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## RESEARCH ARTICLE

# Intraguild predation is increased in areas of low prey diversity in a generalist predator community

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## Abstract

1. Niche differentiation and intraguild predation (IGP) can allow ecologically similar species to coexist, although it is unclear which coexistence mechanism predominates in consumer communities. Until now, a limited ability to quantify diets from metabarcoding data has precluded the use of sequencing data to determine the relative importance of these mechanisms.
2. Here, we pair a recent metabarcoding quantification approach with stable isotope analysis to examine diet composition in a wolf spider community.
3. We compare the prevalence of resource partitioning and IGP in these spiders and test whether factors that influence foraging performance, including individual identity, morphology, prey community and environmental conditions, can explain variation in diet composition and IGP.
4. Extensive IGP is likely the primary coexistence mechanism in this community, and other factors to which foraging variation is often attributed do not explain diet composition and IGP here. Rather, IGP increases as prey diversity decreases.
5. Foragers are driven to IGP where resource niches are limited. We highlight the need to examine how drivers of predator–prey interaction strengths translate into foraging in natural systems.

## KEYWORDS

coexistence, diet, diversity, intraguild predation, Lycosidae, niche differentiation, predator–prey interactions, resource partitioning

## 1 | INTRODUCTION

Ecological theory suggests that sympatric species cannot occupy the same niche without exclusion of the weaker competitor (Gause, 1934; Hardin, 1960; MacArthur & Levins, 1967). Resource partitioning—in which organisms divide resource pools such that each uses only a portion of their fundamental or

historical niche—may provide a solution by reducing competition and maintaining stable coexistence of similar species (Augustyn et al., 2016; Correa & Winemiller, 2014; Friedemann et al., 2016; MacArthur, 1958). Despite this, communities broadly show functional redundancy (Adam et al., 2015; Hutchinson, 1961), supporting multiple “ecologically equivalent” species (Siepielski & McPeck, 2010).

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Intraguild predation (IGP) also may allow the coexistence of species relying on similar food resources. IGP, predation between species in a “guild” (Holt & Polis, 1997), reduces competition by enabling consumers to meet some of their energetic demands through consumption of the competitor and by reducing competitor population size, thereby increasing individual foraging rates. Similarly, cannibalism (a form of IGP) can reduce competition and stabilize populations (Claessen et al., 2002; Rudolf, 2007). Although consumers may reduce competition through various mechanisms, including niche partitioning and IGP, it remains unclear which of these mechanisms predominates in predator communities. This is particularly true for generalist predators, whose diets may be flexible enough to accommodate any of these mechanisms.

Any factor that influences foraging performance may structure diet, and thus coexistence mechanisms, as these factors can determine the accessibility (e.g. gape limitation; Nilsson et al., 2019) or energetic gains (e.g. optimal foraging; Charnov, 1976) of various resource “options”. Morphological traits such as body mass and condition, for example, are powerful predictors of foraging ability (DeLong, 2021; Kalinkat et al., 2011; Uiterwaal et al., 2017; Vucic-Pestic et al., 2010) and may explain why some consumers are better competitors or intraguild predators (Balfour et al., 2003; Samu et al., 1999). Environmental conditions also shape foraging (Contreras et al., 2013; Uiterwaal & DeLong, 2018, 2020a), often by influencing activity, movement or detectability (Gillooly et al., 2001; Hirt et al., 2017; Uiterwaal et al., 2019). Despite this robust body of work examining the factors that influence foraging, it is unclear how these effects are reflected in the foraging of wild consumers.

Here, we address these questions using stable isotope analysis and DNA metabarcoding. Stable isotopes can be used to assess isotopic niche (Blüthgen et al., 2003; Hyodo et al., 2018; Newsome et al., 2007; Potapov et al., 2019). The heavier nitrogen isotope ( $^{15}\text{N}$ ) is preferentially incorporated into tissues such that consumers have higher  $\delta^{15}\text{N}$  values than resources (Wada et al., 1991). The  $^{15}\text{N}$ -enrichment at each trophic step (termed trophic discrimination factor) can be used to estimate trophic levels (Kim, Casper, et al., 2012; Martínez del Rio et al., 2009). There is also  $^{13}\text{C}$ -enrichment with trophic level (Kim, Casper, et al., 2012) but  $\delta^{13}\text{C}$  values primarily represent the producers at the base of an individual's food source (DeNiro & Epstein, 1978; Oelbermann et al., 2008). Thus, carbon isotope composition can be used to compare the dietary importance of primary producers with different baseline  $\delta^{13}\text{C}$  values (DeNiro & Epstein, 1978; Haines, 1976). Combined,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values reflect a consumer's isotopic niche over relatively lengthy periods of time (Kim, Tinker, et al., 2012; Mestre et al., 2013; Newsome et al., 2007).

In contrast, metabarcoding data provides “snapshots” of predation events that can be used to determine diet composition of a group when compiled across individuals (Bonato et al., 2021; Cohen et al., 2020; Hoenig et al., 2021; Lopes et al., 2020; Mata et al., 2021; Trevelline et al., 2018). Although many studies have used metabarcoding to assess dietary overlap between consumer groups, niche overlap calculations require accurate estimates of relative proportions of prey in the diet, which metabarcoding on its own does not

produce (Deagle et al., 2019). This is because prey are digested at different rates, affecting the probability of detection and skewing estimates of dietary proportions (Greenstone et al., 2014). We use a novel method (Uiterwaal & DeLong, 2020b) to correct for this and, for the first time, obtain unbiased estimates of dietary niche overlap from metabarcoding data.

