Negative intraguild interactions drive niche variation in arthropod predators

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With 4 figures and 1 table

Abstract: The niche variation hypothesis states that the population niche width expands with increasing interindividual differences in prey utilization (i.e., individual dietary specialization). The main ecological drivers forming this relationship include a) ecological opportunity, b) food limitation and exploitative competition, and c) intraguild interference. Only a limited number of empirical studies have tested the impact of these drivers on the niche variation–width relationship and focused only on vertebrates. Using molecular gut content analysis, we investigated how prey diversity (proxy for ecological opportunity), prey abundance (proxy for exploitative competition / food-limitation), and activity density of guild members (proxy for intraguild interference) affect the short-term individual dietary specialization and consequently the population niche width in local communities of 13 species of predatory beetles and spiders. The study took place in 10 spring barley fields in Sweden in 2011. We found that the niche variation and consequently the average population niche width of the species in the predator community decreased with prey abundance but increased with activity density of guild members. The results indicate that intraguild interference and exploitative competition / food limitation increased dietary variation. The increased diet variation led to the observed population diet expansion. Our results support the niche variation hypothesis and, in contrast to the traditional view, show that negative intraguild interactions may act as a diversifying force.

Keywords: Araneae; Carabidae; Coccinellidae; ecological opportunity; individual specialization

1   Introduction

Individual dietary specialization means that individuals utilize only a subset of prey utilized by their population (Bolnick et al. 2003) and it occurs across animal taxa (Bolnick et al. 2003; Traugott et al. 2008; Ingram et al. 2018). Individual dietary specialization has a key role in trophic niche dynamics, species coexistence, and interactions in food-webs (Bolnick et al. 2011; Ingram et al. 2018). Among the main drivers of individual dietary specialization (hereafter termed individual specialization) are a) ecological opportunity (i.e., access to diverse prey resources), b) food limitation and exploitative competition, and c) intraguild interference (Araújo et al. 2011). These drivers may affect the trophic niche structure in various ways (Sjödin et al. 2018) depending on a population's general environment (Evangelista et al. 2014) and intensity of antagonistic interaction (Svanbäck & Bolnick 2005; Jones & Post 2016). Previous studies assess-

ing the main ecological drivers of individual specialization have focused primarily on vertebrates and are mostly limited to a single species (reviewed in Araújo et al. 2011 and Ingram et al. 2018). Therefore, it is crucial to study impact of ecological interactions on species' trophic niches in taxa beyond vertebrates in a multi-species context to allow for broader generalization.

Population niches comprise within-individual component (WIC; i.e., average variance of resources utilized by individuals) and between-individual component (BIC; i.e., variance among individuals) (Bolnick et al. 2003; Fig. 1a); both components can change the niche structure independently or simultaneously (Sjödin et al. 2018; Fig. 1b). The niche variation hypothesis postulates that populations with wider niches are also more heterogeneous as individuals occupy different niches (Bolnick et al. 2007; Fig. 1B). Such relationships can develop due to an increased diversity of available prey, i.e., due to ecological opportunity (e.g., Araújo et al.
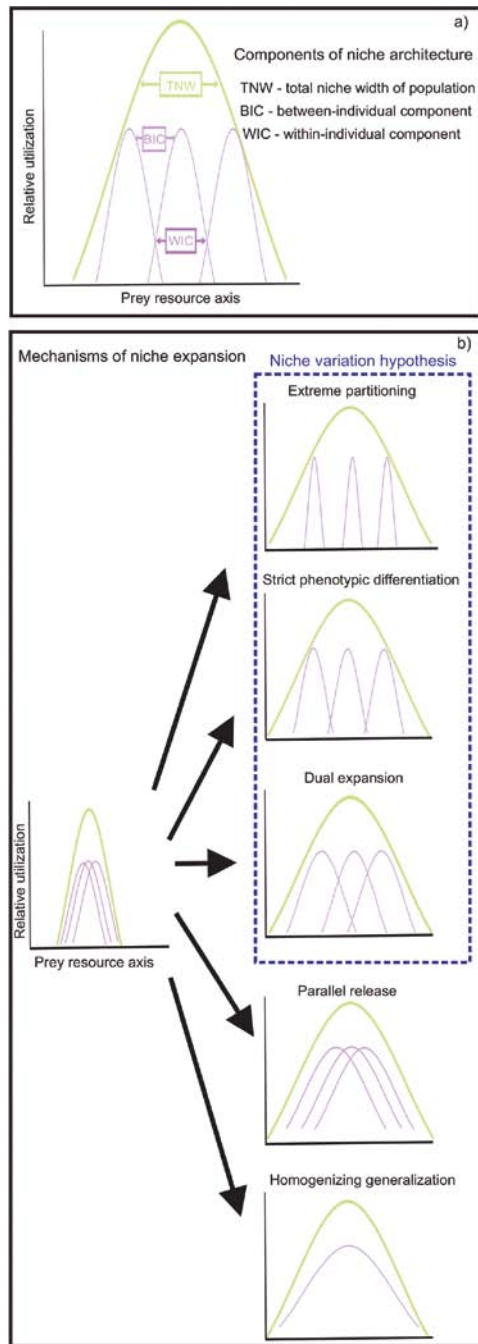
Fig. 1. Conceptual figure of **(A)** components forming niche structure (Bolnick et al. 2003) and **(B)** mechanisms of niche width expansion according to Sjödin et al. (2018). In both panels, the green and purple arcs indicate population and individual niches, respectively. The position of the arcs' humps indicates the position on the niche axis and the width of the arcs represents niche width. Population niche width may expand when WIC decreases while BIC increases (extreme partitioning), WIC remains similar but BIC increases (strict phenotypic differentiation), WIC and BIC increase (dual expansion), BIC remains similar but WIC increases (parallel release), and BIC decreases but WIC increases (homogenizing generalisation). Extreme partitioning, strict phenotypic differentiation, and dual expansion are parts of the niche variation hypothesis (the rectangle delimited by the blue dashed line) that postulates that populations with wider niches are also more heterogeneous.

