent groups (reviewed in Wilcox et al. 2018), most work on niche dynamics focuses on related taxa. In an effort to help fill this knowledge gap, we examined the potential for competition between two phylogenetically distant species (a centipede and a carabid beetle) that overlap in prey and microhabitat use. Although similar in resource use, our focal species are profoundly different in key phenotypic features, including visual acuity, venom, locomotion, and trophic morphology. These unrelated phenotypic traits have the potential to contribute to asymmetric competition between otherwise similar competitors (Wilcox et al. 2018). Our results suggest that species with very different trophic morphology have the potential to compete for shared microhabitat and prey. Future studies might focus on shifts in trophic morphology, or changes in habitat use, by beetles in geographic regions where centipedes do not occur.

Co-occurrence Beneath Cover in the Field and Laboratory

Although there has been much debate about whether or not negative spatial associations in communities can arise randomly and in the absence of competition (reviewed in Hausdorf and Hennig 2007), the idea remains that if interspecific competition is an important factor shaping species distributions then the interaction should result in non-overlapping spatial patterns via exclusion of one or more species (Diamond 1975). Hickerson et al. (2012) used ACOs to demonstrate that the removal of centipedes from open field plots resulted in a significant increase in the number of carabid beetles compared to control plots where no predators were removed. In our study, we examined more specifically, and at smaller scale, co-occurrence beneath cover using removal data from Hickerson et al. (2012) and found that during seasons in which both taxonomic groups were active on the surface, carabid beetles were significantly negatively associated with *S. sexspinosus* under ACOs. Our results corroborate the findings of Hickerson et al. (2012) and suggest that centipedes may exclude beetles from cover in the field.

We next determined that the most abundant carabid beetle species at Hickerson's field site was *P. stygicus* which we paired with the centipede, *S. sexspinosus*, in laboratory arenas to assess which species would gain access to the best quality microhabitat when presented with a gradient of poor to high-quality in simple arenas. While alone in arenas, both species occupied high-quality microhabitat. When paired in arenas, *P. stygicus* was able to inhabit the most desirable microhabitat underneath the cover and exclude