We leverage this approach to explore potential coexistence mechanisms and the factors that affect these mechanisms in a wolf spider community. Wolf spiders (Lycosidae) consume prey from dozens of taxonomic families (Eitzinger et al., 2019; Wirta et al., 2015) and readily engage in IGP (Balfour et al., 2003; Samu et al., 1999). Because spiders in this community broadly use the same resources, we explore which coexistence mechanisms appear to predominate and what determines whether spiders engage in them. First, we hypothesize that spider diets are consistent with interspecific niche partitioning, IGP between wolf spiders, or both. Secondly, we hypothesize that factors known to affect foraging performance, including individual traits and states, prey availability, and environmental conditions, can explain variation in diet composition (how niches are partitioned) and the extent to which individuals act as intraguild predators.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

We collected spiders at Cedar Point Biological Station near Ogallala, Nebraska, USA (41.210, -101.649). Cedar Point sits on the south shore of Lake Ogallala. Close to shore, ground cover consists of grass along a gravel road. This gives way to red cedar *Juniperus virginiana* and mixed deciduous riparian forests, meadows and canyons, before transitioning to upland semi-arid mixed-grass prairie. In early summer of 2019–2020, we collected spiders from 20 sites per year, each approximately 400 m<sup>2</sup>. On sampling days, we recorded 24-h temperature using a shaded Hobo temperature logger at the site's centre. We measured the straight-line distance from the centre of each site to the lakeshore using GoogleMaps.

### 2.2 | Spider collection

We visited sites around 9–9:30pm to collect spiders by headlamp spotlighting. We aimed to collect 20 spiders per site, but this was often not possible due to rain or low spider density, particularly in 2019. We targeted individuals of different species, collecting at least one individual of each species present over 20–40 min. Transport time to the lab was <20 min after collection of the last spider. In the lab, we weighed spiders, photographed spiders with a size standard, recorded species, and (in 2020) recorded sex or stage (“immature” if sex could not be determined). We then killed spiders by freezing them overnight at -20°C. The following morning, we transferred spiders to 2.0 mL tubes in 95% ethanol and stored them at -20°C for

transport to the University of Nebraska-Lincoln. We used ImageJ to measure opisthosoma (abdomen) and prosoma (head) width from photographs, taking opisthosoma: prosoma ratio as a measure of body condition (e.g. energetic state; Anderson, 1974). Ethical approval was not required.

We caught 156 spiders in 2019 and 449 in 2020. We identified eight (morpho)species (*Hogna baltimoriana*, an unidentified morphospecies ("RED"), *Rabidosia rabida*, *Schizocosa bilineata*, *S. mccoocki*, *S. ocreata*, *S. retrorsa*, and *S. saltatrix*) in addition to some unidentified spiders. We focused on the most commonly collected (morpho)species for further analyses (*H. baltimoriana*, RED, *R. rabida*, *S. mccoocki*, *S. ocreata*, *S. saltatrix*). Mean body mass was 98 mg (range: 1 mg [unidentified spiderling]-870 mg [female *H. baltimoriana*]). Mean body condition was 0.955 (0.514 [male *S. mccoocki*]-2.980 [unidentified spiderling]). Mean 24-hour temperature was 23.0°C (17.0°C-28.3°C) in 2019 and 24.1°C (15.0°C-29.2°C) in 2020.

### 2.3 | Arthropod collection

On sampling days in 2020, we used 0.25 m × 0.25 m × 0.25 m boxes to sample the non-Lycosid arthropod community at four locations within the site. These modified box quadrats minimize immigration/emigration of mobile arthropods (Gardiner & Hill, 2006), allowing us to use a handheld vacuum for collection. We paired this method with pitfall traps in an effort to exhaustively collect arthropods within each sample location. We identified arthropods to family, estimated live (wet) mass for each family and calculated the Gini-Simpson's index of diversity for each site:

$$GS = 1 - \frac{\sum_{i=1}^N n_i(n_i - 1)}{N(N - 1)},$$

where  $n_i$  is the number of arthropods in family  $i$  and  $N$  is the total number of arthropod families (Simpson, 1949), a commonly used diversity metric. See Supporting Information for more details on arthropod sampling methods.

### 2.4 | Stable isotopes

From 161 of the spiders, we removed one to six legs. We dried these at 50°C overnight before transport to the Stable Isotope Ecosystem Lab of University of California Merced (SIELO) for stable isotope analysis. Approximately 0.2–0.3 mg of sample were weighed and analysed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values on a Costech Elemental Analyser coupled to a ThermoFisher Delta V Plus isotope ratio mass spectrometer with a ConFlo IV. We used the reference materials USGS 40 and 41a for standardization and ran additional internal reference materials, Cotech Acetanilide and MB Squid, in replicate for drift and mass linearity corrections. The analytical error across the suite of reference materials was

less than 0.2‰ and 0.1‰ for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values, respectively. We report isotope composition in delta notation ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), which reports the ratio of the heavier to lighter isotope and compares the sample to standard (e.g. Vienna PeeDee Belemnite [V-PDB] and Vienna AIR [V-AIR]) in units of per mil (‰).

### 2.5 | Analysis of stable isotope data

To test for isotopic niche differences across species (Hypothesis 1), we performed one-way ANOVAs for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. To examine how individual characteristics, prey community and environmental factors affect trophic position (Hypothesis 2), we additionally tested several linear models using  $\delta^{15}\text{N}$  as the response variable and all combinations of spider species, mass, body condition, sex, distance to the lake, and residuals from a lake distance-prey diversity regression ("diversity residuals", due to a significant positive relationship between distance to the lake and prey diversity) as predictor variables. We selected the best-performing models using Akaike information criterion (AIC; Burnham & Anderson, 2004) and tested whether a random effect of site improved top model performance. We used Matlab (R2021a).