2011). Increased prey diversity enables individuals within a predator population to specialise on certain prey types by exploiting them more efficiently than other individuals due to interindividual differences in cognitive, physiological, or morphological traits (Bolnick et al. 2003). Consequently, the total population niche width (TNW) expands with increasing diversity of available prey through increasing BIC, which may be accompanied by a decrease (i.e., extreme partitioning), no change (i.e., strict phenotypic differentiation), or an increase in WIC (i.e., dual expansion; Sjödin et al. 2018; Fig. 1B). However, the population niche can also respond to ecological opportunity differently than predicted by the niche variation hypothesis. For example, the population niche may expand with expanding WIC while the BIC remains similar (i.e., parallel release) or decreases (i.e., homogenizing generalization; Sjödin et al. 2018; Fig. 1B).

The traditional assumptions are that intraspecific competition increases niche variation and expands population niche width, while interspecific competition and predation have the opposite effects (Polechová & Storch 2008). However, it has recently been shown that resource limitation, competition (intra- and interspecific), and intraguild predation may have more diverse effects on niche structure, including niche constriction and expansion through various mechanisms (Svanbäck & Bolnick 2005; Bolnick et al. 2010; Jones & Post 2016; Sjödin et al. 2018). Intraguild predation drives some individuals to seek refuge in microhabitats that host different prey and results in population niche expansion due to increasing BIC (Bolnick et al. 2010). Alternatively, the population niche could expand from increasing WIC, i.e., through parallel release or homogenizing generalization, when individuals are food-limited due to factors such as exploitative competition (inter- and intraspecific) and may utilize sub-optimal resources (Svänback & Bolnick 2005; Bolnick et al. 2010).

Effects of the ecological forces driving individual specialization and niche dynamics depend on the total environment; therefore, it is likely that the effect will differ between ecosystems (Evangelista et al. 2014; Costa-Pereira et al. 2019; Liang et al. 2020). Most studies have focused on how competition, predation, and ecological opportunity affect individual specialization of vertebrates in natural habitats (Ingram et al. 2018). Arthropods, the most diverse animal group, and agroecosystems, which cover 38% of the global surface (FAO 2021), have so far been neglected in this area of research. From an applied perspective, the structure of trophic niches may influence the importance of generalist consumers as a biological control of pests (Michalko & Pekár 2017; Michalko et al. 2021a) or the choice of control strategies for generalist herbivorous pests (Traugott et al. 2008).

The present study directly addresses these important gaps of knowledge. We investigated how ecological opportunity, exploitative competition / food limitation, and intraguild interference (including predation and non-consumptive

effects) affect individual specialization and the consequent population niche width in local communities of 13 species of arthropod predators (predatory beetles, spiders) in spring barley fields under organic and conventional management. We expected i] according to the ecological opportunity hypothesis, niche variation and total niche width of predators to increase with the diversity of available prey (Araújo et al. 2011). We also predicted that ii] according to the intraguild interference hypothesis, niche variation and the total population niche width would increase with increasing density of guild members as, for example, individuals vulnerable to predation seek refuge in microhabitats with distinct prey composition (Bolnick et al. 2010; Sitvarin & Rypstra 2014). We then expected iii] according to the food limitation and exploitative competition hypothesis, low prey abundance to expand individual niches as individuals become more opportunistic and include sub-optimal resources (Michalko et al. 2021a). This may consequently either narrow, widen, or retain the population niche width (Svanbäck & Bolnick 2005).

