Body size and tree species composition determine variation in prey consumption in a forest-inhabiting generalist predator

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Abstract

1. Due to physiological, behavioural or ecological mechanisms, generalist predators may show individual variation in prey consumption. This individual specialization can result from both environmental and trait variation, with especially body size strongly connected to diet. Environmental variation can thus affect consumer-predator interactions by the joint action of changes in prey community composition and predator size.
2. We studied whether and how changes in forest environmental conditions, such as variation in tree species identity and forest fragmentation, affect predator-prey interactions. More specifically we anticipate tree diversity or spatial context to impact the predator diet directly via prey availability and prey size, but also indirectly through shifts in predator size. We used the orb-weaving spider *Araneaus diadematus* inhabiting forest fragments differing in edge distance, tree diversity and tree species as a model species. The species' diet was quantified by an unprecedented metabarcoding campaign. A total of 983 spiders were subjected to molecular diet analysis, from in total of 53 forest plots.
3. *A. diadematus* showed to be a generalist predator, with 298 prey items detected in total. At the individual level, we found large spiders to consume less different species, but consistently larger species. Tree species composition affected both prey species richness and size in the spider's diet, although tree diversity per se had no influence on the consumed prey. Edges had an indirect effect on the spider diet as spiders closer to the forest edge were larger and therefore consumed larger prey.
4. We attribute the structural complexity of the understory related to tree species composition as a driver of prey composition and its size distribution as reflected in the predator's diet. Although large spiders may specialize on large prey, we found no firm evidence for either ecological opportunism or strong specialization. Finally, we conclude that intraspecific size variation and tree species composition define the consumed prey of this generalist predator, and that the many feeding interactions of this spider underlie the species' success in a large diversity of habitats.

Keywords: Metabarcoding, predator-prey interaction, tree diversity, edge effects, prey-size spectrum

Introduction

Trophic interactions are a key component of ecological networks in ecosystems (Thébault & Loreau, 2005; Landi *et al.*, 2018). The stability and functioning of a food web are strongly impacted by the degree of interaction specialisation. With higher per capita consumption rates, specialist predators may be more effective in prey control than generalists (Diehl *et al.*, 2013), yet opportunistic and generalist predators provide stronger stabilizing effect within a food web (Gross *et al.*, 2009). However, due to physiological, behavioural or other ecological mechanisms, intraspecific variation in prey consumption may occur, rendering generalist species a collection of individuals that specialise on different components of the total prey spectrum (Bolnick *et al.*, 2003; Araújo *et al.*, 2011). This intraspecific variation is known to impact the strength of trophic cascades (Keiser *et al.*, 2015), with widespread consequences for ecosystem functioning (e.g. Post *et al.*, 2008).

Spiders are known to be the principal consumers of insects worldwide (Nyffeler & Birkhofer, 2017), and many species are opportunistic and generalist predators that rely on active hunting or trapping for prey capture (Eitzinger *et al.*, 2019). Orb-web spiders build vertical webs from silk to intercept flying prey, from small insects to smaller vertebrates (e.g. (Brooks, 2012)), and evidence is accumulating that many species are able to adapt their web-building in response to changes in the environment (Schneider & Vollrath, 1998; Bonte *et al.*, 2008; Sensenig *et al.*, 2010; Tew *et al.*, 2015). One such species, *Araneaus diadematus*, is for instance adapting web characteristics in an adaptive way to maximise prey interception in environments with a reduced prey availability (Bonte *et al.*, 2008; Dahirel *et al.*, 2017). By manipulating the size of the mesh, the location of the web and whether to eat or not to eat the prey caught in the web, spiders can adjust both the numbers and biomass of intercepted prey. For instance, when prey is experimentally switched from *Drosophila* to larger mosquitos, *A. diadematus* increases mesh height and web area, and reduces it to the original design when the prey availability is switched back to the smaller *Drosophila* (Schneider & Vollrath, 1998). By adapting their web-building behaviour, *A. diadematus* may therefore show individual-level resource specialization in relation to the prey-availability. Moreover, even though orb-webs are flight interception traps, orb web spiders can choose to eat or leave the prey caught in their webs (Janetos, 1982).

Body size is often considered a key-trait to explain intraspecific variation in resource consumption (Bolnick *et al.*, 2011). First, body size changes individual metabolism and metabolic efficiency through well-known allometric rules, and may hence translate into differential resource uptake (Brown *et al.*, 2004). More specifically, metabolic theory predicts the need of higher energy intake for large predators (Brown *et al.*, 2004), which can be obtained by either consuming larger, or more prey. While the consumption and handling of large prey is more energy-efficient, large prey are usually not as abundant as small ones (Venner & Casas, 2005). Hence, when spiders can chose, large prey items should be selected over smaller ones. Second, body size is allometrically related to traits that impact resource uptake, for instance to prey handling capacity and mobility (Hillaert *et al.*, 2018). Since predator body size determines the maximum prey size that can be caught (as shown in spiders by (Nentwig & Wissel, 1986)), large predators can be expected to have access to a wider range of prey species (Woodward & Hildrew, 2002).