### 2.6 | Estimating trophic levels

To test for IGP (Hypothesis 1), we estimated trophic level (TL) of individual spiders using:

$$TL = \lambda + \frac{(\delta^{15}\text{N}_s - [\delta^{15}\text{N}_{\text{Abase}} \times \alpha + \delta^{15}\text{N}_{\text{Tbase}} \times (1 - \alpha)])}{\Delta_n}, \quad (1)$$

where  $\delta^{15}\text{N}_s$  is the  $\delta^{15}\text{N}$  value of the spider,  $\delta^{15}\text{N}_{\text{Abase}}$  and  $\delta^{15}\text{N}_{\text{Tbase}}$  are the  $\delta^{15}\text{N}$  value of organisms at the base of the aquatic and terrestrial (respectively) food webs,  $\lambda$  is the trophic level of the bases used to estimate  $\delta^{15}\text{N}_{\text{base}}$ ,  $\alpha$  is the proportion of nitrogen derived from the aquatic food web and  $\Delta_n$  is the trophic discrimination factor (Post, 2002). This equation allowed us to calculate trophic level while accounting for the systematic enrichment of  $^{15}\text{N}$  in aquatic food webs. We used herbivores ( $\lambda = 2$ ) for both the terrestrial and aquatic  $\delta^{15}\text{N}_{\text{base}}$ . We used the relationship between lake surface area and  $\delta^{15}\text{N}_{\text{base}}$  (Post, 2002) to estimate  $\delta^{15}\text{N}_{\text{Abase}}$  as 10.4‰ for the littoral food web of Lake Ogallala (129 ha). We estimated  $\alpha$  as 0.088, using the proportion of the diet (by biomass) coming from aquatic prey families in the metabarcoding data. Wolf spider  $\Delta_n$  values tend to be low (attributed to guanine excretion, Vanderklift & Ponsard, 2003), between at 0.5‰–2.5‰ (Oelbermann & Scheu, 2002; Rickers et al., 2006; Vanderklift & Ponsard, 2003; Wise et al., 2006). We drew  $\Delta_n$  values from a uniform distribution between 0.5‰–2.5‰ (see Supporting Information for analysis using  $\Delta_n = 3.4$ , the mean from Post (2002)). We drew  $\delta^{15}\text{N}_{\text{Tbase}}$  values from a uniform distribution between 0.15‰–1.7‰, the minimum and maximum grasshopper  $\delta^{15}\text{N}$  means from three studies (Halaj et al., 2005; Karpeštam & Forsman, 2011; Laiolo et al., 2015). We chose grasshoppers because

they are a herbivorous and terrestrial prey group. We repeated this 1000 times to obtain estimates of spider trophic levels.

## 2.7 | Metabarcoding

We used DNA metabarcoding to assess diet composition and determine dietary niche overlap between species. We rinsed spiders with three consecutive washes: deionized water, 10% bleach, and deionized water. We then dried either the opisthosoma or the whole body (sans the legs for isotope analysis; Macías-Hernández et al., 2018) at 56°C for 45 min. We used QiaGen Blood and Tissue Kits to extract DNA, following the QiaGen Supplementary Protocol for purification of insect DNA. We normalized DNA to 100 µg/mL (when possible) before sending samples for sequencing with two primer pairs: ZBJ-ArtF1c/ZBJ-ArtR2c ("Zeale", (Zeale et al., 2011)) and ARCF3/ARCR6 ("Arc", (Schmidt et al., 2018)). Both primer pairs amplify *cytochrome c oxidase subunit I* (COI) fragments in arthropods (157bp, Zeale; 69bp Arc) and have been used for metabarcoding arthropod prey (Eitzinger et al., 2019; Zeale et al., 2011). The University of Minnesota Genomics Center performed library preparation and Illumina sequencing using 2x150bp paired-end reads on a MiSeq platform. We performed quality trimming and adapter trimming using *cutadapt* 3.2. Using *vsearch* v2.18.0, we merged paired-end reads and performed quality filtering, dereplication and denoising to produce ZOTUs (zero-radius OTUs, Edgar, 2016). We used *vsearch* to remove chimeras and map ZOTUs back to spider samples, resulting in 1,051,512 Zeale reads and 2,144,579 Arc reads. We used *blast* 2.12.0 to perform a remote blast to the NIH database to assign taxonomic information to reads and the package *TAXONOMIZER* in R (4.1.2) to match taxon IDs to families. We discarded sequences that could not be identified with a 95% similarity threshold or which could not be identified to family. We considered a family "present" in a sample if it comprised ≥1% of that sample's reads (Deagle et al., 2019).

## 2.8 | Diet composition

We analysed metabarcoding data in Matlab (R2021a). To examine how the number of spiders tested influenced apparent diet breadth (number of prey families detected) across species, we constructed rarefaction curves for each species from 1000 bootstraps.

To estimate diet compositions, we first accounted for differences in prey DNA digestion rates, which may lead some prey to be underestimated in the diet, precluding accurate comparisons of diet composition. These digestion rate differences are quantified using DNA detectability half-lives,  $h$ , that describe the time after a predation event when the prey is no longer detected in half the predators who consumed the prey (Greenstone et al., 2014; King et al., 2008). These half-lives shape detection curves, which typically take the form:

$$p_d = \frac{1}{1 + e^{-k(t-h)}}$$

where  $p_d$  is the probability of detection given consumption,  $t$  is the time after the predation event and  $k$  is the slope of the decay.

To account for differences in digestion rates across prey, we adjusted the observed diet composition using half-lives. To do this, we first estimated a half-life for each family detected in each spider species (pooled across sites) or each site (pooled across species), using the mean spider mass, estimated prey family mass, mean temperature, amplicon lengths, and the estimated effects of these variables on DNA detectability half-lives (Uiterwaal & DeLong, 2020a). We slightly modified the approach from Uiterwaal and DeLong (2020a, 2020b) for prey detected by both primers: rather than using the reported mean Lycosidae  $k$  of  $-0.067$ , we estimated  $k$  using:

$$k = -0.855 \times h^{-0.623},$$

which better captures the more negative values of  $k$  observed for short half-lives (Figure S1).