2   Material and methods

2.1   Data collection

2.1.1   Molecular gut-content analyses
All data came from previously published studies (Roubinet et al. 2017, 2018), where a detailed description of the methods can be found, and we only provide the necessary details here. The data were collected in 10 spring barley fields around the city of Uppsala in Sweden in 2011. The fields were paired in five blocks with one field under conventional management and the other field under organic management. The differences between the management types lied mainly in application of herbicides and inorganic fertilizers in fields under conventional management. Application of insecticides in the conventional fields was low. The data were collected in each field during two periods of barley growth: early period (barley tillering stage, 22–23 week) and late period (barley stem extension/heading stage, 25–26 week).

For the molecular gut-content analyses the spider and beetle predators (see the subsection '*Predator groups*' in the section 2.2. Computation of individual specialization and total niche width below) were collected using dry pit-fall traps (Roubinet et al. 2017). In each field, 12–35 traps (number depending on predator abundances) were opened for 24 h within each week (Period 1: weeks 22 and 23; Period 2: weeks 25 and 26) of the two time periods (see above). There was no rainfall during the 24 h periods. All arthropod predators were collected individually and to reduce potential predation within traps, clay balls were put into the traps. Prey remains in visually inspected traps were found in only 4% of the emptied traps, suggesting that within trap predation was minor. The molecular gut content analyses provided presence-absence data for the DNA of each prey type in each predator individual. The samples from the two weeks within each period were then pooled into one sample for further analyses, i.e. population-level information was taken per two-week period.

The diagnostic multiplex PCR approach was used to detect the prey. A first group-specific multiplex PCR assay (MPI) targeted aphids, dipterans, springtails, earthworms, lacewings, spiders, beetles, and thrips as prey groups. Two following additional assays enabled lower taxonomic resolution for spiders: Lycosidae, Linyphiidae, *Pachygnatha*; and for beetles: *Pterostichus, Poecilus, Harpalus, Bembidion, Coccinella septempunctata* (Linnaeus 1758).

2.1.2   Ecological drivers of niche variation
Following previous studies, we used proxies for the intensity of interactions (e.g., Costa-Pereira et al. 2019). The total activity density of local ground-dwelling predators was used as a proxy for intraguild interference that may include predation as well as non-consumptive effects. We used overall prey abundance as a proxy for exploitative competition / food-limitation; prey diversity measured by the Shannon index (Krebs 2014) was used as a proxy of ecological opportunity (Costa-Pereira et al. 2019; Sánchez-Hernández et al. 2021).

The activity densities of predators were investigated each week during the early and late periods. The ground-dwelling predators were collected by six pitfall traps per field (11.5 cm diameter × 11 cm depth). Traps were emptied weekly. Activity densities of spiders and carabid beetles were summed for further analyses (i.e. number of individuals / 6 pitfall traps).

Abundances of prey in each field were investigated during the growing season using tiller counts (aphids on 100 tillers/week during each period, from 10 spatially clustered batches of 10 tillers), soil samples (springtails, earthworms, and thrips in 10 soil samples of 5 cm diameter × 10 cm depth once in each period; extracted into ethanol via a Tullgren funnel over 48 hours), and sweeping (Diptera, in 100 sweeps with sweep nets of 35 cm diameter × 80 cm shaft length) weekly during each period. Prey densities per sampling unit were averaged per week in the early and late periods for each field. Prey densities were estimated on the same day within field pairs, and within a maximum of four days among field pairs.

2.2   Computation of individual specialization and total niche width

2.2.1   Individual specialization
We distinguished eight prey types to compute the individual specialization and the population niche width of predators: earthworms, spiders, springtails, thrips, aphids, neuropterans, beetles, and dipterans (Roubinet et al. 2017). These prey groups are the major prey of the studied predator species

and are highly abundant in cereal crops (e.g., Sunderland 1975; Cuff et al. 2022). We computed the V-index that is commonly used to quantify the individual specialization (Bolnick et al. 2003). The V-index is the mean Bray-Curtis distance between the trophic niche of each individual and its population (Bolnick et al. 2003). We used Bray-Curtis distance because the population niche was quantitative and because beetle and spider prey could reach values from 0 to 4 instead of 0–1 as beetle and spider prey groups were clumped from a higher taxonomic resolution (see the sub-section *Molecular gut-content analyses* in the section 2.1. Data collection, Fig. S2, and Roubinet et al. 2017). However, there was only 6% of predator individuals where value of these prey groups was higher than 1 (Fig. S2). When computing the distance between an individual and its population, we included the diet of that individual into the population diet and the index can therefore reach values from the half-open interval [0,1]. The degree of individual specialization increases with the V-index value (Bolnick et al. 2003). Given the character of the data, the index value expresses a probability that any two individuals from a population differ in their recent prey choice.