The potential prey spectrum, is however, equally determined by the environment. Insect diversity depends, for instance, largely on the prevailing plant community composition and plant diversity which form the basis of their trophic interactions (Price, 2002; Scherber *et al.*, 2010; Rzanny *et al.*, 2013). By providing more resources, increases in plant diversity have been shown to promote the occurrence of more diverse groups of herbivores and predators, thereby inducing shifts in trophic structure (Haddad *et al.*, 2009; Hertzog *et al.*, 2016; O'Brien *et al.*, 2017). The diet of generalist and opportunistic predators is therefore expected to reflect the species richness of the prey community (Bison *et al.*, 2015; Schmidt *et al.*, 2018), and to be characterised by an increasing number of prey-predator links width increasing plant diversity (Tiede *et al.*, 2016). Additionally, as plant diversity is linked to an increases in productivity (Loreau *et al.*, 2001; Hooper *et al.*, 2005), mean prey size should increase as well (Allen *et al.*, 2006). Despite the general prediction of plant diversity increasing insect diversity (Scherber *et al.*, 2010), plant species identity may have larger effect on the community composition of arthropods than its diversity per se (Vehviläinen *et al.*, 2008; Scherber *et al.*, 2014; van Schrojenstein Lantman et al. 2019). However, predators are not as directly linked to the plant community as herbivores are, since plants are the food resource for herbivores. The dependence of predators to plant community is due to the prey those plants harbour, or due to structural resources that those specific plant species provide (Price, 2002). This generally makes the effect of plant diversity, but also their identity effects, less pronounced in comparison to lower trophic levels (Scherber *et al.*, 2010).

Arthropod, and hence putative prey communities are also affected by the spatial dimensions of their habitat, especially by habitat size and isolation (Debinski & Holt, 2000; Krauss *et al.*, 2010). According to the trophic rank hypothesis, higher trophic levels are generally more affected by habitat fragmentation than lower trophic levels (Holt, 2002; Cagnolo *et al.*, 2009; Martinson & Fagan, 2014). And due to the higher energy requirements, need for larger home ranges and slower development time, larger organisms are more vulnerable to habitat fragmentation per se (Hillaert *et al.*, 2018). Because of deforestation, 20% of the current forest area is for instance located within 100m of the forest edge (Haddad *et al.*, 2015). While prey availability as edges may be higher because of influxes from the matrix (Debinski & Holt, 2000; Rand *et al.*, 2006), edges are also know to show microclimatic gradients which directly affect arthropod diversity (Murcia, 1995; Schmidt *et al.*, 2017). Warmer microclimate at forest edges, have for instance been demonstrated to favours smaller arthropods (Atkinson & Sibly, 1997; Kingsolver & Huey, 2008). To date, however, we lack any synthesis on how edge effects affect arthropod community structure and biomass.

The prey spectrum of generalist predators may hence be largely affected by prey community composition, but also by potential intraspecific specialisation as related to variation in body size (Bison *et al.*, 2015; Staudacher *et al.*, 2018), thereby impacting species fitness (Dahirel *et al.*, 2019). In orb-web spiders larger prey -so called life-saving catches- may be especially key to reproduction (Venner & Casas, 2005). Describing and understanding trophic interactions in complex habitats, such as forests, rather than in experiments or simple agricultural sites is a challenging endeavour. Recent advances within the field of metabarcoding enable the investigation of trophic interactions on a larger extent (O'Rorke *et al.*, 2012; Pompanon *et al.*, 2012). Here, we engaged in a to date unprecedented barcoding campaign to understand whether environmental or intraspecific variation are more important in defining the diet of a generalist arthropod predator. We analysed the gut content of the orb-weaving spider *A. diadematus* from a heavily fragmented forest complex. This allowed us to study the interacting effects of edge distance and tree diversity or tree species composition as well as individual spider size on various aspects of the diet. We specifically hypothesised that (i) large spiders have a wider range of prey species in their diet, mainly due to the ability to eat prey at the upper limit of the prey-size spectrum. Therefore, (ii) large spiders are also expected to include larger prey in their diet. In relation to environmental variation, we assume (iii) that prey richness in the diet increases with both tree diversity and forest edge proximity, due to an increase in prey species availability. In terms of prey size, more diverse forests should have larger prey available, and therefore (iv) prey size in the diet should increase.