We then weighted metabarcoding detections using these half-lives to estimate diet composition for each spider species (Uiterwaal & DeLong, 2020b). To compare diets across spider species with different sample sizes, we additionally estimated diet composition of 20 randomly selected individuals of each species (repeated for 1000 bootstraps). We chose to sample 20 per species because the least represented morphospecies ("RED") comprised 20 individuals. We calculated pairwise niche overlap for diet composition between species using Pianka's index (Pianka, 1974), which ranges from 0 (no overlap) to 1 (identical) to test the extent to which interspecific niche partitioning occurred in this community (Hypothesis 1).

To test whether factors that commonly affect foraging performance could explain diet variation (Hypothesis 2), we pooled all spiders and again randomly selected groups of 20 spiders to compare, repeated 1000 times, and tested for correlations between Pianka's index and potential explanatory factors such as mean body size difference and mean body condition difference. We also calculated Pianka's index between sites, using both diet data and arthropod collection data to determine whether similarities in arthropod community composition can explain similarities in diet composition.

Lastly, to understand whether isotopic differences between spiders collected at different sites may reflect the effect of an aquatic subsidy, we tested for a correlation between distance to the lake and proportion of aquatic prey in the diet.

## 2.9 | Comparing trophic levels between metabarcoding and stable isotope analysis

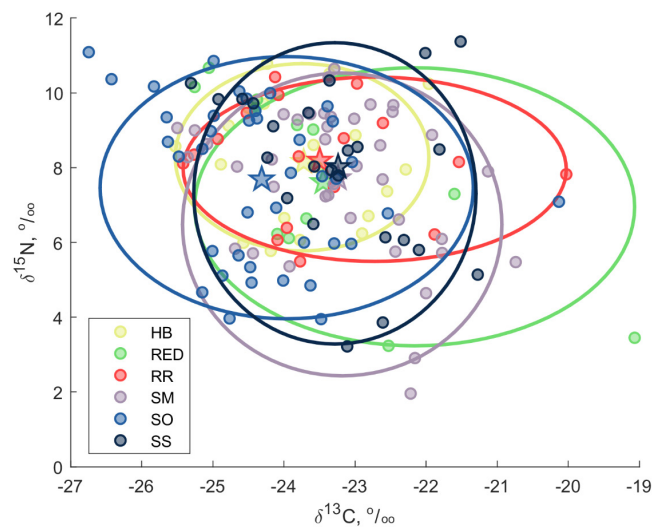
To further explore Hypothesis 1, we determined whether trophic level estimates from stable isotopes were consistently higher than estimates from metabarcoding, as would be expected if IGP was driving high  $\delta^{15}\text{N}$  values (since metabarcoding cannot account for IGP, including cannibalism). To estimate trophic level from metabarcoding data, we used diet composition for spiders grouped into species-site combinations. We grouped spiders because metabarcoding data

provides individual dietary snapshots and can better represent diet composition when combined across multiple individuals. We only used data from species-site combinations with at least four individuals (i.e. when at least four individuals of the same species from the same site were sequenced). For spiders in each species-site combination, we calculated the mean trophic level of consumed prey, weighted by dietary proportion, and added 1 to obtain an estimate of the spiders' mean trophic level. We then tested for a correlation between mean metabarcoding trophic level and mean  $\delta^{15}\text{N}$  trophic level of spiders in the same species-site combination.

### 3 | RESULTS

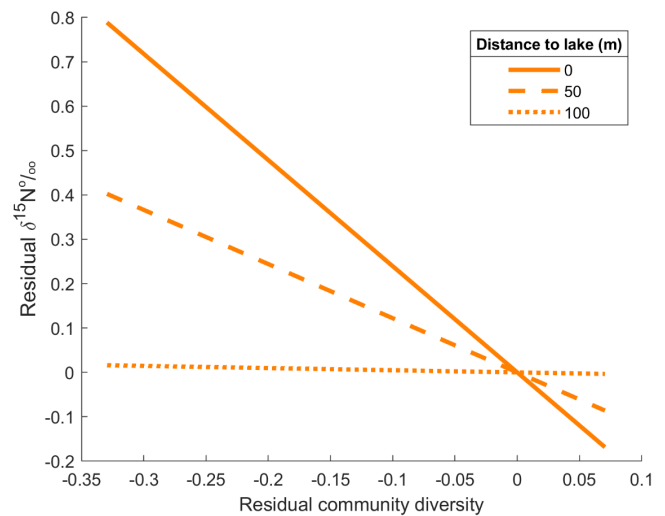
#### 3.1 | Stable isotope analysis

The  $\delta^{13}\text{C}$  values for individual spiders ranged between  $-26.8$  to  $-19.1\text{‰}$  (mean,  $-23.6$ ) and  $\delta^{15}\text{N}$  values ranged from  $1.9$  to  $11.3\text{‰}$  (mean,  $7.85$ ). Median spider trophic position was  $5.94$  (95% CIs:  $2.96$ – $14.78$ ) with individual trophic levels ranging from  $2.14$  (a female *S. mccooki*, 95% CIs:  $1.51$ – $3.05$ ) to  $8.49$  (a female *S. saltatrix*, 95% CIs:  $5.88$ – $19.05$ ). There was no difference in  $\delta^{15}\text{N}$  between species ( $F_{5,146} = 0.34$ ,  $p = 0.89$ , Figure 1). There was a difference in  $\delta^{13}\text{C}$  ( $F_{5,146} = 4.10$ ,  $p = 0.002$ , Figure 1), with *S. ocreata* showing lower  $\delta^{13}\text{C}$  values than *S. saltatrix* and *S. mccooki*, and no difference between the remaining 13 species pairs. The best supported model for  $\delta^{15}\text{N}$  values contained species and an interaction between distance to the lake and residual prey diversity (Table S1). This model explained