To investigate the mechanism behind the relationship between niche variation and total niche width (Sjödin et al. 2018), we also computed the WIC and BIC for each population. WIC is mean number of prey per individual and BIC is simply the variance of the number of prey types per individual.

2.2.2   Population niche width
The measure of the population niche width was computed using the Levin's standardized niche width (Levin's B) that accounts for the proportion of predators that fed on a certain prey type in each population. Levin's B can reach values between 0 and 1; the higher the value, the wider the niche (Krebs 2014).

2.2.3   Predator groups
For the computation of individual specialization and total niche width, we considered predator populations as individuals from a predator group (see later for the definition of predator group) collected in a field and in a period. We included the populations where prey was detected in at least eight individuals, indicating that a population might theoretically individually specialize on each prey type equally. According to data availability, we considered the following 15 predator groups of spiders and predatory beetles (Table 1). Individual specialization is defined as niche variation that is not attributed to differences in sex, age, and discrete morphs (Bolnick et al. 2003). We therefore separated the adult males and females in spiders and treated them as separate groups in the analyses because they could show distinct prey preferences and optimization criteria influencing prey selection.

Table 1. The list of predator groups used to compute individual specialization.

Predator groups	Family
Adult males *Agyneta rurestris* C. L. Koch, 1836	Linyphiidae
Adult males *Oedothorax apicatus* Blackwall, 1850	Linyphiidae
Adult females *O. apicatus*	Linyphiidae
Adult males *Pardosa lugubris* Walckenaer, 1802	Lycosidae
Adult females *P. lugubris*	Lycosidae
Subadult *Trochosa* sp.	Lycosidae
Coccinella septempunctata	Coccinellidae
Bembidion lampros Herbst, 1784	Carabidae
Bembidion quadrimaculatus Linnaeus, 1761	Carabidae
Harpalus rufipes Degeer, 1774	Carabidae
Poecilus cupreus Linnaeus, 1758	Carabidae
Poecilus versicolor Sturm, 1824	Carabidae
Pterostichus melanarius Illiger, 1798	Carabidae
Pterostichus niger Schaller, 1783	Carabidae
Trechus secalis Paykull, 1790	Carabidae

2.3   Statistical analyses
All analyses were performed within the R environment (R Development Team 2021, ver. 4.0.4). We used the generalized mixed effects models (GLMM) from the R package 'mgcv' (Wood 2017) to investigate 1) the effect of activity density of guild members, prey diversity, and prey abundance on individual specialization. We then tested 2) how the variables that affected individual specialization affected the population total niche width. We also used GLMM to 3) test the niche variation hypothesis.

2.3.1   Drivers of individual specialization
We used GLMM with gamma error structure (GLMM-g) and inverse link function to investigate how activity density of guild members, prey diversity, and prey abundance affect the individual specialization since the values of the indices were continuous and heteroscedastic (Zuur et al. 2015). We also inversely transformed the activity density of guild members to account for the asymptotic trend in the data (Appendix S2).

In all analyses, we first determined the correct structure of the random effects (Zuur et al. 2015; Appendix S2) that were represented by predator group, locality, and field. The crossed random effects in the final models differed among the models (Appendix S2).

Initially, we considered management, period, prey diversity (Shannon index of diversity), prey abundance, and predator activity density as the additive fixed effects. However, we excluded the variable 'period' from all analyses because it defined the prey abundance (LME, $P < 0.001$) and consequently there was high collinearity among variables (vari-

ance inflation factor = 3.3). After exclusion of the variable 'period,' the collinearity among the fixed effects was at an acceptable level (variance inflation factor < 2.4; Zuur et al. 2015). There still might be a possibility that the predator density and prey density / diversity would be interrelated but the pairwise correlation across fields was weak (Spearman $\rho < -0.13$). We included management among fixed effects to account for a possible influence on individual specialization as exposure to agrochemicals can alter prey preferences (Petcharad et al. 2018).

As the samples were of different quality by means of the number of screened individuals per population in the molecular gut-content analysis, we weighted each sample by the number of screened individuals. The final model was selected by backward selection and the rule of marginality (Zuur et al. 2015).