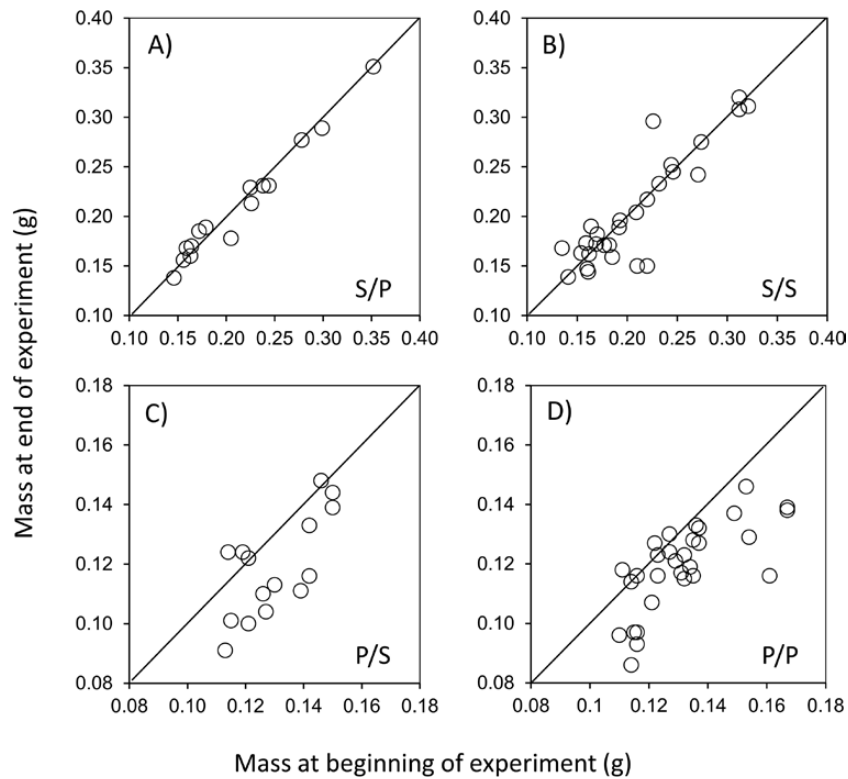


Fig. 4. Equal probability plots illustrating mass gain and loss in three mesocosm treatments: two intraspecific pairings and the interspecific pairings. Points above the line indicate a mass gain by the end of the first 4 wk of the experiment, and points below the line represent individuals that lost weight during the same period. The further away the point is from the line, the greater the change in mass. (A) Changes in mass of *S. sexspinosus* (S) in interspecific pairings with *P. stygicus* (P). (B) Changes in mass of *S. sexspinosus* (S) when paired with a conspecific (S). (C) Changes in mass of *P. stygicus* (P) when paired with *S. sexspinosus* (S). (D) Changes in mass of *P. stygicus* (P) when paired with a conspecific (P). There are more points in intraspecific trails because both animals were included in the same plot.

Table 1. Mean (SE) numbers of invertebrates in control and experimental treatments

Taxa	Control		Predator	
	Pre	Post	<i>S. sexspinosus</i>	<i>P. stygicus</i>
Collembola	8.73 (1.18)	19.53 (6.75)	3.43 (1.47)	3.40 (1.41)
Hymenoptera	0.13 (1.84)	0 (0.00)	0 (0.00)	0 (0.00)
Formicidae	1.27 (0.09)	0 (0.00)	0 (0.00)	0.07 (0.07)
Acari	43.67 (0.28)	16.07 (2.87)	36.64 (9.68)	30.93 (10.37)
Isopoda	0.4 (12.47)	0.4 (0.19)	0.14 (0.10)	0.53 (0.22)
Coleoptera (adult)	0.2 (0.22)	0.33 (0.19)	0.07 (0.07)	0 (0.00)
Coleoptera (larvae)	1.53 (0.11)	0.73 (0.25)	0.21 (0.11)	0.8 (0.26)
Rove Beetle	0.2 (0.67)	0.2 (0.11)	0.07 (0.07)	0.33 (0.13)
Lepidoptera (larvae)	1.33 (0.11)	0.67 (0.32)	0.36 (0.17)	0.27 (0.15)
Araneae	0.2 (0.46)	0.33 (0.16)	0 (0.00)	0.13 (0.09)
Diptera (adult)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
Diptera (larvae)	0.47 (0.00)	0.73 (0.32)	0.64 (0.23)	0.07 (0.07)
Diplopoda	1.067 (0.17)	3.53 (1.41)	0.29 (0.16)	0.8 (0.28)
Annelida	0.2 (0.31)	0.27 (0.21)	0.29 (0.16)	0.67 (0.35)
Pseudoscorpionida	0.53 (0.15)	0.13 (0.09)	0.43 (0.17)	0.4 (0.16)
Thysanoptera	0.53 (0.17)	0.33 (0.33)	0 (0.00)	0 (0.00)
Nemotoda	0.4 (0.41)	0 (0.00)	0 (0.00)	0 (0.00)
Hemiptera nymph	0.27 (0.22)	0.4 (0.16)	0.07 (0.08)	0.07 (0.07)
Gastropoda	0.73 (0.16)	0.07 (0.07)	0 (0.00)	0.2 (0.20)
Chilopoda	0.4 (0.49)	0.2 (0.11)	0 (0.00)	0 (0.00)

S. sexspinosus in most pairings. *Pterostichus stygicus* quickly located the cover objects upon being placed in the arenas in all treatments (solitary and interspecific pairings). However, when *S. sexspinosus*

were placed within the arenas, all individuals explored the arena perimeter prior to settling in a location. Differences in behavior between the two species may be due to the inability of *S. sexspinosus* to see