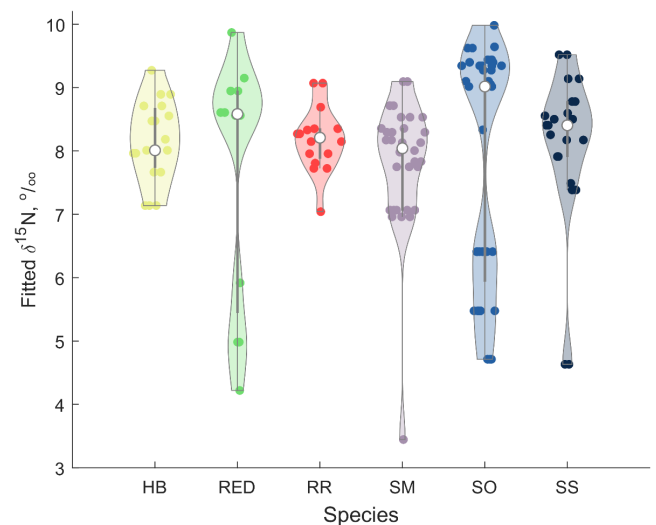


**FIGURE 1** The  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values and 95% confidence interval ellipses for six spider species. Stars represent mean values for each species. There is no difference in  $\delta^{15}\text{N}$  between species ( $F_{5,146} = 0.34$ ,  $p = 0.89$ ). There is a difference in  $\delta^{13}\text{C}$  ( $F_{5,146} = 4.10$ ,  $p = 0.002$ ), with *S. ocreata* showing lower  $\delta^{13}\text{C}$  values than *S. saltatrix* and *S. mccooki*, and no differences between the remaining 13 species-species pairs. (HB, *Hogna baltimoriana*; RED, unidentified morphospecies; RR, *Rabidosa rabida*; SM, *Schizocosa mccooki*; SO, *Schizocosa ocreata*; SS, *Schizocosa saltatrix*).

nearly half of the observed  $\delta^{15}\text{N}$  variation ( $R^2 = 0.49$ ). Model support was not increased by addition of a random site effect ( $\Delta\text{AIC} = 2.0$ ). Four additional models with  $\Delta\text{AICs} < 2$  additionally contained either mass, mass and sex, body condition, or mass and body condition (Table S1). These additional terms were not significant. All five top models supported a negative effect of distance to the lake, a negative effect of residual arthropod diversity and a positive interaction between lake distance and diversity residuals (Table S2, Figure 2). All five models suggested that, although most species did not differ in  $\delta^{15}\text{N}$  values, *S. ocreata* had higher  $\delta^{15}\text{N}$  values than other species (in the top model: *S. saltatrix*, *S. mccooki*, *H. baltimoriana*, and *R. rabida*; Table S2, Figure 3).



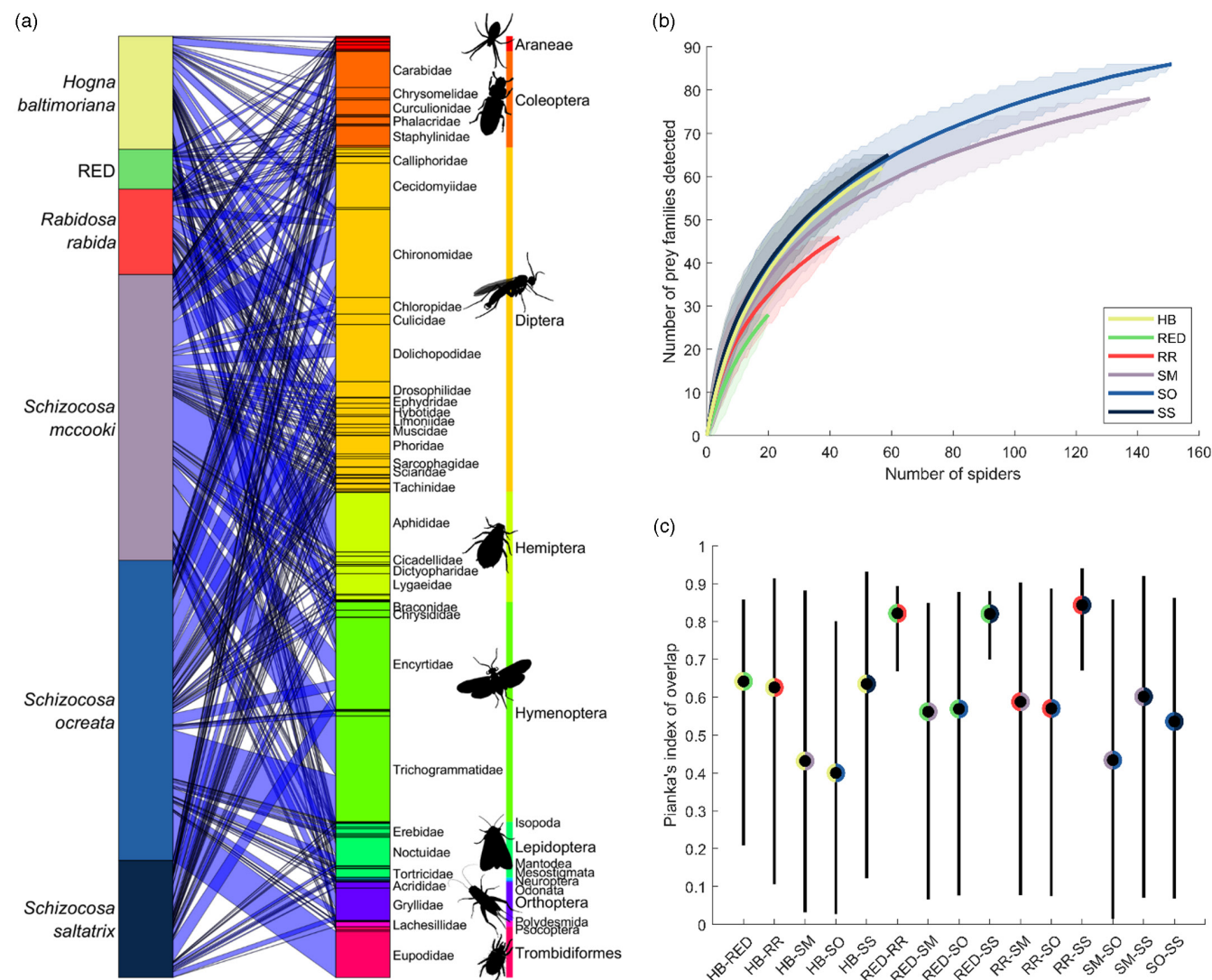
**FIGURE 2** Partial correlation plot for  $\delta^{15}\text{N}$ , arthropod community diversity, and distance to the lake, based on the best supported model.