As top predators and mesopredators can be distinguished in the predator community (Roubinet et al. 2017), we also run the analyses separately for top predators and mesopredators to see whether they may respond differently. We used only the final model selected when analysed together. We distinguished the top predators and mesopredators based on their body sizes (Rypstra & Samu 2005) and trophic niche (Roubinet et al. 2017, 2018). The top predators (maximum body size > 12 mm) were *H. rufipes, Poecilus* spp., *Pterostichus* spp., and *Trochosa*. The mesopredators were (maximum body size < 12 mm): *A. rurestris, Bembidion* spp., *C. septempunctata, O. apicatus, P. lugubris*, and *T. secalis*. The results are presented in the supplementary material (see Appendix S1 in Supporting Information).

2.3.2 Drivers of population niche width

We investigated how the variables that affected individual specialization in previous analyses (see the above section *Drivers of individual specialization*) affected the population niche width. We used GLMM-g with identity link function for the population niche width measured by Levin's B as the index values are continuous and heteroscedastic (Zuur et al. 2015).

2.3.3 Niche variation hypothesis

We investigated the relationship between individual specialization and population niche width to test the niche variation hypothesis' assertion that more generalized populations are also more heterogeneous (Bolnick et al. 2007). We then investigated the relationship between BIC and WIC to test the mechanism of niche expansion (Sjödin et al. 2018). We tested the relationship between population total niche width and the V-index as well as the relationship between WIC and BIC by GLMM-g and with identity link function as the data were continuous but non-normally distributed (Zuur et al. 2015). Since gamma distribution is defined only for positive values, we added the lowest non-zero value (0.066) to the BIC that acted as the response variable.

3 Results

3.1 Drivers of individual specialization

The management type (GLMM-g, $F_1 = 0.06$, P = 0.814) had no significant effect on the individual specialization. The diversity of potential prey, a proxy for ecological opportunity, did not affect the individual specialization (GLMM-g, $F_1 = 1.04$, P = 0.311). The individual specialization increased with activity density of guild members as a proxy for intraguild interference (GLMM-g, $F_1 = 15.14$, P < 0.001; Fig. 2a). In line with our third hypothesis individual specialization decreased with increasing prey abundance as a proxy for food limitation and exploitative competition (GLMM-g, $F_1 = 10.82$, P = 0.001; Fig 2b). The model explained moderate variability ($R^2_{adj} = 0.44$).

Individual specialization in the mesopredators and the top predators showed similar patterns. Individual specialization of both increased with activity density of guild members but only individual specialization of mesopredators decreased with increasing prey abundance (Appendix S1).

3.2 Drivers of population niche width

The population total niche width was not significantly influenced by activity density of guild members (GLMM-g, $F_1 = 0.14$, P = 0.708). The total niche width decreased with increasing prey abundance (GLMM-g, $F_1 = 6.98$, P = 0.001, $R^2_{adj} = 0.19$; Fig. 3).

3.3 Test of the niche variation hypothesis

The population niche increased with individual specialization (GLMM-g, $F_1 = 31.31$, P < 0.001, $R^2_{adj} = 0.15$; Fig. 4a). The BIC component increased with the WIC component (GLM-g, $F_1 = 657.1$, P < 0.001, $R^2_{adj} = 0.68$; Fig. 4b).