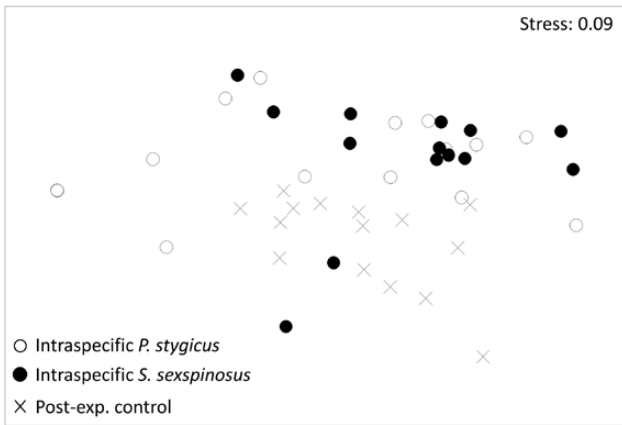


Fig. 5. nMDS plot of invertebrate prey composition in the leaf litter from intraspecific *Pterostichus stygicus* mesocosms (white circles), intraspecific *Scolopocryptops sexspinosus* mesocosms (black circles), and the post-experimental control mesocosms which did not contain either predator (X). Each point represents invertebrate prey from a single replicate mesocosm. The closer the points are to one another on the plot, the more similar they are in invertebrate composition. Invertebrates from the leaf litter of the two intraspecific treatments were not significantly different (Global R = 0.005, $P = 0.351$). There was a significant difference between the two predator treatments and the control mesocosms (ANOSIM, Global R = 0.244, $P = 0.003$ [*S. sexspinosus*]; ANOSIM, Global R = 0.214, $P = 0.002$ [*P. stygicus*]).

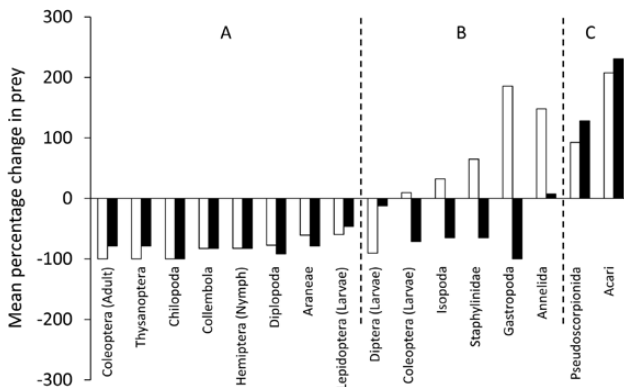


Fig. 6. Changes in mean prey abundance within intraspecific mesocosms relative to control mesocosms. Region A shows prey taxa that were similarly reduced by *Pterostichus stygicus* (white bars) and by *Scolopocryptops sexspinosus* (black bars). Region B illustrates instances where diets of predators may differ. Region C contains prey that was avoided by both species of predator.

(Shelley 2002) and the ability of many species of carabid beetles to at least sense light and dark areas in their environment (Thiele 1977). In simply constructed arenas, *P. stygicus* was able to easily detect the cover object and go directly to it, but *S. sexspinosus* took more time to determine its location. This delay in locating the cover object may have allowed the beetles to reach the high-quality microhabitat first and provided them with a residency advantage when defending the cover object from the centipede (Sensu Alcock and Bailey 1997, Gall et al. 2003). Our results indicate that although these two groups utilize similar microhabitat beneath cover, they do not do so at the same time. Results from Hickerson et al. (2012) showing that carabid beetles invaded cover objects that centipedes were removed from, and the data presented herein, suggest that competition may

be preventing the co-occurrence of our focal predators. Other studies have found evidence in support of competition between species by examining negative co-occurrence. For example, Eastern Red-backed Salamanders (*Plethodon cinereus*) exhibit negative associations with centipedes (Anthony et al. 2007, Hickerson et al. 2004) and spiders (Hickerson et al. 2018); behavioral studies suggest that these spatial distributions arise via aggressive interference. During our mesocosm cover object experiment, we recorded instances of aggression. This behavior may be indicative of territorial defense of cover objects, but homing studies and laboratory observational trials to measure advertisement, defense and expulsion of intruders would be necessary prerequisites to drawing conclusions about territoriality.