**FIGURE 3** Fitted  $\delta^{15}\text{N}$  values (from the best supported model) for the six focal species. Filled: individuals, open: medians.

### 3.2 | Metabarcoding

We obtained gut content sequences from 57 *H. baltimoriana*, 20 RED, 43 *R. rabida*, 144 *S. mccooki*, 151 *S. ocreata* and 59 *S. saltatrix* individuals. We detected 122 prey families from 15 orders (Figure 4a). The most detected families were Trichogrammatidae, Encyrtidae, Chironomidae, Aphididae and Dolichopodidae. Detected families included primary consumers (e.g. Aphididae, Eupodidae and Cecidomyiidae), predators (e.g. Dolichopodidae, Carabidae, and Staphylinidae), insect parasitoids (e.g. Trichogrammatidae, Encyrtidae and Braconidae) and spider parasitoids (Acroceridae). The number of families detected depended on the number of spiders sampled (Figure 4b). Mean species diet overlap ranged from 0.40 (*H. baltimoriana*-*S. ocreata*) to 0.84 (*R. rabida*-*S. saltatrix*) (Figure 4c). Diet overlap was not correlated with body mass differences ( $p = 0.178$ ,  $R^2 = 0.01$ ) or body condition differences ( $p = 0.202$ ,  $R^2 = 0.01$ ).



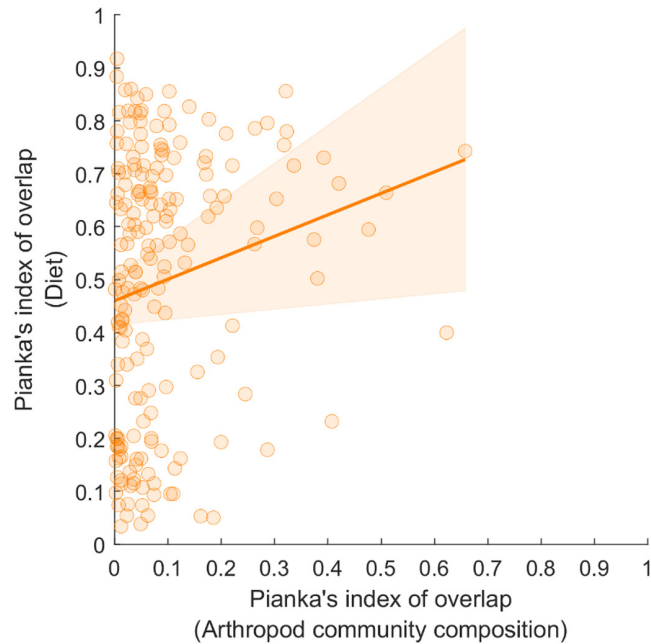
**FIGURE 4** (a) Diet composition, including only non-Lycosid prey. Wolf spider bar height shows number of sampled individuals. Arthropod family bar height shows estimated number consumed, corrected for detectability. Widths of connecting lines show number consumed by each spider species. Names shown for families constituting >0.5% of prey consumed. (b) Mean rarefaction curves and 95% confidence intervals. (c) Pianka's index of niche overlap for species pairs (means and 95% CIs).

When diet overlap was compared across sites, there was no correlation between diet overlap and difference in distance to the lake ( $p = 0.43$ ,  $R^2 = 0.001$ ) and a weak, positive correlation between diet overlap and arthropod community composition overlap ( $p = 0.010$ ,  $R^2 = 0.035$ , Figure 5). There was no correlation between distance to the lake and proportion of aquatic prey in the diet ( $p = 0.082$ ,  $R^2 = 0.10$ ).

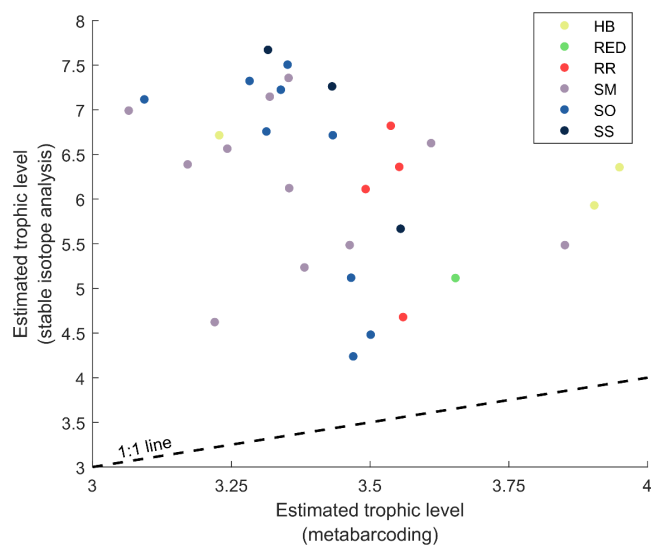
### 3.3 | Comparing trophic levels between metabarcoding and stable isotope analysis

Trophic level estimates were consistently higher from stable isotopes than from metabarcoding. There was a slight negative correlation between the two estimates ( $p = 0.054$ ,  $R^2 = 0.12$ , Figure 6).





**FIGURE 5** Pianka's index of niche overlap between sites plotted against Pianka's index of overlap for arthropod communities at those sites. Regression and 95% confidence intervals shown ( $R^2 = 0.01$ ).