4 Discussion

We studied how activity density of guild members (a proxy for intraguild interference), prey diversity (a proxy of ecological opportunity), and prey abundance (a proxy for exploitative competition and food-limitation) affect individual specialization and niche expansion in a community of 13 species of arthropod generalist predators from organically or conventionally managed barley fields. We did not find support for our first hypothesis about the ecological opportunity expecting increasing niche variation and population niche width with increasing diversity of prey. In accordance with our second hypothesis, we found that individual specialization was higher in populations with stronger intraguild interference. Nevertheless, we did not find the impact of intraguild interference on total population niche width. In accordance with our third hypothesis about the food limitation / exploitative competition, we found that individual specialization and population total niche width were higher
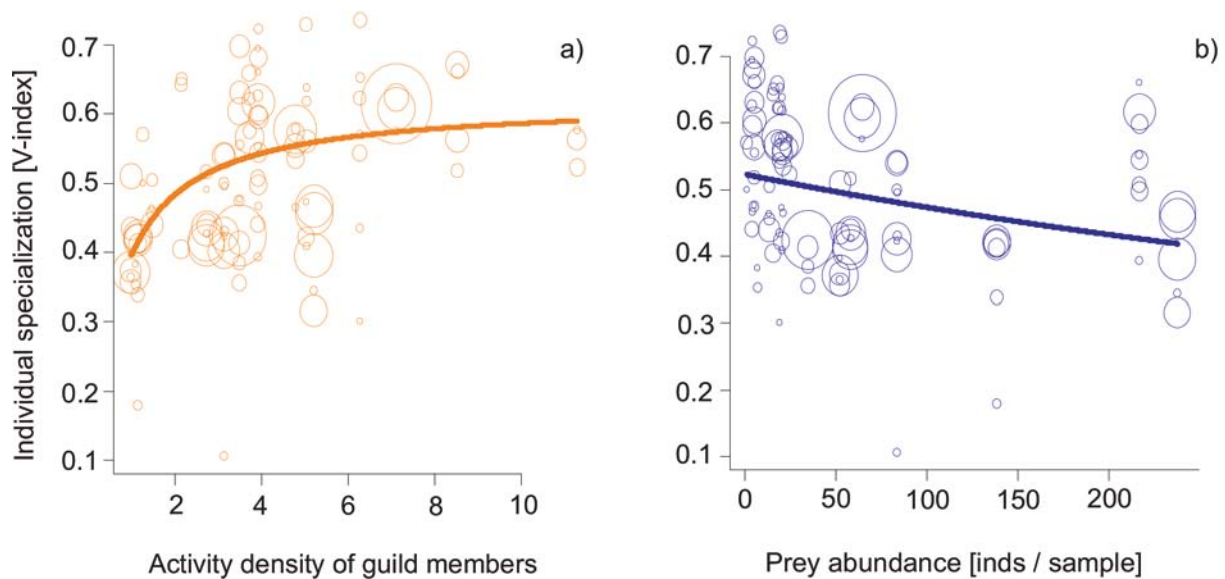
Fig. 2. The partial graphs showing the factors driving the individual specialisation in local communities of 13 species of generalist predators in cereal crops. The ecological factors that drive the individual specialisation are activity density of guild members (predatory beetles, spiders) **(a)** and prey abundance **(b)**. The thick lines are the estimated relationships and the points are individual predator populations. The size of points corresponds with their weights in the analyses.
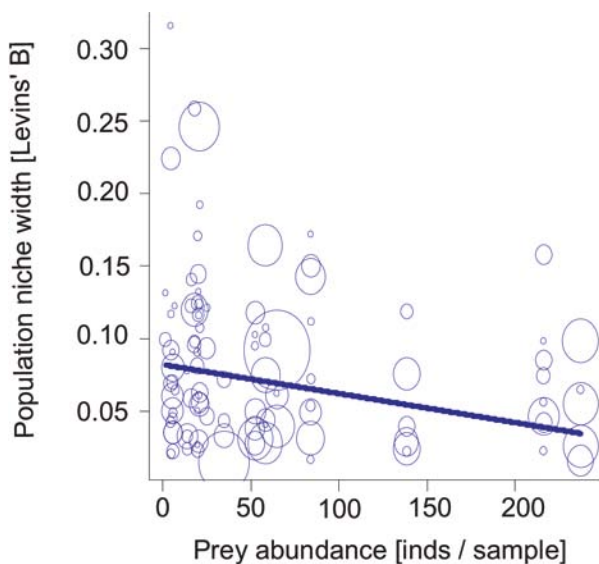

Fig. 3. The effect of prey abundance on the population niche width of generalist predators. The thick line is the estimated relationship, and the points are individual predator populations. The size of points corresponds with their weights in the analyses.

in populations with lower prey abundance. The results therefore suggest that intensified intraguild interactions, intraguild interference, and exploitative competition / food-limitation increased individual specialization in the local predator populations, which consequently resulted in niche expansions. The population niches expanded due to the dual expansion of the between- and within-individual components.