IGP and Cannibalism

Laboratory mesocosms that mimicked forest floor leaf litter microhabitat allowed us to assess how shared, limited resources affect interactions between *P. stygicus* and *S. sexspinosus*. These predators experienced unequal, reciprocal IGP, *S. sexspinosus* consumed *P. stygicus* in 40% of pairings, and *P. stygicus* consumed *S. sexspinosus* in only 13% of pairings. Predation upon guild members is expensive and risky behavior because large amounts of energy are required to subdue prey that are similar in size and fighting ability to the predator (Polis et al. 1989). Despite the risks, there is a large and immediate energy gain for the predator, the elimination of a competitor, and possibly the elimination of predation threats on juveniles of the predator species (Polis et al. 1989). *Scolopocryptops sexspinosus* is venomous and larger in mass and length than *P. stygicus*, which may have given centipedes an advantage in mesocosms via interference. Also, carabid beetles are known to be voracious feeders (Lövei and Sunderland 1996) and likely depleted prey within the mesocosms during the experiment. Thus, although we cannot rule out other mesocosm related effects, the high mortality rate by week 9 in solitary mesocosms may have been due to starvation. *Pterostichus stygicus*, if weakened by starvation, would have been vulnerable to predation by venomous centipedes. *Scolopocryptops sexspinosus* appeared to better handle the stress of reduced prey abundance over time and benefited from preying upon *P. stygicus*, indicated by their significant gains in mass following predation events. Polis et al. (1989) suggested that at lower prey densities, predators may expand their diet to include guild members, stabilizing predator-prey cycles and releasing pressure on non-guild prey. Low prey density, leading to IGP, has been documented in other terrestrial arthropods, including spiders (Turner 1983), scorpions (Polis and McCormick 1986), and ants (Mabelis 1984, Rosengren 1986). Many of the risks and benefits of IGP are similar to those of cannibalism (Polis 1981). Cannibalism in intraspecific *S. sexspinosus* pairings was relatively uncommon, occurring in 2 out of 15 pairings. However, cannibalism was much more common among conspecific pairings of *P. stygicus* (10 out of 15 mesocosms), suggesting that intraspecific competition was much more intense within *P. stygicus* pairings than in *S. sexspinosus* pairings.

High instances of IGP and cannibalism in laboratory mesocosms suggest that coexistence of these two species would be unlikely. However, there are many examples in which species partition niche space to alleviate strong effects of competition (Ross 1986, Martin et al. 2004, Proffit et al. 2007). Habitat complexity can play a role in the trophic interactions between intraguild predators by allowing them to occupy different microhabitats and thereby decreasing encounter rates. For example, Denno et al. (2004) found that *Pardosa* wolf spiders and *Grammonota* web-building spiders avoided cannibalism and IGP in complex habitats relative to simple laboratory

arenas. Results from our studies indicate that being confined to mesocosms without resource replenishment elevated the chance of IGP and cannibalism. In the field, centipedes and carabid beetles can leave the simple microhabitat beneath cover and forage in the leaf litter thus avoiding predation or interference competition.