**FIGURE 6** Comparisons of trophic level estimates from metabarcoding and stable isotopes. Each point represents mean values from at least four individuals of the same species at the same site. Points fall above the 1:1 line, suggesting that stable isotope estimates of trophic level are higher than expected from metabarcoding. Thus, predation events that cannot be detected by metabarcoding (cannibalism and intraguild predation) are driving  $\delta^{15}\text{N}$  values. Not all spiders were used for stable isotope analysis, so  $\delta^{15}\text{N}$  means sometimes represent fewer individuals than metabarcoding means.

## 4 | DISCUSSION

The relative importance of two key coexistence mechanisms, interspecific niche partitioning and IGP, remains understudied in

natural systems. In particular, the diets of small predators, such as arthropods, must often be studied using metabarcoding, which has historically been hard to quantify, precluding accurate dietary comparisons (Greenstone et al., 2014). Our study is the first to use DNA detectability half-life corrections to determine diet compositions for a community of foragers, allowing us to assess the prevalence of resource partitioning. By pairing metabarcoding with stable isotopes, we revealed that IGP is an important mechanism supporting coexistence of multiple spider species and that the extent of IGP depends on prey community diversity.

Metabarcoding showed that Cedar Point wolf spiders are generalists with extremely broad diets, even compared to other wolf spiders (Eitzinger et al., 2019; Nentwig, 1986; Wirta et al., 2015). The large number of prey families detected shows that these spiders can access many prey types, suggesting that these spiders have the dietary flexibility to partition resources. Despite this, 12/15 species pairs showed high (>0.5) dietary overlap (Hubbell, 2001), with only the *S. ocreata*-*H. baltimoriana*, *S. ocreata*-*S. mcooki*, and *H. baltimoriana*-*S. mcooki* pairs showing moderate, rather than high, overlap (between 0.4 and 0.5). Similarly, most species had comparable  $\delta^{15}\text{N}$  values. *S. ocreata* was an exception, although an ANOVA of  $\delta^{15}\text{N}$  shows that other sources of  $\delta^{15}\text{N}$  variation cancel out any differences between *S. ocreata* and other species and that all spider species, in practice, overlapped in trophic niche (Figure 1). In addition, most species pairs did not differ in  $\delta^{13}\text{C}$  values (although *S. ocreata* was again slightly different from two species) suggesting that the species' prey assimilate carbon from the same basal sources. This broad overlap in dietary niches as revealed by both metabarcoding and stable isotopes indicates that interspecific dietary niche partitioning is, for the most part, not occurring (Hubbell, 2001; Wirta et al., 2015), although the diet of *S. ocreata* appears somewhat distinct. Increased prey identity resolution (e.g. to species) may uncover hidden dietary differences between spider species (Greene & Jaksic, 1983).

We note that some metabarcoding detections may not reflect direct predation. For example, although we detected insect parasitoids, we cannot distinguish between consumption of free-living parasitoids versus parasitized prey. Similarly, we cannot tell whether detections of spider parasitoids represent predation by or parasitism of wolf spiders. Metabarcoding also cannot account for secondary predation (Hosseini et al., 2008; King et al., 2008): when a focal predator consumes another predator that itself has eaten prey, metabarcoding cannot distinguish that the prey was originally eaten by the second predator, rather than by the focal predator. Given the high trophic levels we observed, we suspect that secondary predation played a role in our metabarcoding dataset.

Our data show that IGP is an important coexistence mechanism in this community (Hypothesis 1). With a  $\delta^{15}\text{N}$  range of nearly 10‰, wolf spider trophic levels in this community ranged from just above herbivores to trophic level 8 (six trophic steps above herbivores), averaging around trophic level 5. Although trophic levels estimated using laboratory trophic enrichment factors may not reflect enrichment processes occurring in the field (Caut et al., 2008; Semenina & Tiunov, 2011), our results are generally in line with ranges of

2–5 trophic levels reported within communities of spiders (Mestre et al., 2013; Sanders et al., 2015; Zuev et al., 2020) and other arthropods (Chahartaghi et al., 2005; Schneider et al., 2004). Trophic estimates from metabarcoding data severely underestimated spiders' trophic position (Figure 6), suggesting that much trophic enrichment is driven by predation that is not detectable via metabarcoding (i.e. wolf spiders consuming other wolf spiders). We conclude that IGP is the driver of  $\delta^{15}\text{N}$  enrichment. Given the considerable risk of IGP faced by these wolf spiders, we further suggest that predator interference may act as an additional coexistence mechanism in this community (Amarasekare, 2002; Schmidt et al., 2014).

Because spider species identity did not underlie dietary differences, there remains an enormous amount of unexplained variation: broad confidence intervals on dietary overlap indices suggest that estimates of interspecific niche overlap—and therefore estimates of species diet composition—depend strongly on which individuals were randomly selected during bootstrapping. Similarly, individual  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values differed greatly. Individual variation is a hallmark of intraspecific competition, which tends to maintain intraspecific variation (Araújo et al., 2011; Cloyd & Eason, 2017; Roughgarden, 1972; Svanbäck & Bolnick, 2007). There is growing interest in assessing the ability of intraspecific competition to explain diet structure in generalist predators (Kim, Tinker, et al., 2012; Rossman et al., 2015; Smith & Skulason, 1996). However, dietary “snapshots” obtained from metabarcoding do not necessarily reflect the long-term foraging differences described by intraspecific niche partitioning. Because stable isotopes, which reflect diets over longer time spans than metabarcoding (Kim, Tinker, et al., 2012; Mestre et al., 2013), also showed extensive intraspecific variation in both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , we suggest that sustained intraspecific niche partitioning occurs in this community. Such individual variation may further support coexistence by muddling competitive differences between species or increasing capacity for resource partitioning (Hart et al., 2016; Hausch et al., 2018).