4.1 Population niche width of predators expanded with niche variation according to the dual expansion scenario

Niche width expanded with increasing niche variation so these results support the niche variation hypothesis. The support of the niche variation hypothesis was observed also in other studies on vertebrates (Bolnick et al. 2007; Sjödin et al. 2018). In our study, BIC and WIC showed a strong positive relationship, which consequently resulted in population niche expansion. This corresponds with the dual expansion scenario (Sjödin et al. 2018), as recently observed in bird and frog communities (Liang et al. 2020). However, according to a review of 15 vertebrate species and an evolutionary model, Sjödin et al. (2018) concluded that the dual expansion scenario is unlikely because the simultaneous expansion of BIC and WIC is mutually exclusive when there are costs to individual generalization. The discrepancies between this conclusion and our results may be explained by the fact that the evolutionary model was based solely on the energy limitation and fitness costs imposed on individual generalization (Sjödin et al. 2018). In contrast, most arthropod generalist predators are nutrition- rather than energy-limited (Toft et al. 2019) and they require a certain composition of nutrition (Jensen et al. 2012). Therefore, they include prey species with distinct nutritional composition to balance the nutritional intake (Toft & Wise 1999; Michalko et al. 2021b) as a single prey species rarely contains an optimal nutritional composition (Toft & Wise 1999). Hence, there are fitness costs connected not only to individual generalization but also to specialization in generalist predator species (Toft & Wise 1999; Michalko et al. 2021b). Further evolutionary models
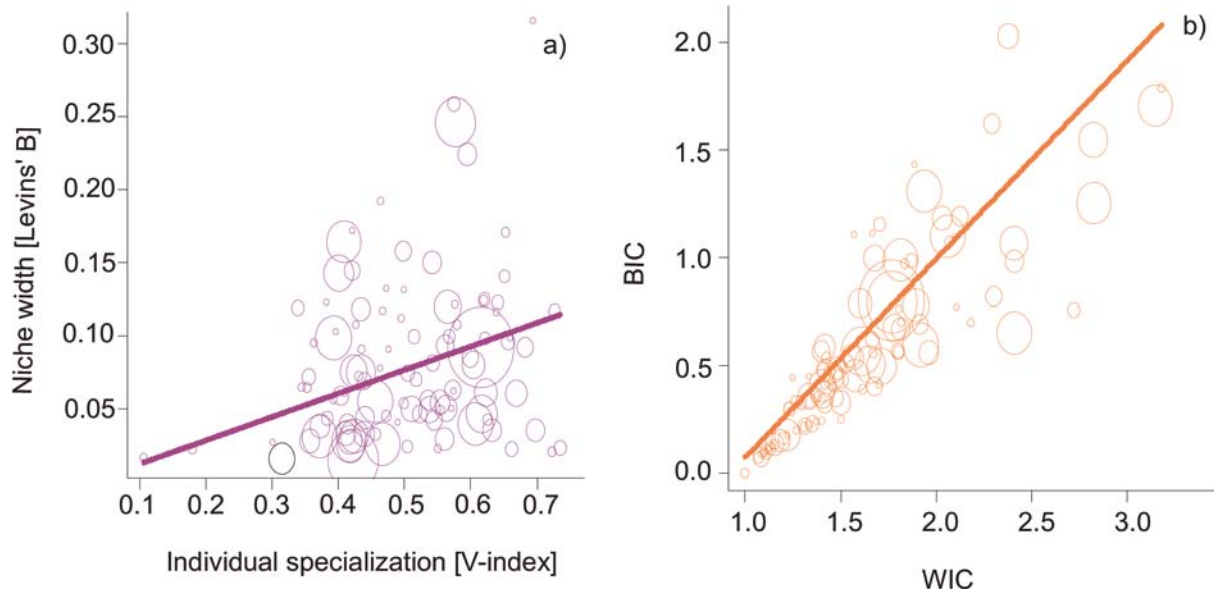
Fig. 4. Test of the niche variation hypothesis. The relationship between individual specialisation and the population total niche width **(a)** and the relationship between within-individual component (WIC, mean number of prey types per individual) and between-individual component (BIC, variance in the mean number of prey types per individual) **(b)**. The thick lines are the estimated relationships and the points are individual predator populations. The size of points corresponds with their weights in the analyses.

that include fitness costs also for individual specialists may find types of niche expansions that have been considered unlikely by the model in Sjödin et al. (2018).

4.2 Intensifying intraguild interactions increase individual specialization and expand population trophic niche

4.2.1 Intraguild interference increases individual specialization

The activity density of guild members increased individual specialization. Our results agree with previous studies on philodromid spiders (Michalko & Pekár 2014), sticklebacks (Bolnick et al. 2010), and frogs (Costa-Pereira et al. 2019) that showed that intensifying intraguild predation heterogenized population niches.

The overall activity density of predators is a rather broad proxy of intraguild interference as it includes consumptive and non-consumptive interactions with various degrees of asymmetry in pair-wise interactions (Roubinet et al. 2017) and community-level effects (i.e., multiple-predator effect; Sitvarin & Rypstra 2014). We aim to disentangle these complex interactions by further study. The individual specialization of mesopredators and top predators responded similarly to the activity densities of guild members. Mesopredator individuals in a population often differ in exposure to predation risk (Toscano et al. 2016), responsiveness to a predation-risk (Steinhoff et al. 2020), and vulnerability (Rypstra & Samu 2005) resulting in higher individual specialization (Toscano et al. 2016). Responsive and vulnerable mesopredator indi-

viduals may change microhabitats (e.g., by climbing from the ground onto vegetation or by seeking more complex vegetation; Sitvarin & Rypstra 2014) or may alter their activity patterns and hunting strategy. Changes in microhabitat use and hunting strategy might then result in dietary changes and trophic niche separation between responsive and non-responsive individuals (Toscano et al. 2016).