Leaf Litter Mesofauna—Diet Overlap

We detected no significant difference in mesofauna composition between the two predator treatments at the end of the experiment. The composition of mesofauna from the intraspecific mesocosms was significantly different than the post-experimental control mesocosms, indicating that the predators feeding habits were influencing mesofauna abundance and composition. The fact that *P. stygicus* and *S. sexspinosus* intraspecific treatments had a similar composition of mesofauna suggests that their diets may overlap, at least seasonally. Relative to the controls, centipedes and beetles reduced Collembola and millipede abundance by over threefold. Collembola represents a common prey for many generalist food web predators (Clarke and Grant 1968, Maerz et al. 2005) and in a laboratory study, *Pterostichus melanarius* consumed millipedes in feeding trials (Brunke et al. 2009). Therefore, a reduction in the numbers of these taxa may be a result of direct predation by predators in our mesocosms. Mite numbers were 2.28 times higher in the *S. sexspinosus* mesocosms and 1.92 times higher in *P. stygicus* mesocosms relative to controls. Increased mite numbers suggest that mites may have benefited by the presences of the predators and that the predators were not actively consuming them. Several studies have shown that feces and nitrogenous waste can contribute to predator effects on lower trophic levels in terrestrial above-ground ecosystems (Pastor et al. 1993, McNaughton et al. 1997, Walton and Steckler 2005). For example, the presence of red-backed salamanders enhances the densities of Collembola and mites in laboratory mesocosms by promoting the growth of microflora (Walton and Steckler 2005). Microflora serves as a food resource for Collembola and many mite species are predatory on Collembola (Koehler 1999). In our mesocosms, feces and other wastes produced by centipedes and beetles may have contributed to the growth of fungal hyphae and ultimately contributed to increases in mite numbers.

Mass Changes Within Mesocosms

Over the course of the 9-wk experiment, mortality was high within mesocosms and instances of IGP and cannibalism made it difficult to detect the strength of interspecific competition using changes in mass. *Scolopocryptops sexspinosus* and *P. stygicus* lost weight in both intra- and interspecific treatments, but treatment type had no effect on the amount of weight lost by the two predators. However, *S. sexspinosus*, on average, maintained their weight much better than *P. stygicus*. Although these results suggest that the pressures of intra- and interspecific competition more negatively affected *P. stygicus*, it is also possible that beetles simply do not thrive in mesocosms. For example, in our control (solitary) treatments, mortality and loss of body mass by beetles necessitated using only the first 4 wk of data to assess the strength of competitive interactions. For both species, inter- and intraspecific competition had similar negative effects on mass change within mesocosms at low resource levels, but we interpret these results with some caution because we only marked individuals in intraspecific trials. If the marking technique had negative effects, we may have over-estimated the effects of intraspecific competition. However, we detected no differences in mortality between marked and unmarked individuals, so we doubt that limb clipping had a significant effect. Future studies could be conducted using leaf

litter collected during higher periods of secondary productivity, either in mid-spring or early fall, when moisture levels are higher and when leaf litter mesofauna are more abundant.

Evidence from this study suggests that *P. stygicus* and *S. sexspinosus* compete for similar resources in mesocosms, and may compete in the field, indicated by their negative spatial associations in the field and laboratory. In temperate forest floor ecosystems, seasonal fluctuations in leaf litter mesofauna, which are more abundant in the spring and fall, and less abundant in the summer, may change the outcome of intra- and interspecific competition within these communities. The estimated similarity in diet and negative co-occurrence under cover objects of the focal predators in this study suggests that exploitative competition may be occurring between these two species. The high rate of IGP on *P. stygicus* by *S. sexspinosus* adds to the growing evidence that IGP is a widespread occurrence and probably important in helping explain food web dynamics (Polis et al. 1989, Polis and Strong 1996, Holt and Polis 1997). Although *S. sexspinosus* preyed heavily on *P. stygicus* in our mesocosms, intraspecific competition appears to be more intense than interspecific competition for both species. Mechanisms that allow coexistence in natural systems with multiple competitors (more than two) are understudied, and we do not fully understand how community structure affects coexistence and ultimately species richness (Levine et al. 2017). Future research aimed at examining the effects of IGP on competitive outcomes could include density manipulations of more than two intraguild predator species crossed with intra- and interspecific treatments and should include estimates of interaction strengths for each treatment. Such an experimental design may help us better understand how such mechanisms of coexistence in forest floor systems maintain stability.

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