We examined how sex, body condition and mass may structure diet and explain individual foraging variation (Hypothesis 2). Body condition can indicate energetic state (Anderson, 1974; Uiterwaal & DeLong, 2019), but also may reflect structural differences in morphology. Although both energetic state and morphological structure can influence foraging (DeLong et al., 2021; Lyon et al., 2018; Samu et al., 1999), body condition did not explain individual variation in trophic level or diet composition across species in our study (Table S2). Body mass similarly influences foraging performance (Cuthbert et al., 2020; Rall et al., 2012; Uiterwaal et al., 2017; Uiterwaal & DeLong, 2020a; Vucic-Pestic et al., 2010). Larger predators are expected to have higher trophic levels (Riede et al., 2011) and access to larger prey, potentially broadening their resource pool (Costa, 2009) and imparting an IGP advantage (Rypstra & Samu, 2005; Samu et al., 1999). Despite this, we found no evidence that spiders more similar in body mass had more similar diets, nor did we find any effect of body size on trophic level (Klarner et al., 2013). Foraging also may differ by sex and stage (Coblentz et al., 2022; Walker & Rypstra, 2001), but we saw no effects of sex on individual trophic

level (Table S2). Thus, the limited explanatory ability of individual identity and morphological variation, surprising in light of laboratory work experiments, suggests that foraging variation is decoupled from morphology in this community (Araújo et al., 2009; Ingram et al., 2011; Zuev et al., 2020).

We tested whether a spider's surroundings, such as the composition of the resource pool or environmental conditions, may explain diet variation (Hypothesis 2). In theoretical and experimental work, resource availability strongly influences both the number of prey taxa consumed and the relative proportions of prey in the diet (Chan et al., 2017; Charnov, 1976; Holling, 1959; Kalinkat et al., 2011). Similarly, environmental conditions such as temperature, humidity, and habitat complexity often affect foraging (Contreras et al., 2013; DeLong & Uiterwaal, 2022; Englund et al., 2011; Hoddle, 2003; Uiterwaal & DeLong, 2018, 2020a). Yet studies of dietary generalists in nature suggest that predators broadly maintain foraging characteristics (e.g. foraging rates, diet composition) despite variation in prey availability and environmental conditions (Eitzinger et al., 2019; Smout et al., 2013). We show that diet similarity between spiders from different sites is extremely variable, with Pianka's overlap indices ranging from nearly 0 to 0.9 between sites (Figure 5). Distance to the lake, representing a putative environmental gradient (moisture, plant community) was unrelated to diet composition. Arthropod community composition did explain some diet variation, suggesting that spiders in more similar communities have more similar diets (Figure 5), although an  $R^2$  of 0.01 indicated that most variation remains unexplained.

Trophic level variation, on the other hand, was related to both community composition and distance to the lake. Our results show reduced  $\delta^{15}\text{N}$  values for spiders collected at sites with more diverse prey communities, although this was mitigated by increased distance to the lake (Figure 2). This effect of lake distance could potentially be explained by an aquatic subsidy, whereby food webs closer to lakes are systematically enriched in  $\delta^{15}\text{N}$  as aquatic prey becomes more common in the diet. However, our metabarcoding data reveals no correlation between the distance from the lake at which a spider was collected and the proportion of its diet comprising aquatic prey families, so the variation in  $\delta^{15}\text{N}$  is more likely due to differences in the extent of IGP rather than differences in allochthonous prey consumption. Thus, our results show that wolf spiders are driven to higher trophic levels in the absence of a diverse prey pool, suggesting that individuals are more likely to engage in IGP when resource niches are limited. This result supports the conclusion that, when decreased resource diversity hinders niche partitioning ability by forcing consumers to rely on a shared resource pool, IGP can nonetheless allow several predator species to occur.

Our study reveals that, after accounting for differences in prey detectability, diet composition is largely similar across spider species in this community, with multiple species relying on the same prey families. The high trophic levels and minimal evidence of interspecific niche partitioning indicate that IGP likely acts as a primary mechanism for reducing competition among these spiders. We further show that morphology does not explain variation in dietary

niche or the extent to which IGP occurs. Environmental conditions similarly explained little dietary variation, highlighting a growing need to understand how determinants of predator–prey interaction strengths can explain diet composition. In contrast, resource community structure—mitigated by the effects of environmental conditions—underlies the extent to which individuals engage in IGP. Thus, although individual and species-level diet composition is hard to predict from individual identity, morphology, environmental conditions, and prey community, limited niche availability can increase IGP, supporting a community of ecologically similar predators. Our results underscore that diet composition is more complex than laboratory work might suggest, and much work is needed to understand the mechanisms underlying diet composition and how these mechanisms allow predators to persist.

## AUTHOR CONTRIBUTIONS

Stella F. Uiterwaal and John P. DeLong conceptualized the study, Stella F. Uiterwaal and Amber J. Squires collected arthropods and processed spiders, Bennett A. Grappone identified prey arthropods, Stella F. Uiterwaal and Brian Dillard conducted bioinformatics analyses, Ariadne Castaneda and Sora L. Kim performed stable isotope analyses, Stella F. Uiterwaal and John P. DeLong analysed data, Stella F. Uiterwaal wrote the first draft. All authors contributed to the final version.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.n02v6wx1w> (Uiterwaal et al., 2023).

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## SUPPORTING INFORMATION

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

**Figure S1.** Half-life and  $k$  estimates from (Uiterwaal and DeLong, 2020), showing the improved ability of the power function to capture the more negative value of  $k$  for short half-lives.

**Table S1.** Comparison of the 10 best supported models for  $\delta^{15}\text{N}$ . Lake = distance to the lake (m). Cond = body condition. DivResids = residuals from a regression of arthropod diversity against distance to the lake. LL = Log likelihood.

**Table S2.** Results for the best supported model for  $\delta^{15}\text{N}$ .

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