The individual specialization in top-predator populations might arise from mesopredators becoming more available as prey for top-predators (Roubinet et al. 2017). Individual top-predators often differ in their willingness to capture dangerous mesopredator prey that can seriously harm or kill them (Michalko & Pekár 2017). Therefore, only some individual top-predators might expand their niches by incorporating mesopredators into their diet. The intensifying intraguild interference might therefore reinforce the individual specialization through inter-individual differences in an anti-predator response of mesopredators and different prey preferences among top-predator individuals.

4.2.2 Exploitative competition and food-limitation increase individual specialization and population niche width

Individual specialization and population niche width decreased with increasing prey abundance. Prey diversity had no significant effect on individual specialization. This contrasts with previous studies showing that niche variation and width increase with ecological opportunity (Evangelista et al. 2014; Sánchez-Hernández et al. 2021). Instead, our results correspond with the studies showing that exploita-

tion and food limitation increase niche variation and width (Svanbäck & Bolnick 2005).

The increasing inter-individual differences (i.e., BIC) occurred as some individuals incorporated more prey types than other individuals. The pattern is similar to that of a philodromid spider species where individuals from prey-rich patches in an apple orchard have their trophic niches nested in the niches of individuals from prey-poor patches (Michalko & Dvoryankina 2019). Therefore, the results correspond with the optimal foraging theory that generalist predators are selective and primarily utilize high-quality prey or few complementary prey if they are not prey-limited. But if generalist predators are prey-limited they become opportunistic and hunt also sub-optimal prey (Stephens et al. 2008).

Management of the barley fields had no significant effect on individual specialisation. The nonsignificant effect of management in this study might result from the fact that the conventional management used in our studied barley fields was not typical because the usage of insecticides was low.

4.3 Study limitations
Our approach does not allow precise quantification of individual specialization and we could miss some important details lying in proportional changes of utilized prey. However, our approach still enables inter-population comparisons based on the presence or absence of major prey types utilized by the predator species. Our approach basically expresses a probability that any two individuals from a population differ in their very recent prey choice and we expect that the probability is higher in populations where the utilization of prey resources is more heterogeneous. Another limitation is that we investigated the presence of only eight prey groups and we might miss niche expansion towards other prey. The eight groups, however, represent the major prey of the studied predators and are highly abundant in cereal crops (Sunderland 1975; Cuff et al. 2022). These prey groups also differ in major traits such as body size, defensiveness, dangerousness and nutritional content that drive prey choice in generalist predators (Michalko et al. 2019). The observed niche expansion, therefore, represents expansion in the trait space of prey utilized by the predators and we believe that the observed niche expansion also mirrors the overall niche expansion. However, the combination of novel molecular gut content analyses such as prey-group specific metabarcoding and individual-based stable isotope analyses could provide a more detailed picture in the future.

4.4 Conclusions
We investigated how ecological opportunity, exploitative competition / food limitation, and intraguild interference affect individual specialization in local communities of 13 species of arthropod generalist predators in spring barley fields. The intensifying negative intraguild interactions (interference, exploitative competition), rather than ecological opportunity, increased niche variation and consequently expanded the population niche widths. We have demonstrated that intraguild interactions can drive the positive niche variation–width relationship (Bolnick et al. 2007) in arthropod food-webs. A test of these hypotheses using empirical data from a real-world system for arthropods was previously missing and we encourage further studies on this topic to test the generality of the current findings. However, we found that the population niche expansion was due to the dual expansion of between- and within-individual components of population niche. The dual expansion has been considered unlikely by a previous theoretical model based on energy-limitation and imposed fitness costs on individual generalization (Sjödin et al. 2018). Most arthropod generalist predators are nutrient- rather than energy-limited (Toft et al. 2019), which may explain the discrepancy between the theoretical model and our results. Generalist predators combine various prey to balance their nutritional intake if there is not enough high-quality prey that would meet all their nutritional demands (Jensen et al. 2012). Future theoretical models should therefore include context-dependent fitness costs to individual specialization. Overall, the study supports the niche variation hypothesis and, in contrast to the traditional view, shows that negative intraguild interactions may act as a diversifying force.

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Figure S1–S4, Appendix S2