Materials and methods

Study site

This study was conducted within the TREEWEB research platform (www.treedivbelgium.ugent.be/pl_treeweb.html) situated in the fragmented landscape of northern Belgium (50.899°N, 3.946°E – 50.998°N, 3.584°E; Figure S1 in supplementary material). This platform consists of 53 research plots of 30 x 30 m. All have a similar land-use history (forest since at least 1850), management (no forest management in the last decade) and soil (dry sandy-loam). *Quercus robur* L. (pedunculate oak), *Quercus rubra* L. (red oak) and *F. sylvatica* L. (common beech) are the focal tree species in these forests. Plots of the three monocultures and all possible species mixtures (7 different stand compositions in total) were replicated 6 to 8 times along a fragmentation gradient. Edge distance (ranging from 7.0 to 215.5 m) was used as a proxy for edge effects. Edge distance was not correlated to tree diversity, neither did it differ between tree species combinations. Tree diversity was calculated by taking the exponent of the Shannon diversity index, based on the basal stem area of the tree species per plot. for more information on the setup of the study plots see (De Groote *et al.*, 2017).

Study species

We sampled common orb-weaver spiders (*Araneus diadematus* Clerk, 1757) for this study, as they are abundant in the study area and present in all of our study plots. We collected, if possible, 20 adult female *A. diadematus* in each plot from the 29th of August till 8th of September 2016. The spiders were taken from their webs, which were located at breast height. Collected spiders were immediately killed and stored in 99.6% alcohol. In some plots we could not collect 20 spiders, even after multiple visits. Spider size was taken by measuring the maximum width of the cephalothorax (i.e. carapace) under a stereomicroscope using a calibrated eyepiece graticule. Cephalothorax or carapace width has been a common used proxy for body size (Hagstrum, 1971; Greenstone *et al.*, 1985).

Molecular analysis

To establish the diet of the spiders, we used a proven metabarcoding protocol for spiders and other invertebrate predators (Vesterinen *et al.*, 2013; Kaunisto *et al.*, 2017; Eitzinger *et al.*, 2019). Shortly, we extracted DNA from the spiders' abdomen using NucleoSpin ® Tissue kit (cat. nr. 740952.250, Germany). To amplify mitochondrial COI gene, we used primers ZBJ-ArtF1c and ZBJ-ArtR2c from (Zeale *et al.*, 2011). As these primers also amplify the spiders themselves, we designed a blocking primer to decrease predator amplification in favour of prey amplification (Vestheim & Jarman, 2008). To prepare the blocking primer, we first downloaded all unique *A. diadematus* sequences from BOLD and GenBank and aligned them with multiple potential prey sequences using Geneious (Kearse *et al.*, 2012). Then we designed three primer sequences that overlapped the reverse primer ZBJ-ArtR2c and that were specific for *A. diadematus* (zero mismatches) but that did not match to any potential prey. The blocking primers were tested using primer BLAST (Koressaar & Remm, 2007; Untergasser *et al.*, 2012; Ye *et al.*, 2012). The best candidate (that did not bind to anything in the database except *A. diadematus*) was chosen. This primer sequence was ordered with C3 spacer modification at the 3' end (Aradia-R-blk-C3: 5'- CCA AAT CCC CCA ATT AAA ATA GGT ATA-C3 spacer -3'). PCR conditions and library preparation followed (Kaunisto *et al.*, 2017) and (Vesterinen *et al.*, 2018). To minimize the risk of contamination, all the extraction steps were carried out in carefully cleaned lab space, using purified pipettes with filter tips. All the extraction batches included negative controls to account for contamination issues.[1] Negative controls containing all but template DNA were included in each PCR assay. PCR products were never introduced to the pre-PCR space. All the uniquely dual-indexed reactions were pooled and purified using SPRI beads as in (Vesterinen *et al.*, 2016). The pool in this study was combined with another sample to increase nucleotide diversity. Sequencing was performed by Macrogen Korea (Macrogen Inc., Seoul, Rep. of Korea) using HiSeq4000 with TruSeq 3000 4000 SBS Kit v3 chemistry and 151 bp paired-end read length following HiSeq 3000 4000 System User Guide (Document #15066496 v04 HCS 3.3.52).

After sequencing, the reads separated by each original sample were uploaded on CSC servers (IT Center for Science, www.csc.fi) for trimming and further analysis. Trimming and quality control of the sequences were carried out as in (Vesterinen *et al.*, 2018). Briefly, paired-end reads were merged, trimmed, and collapsed using 64-bit software VSEARCH (Rognes *et al.*, 2016). For chimera-filtering, denoising, and clustering into ZOTUs ('zero-radius OTU'), we used 32-bit USEARCH (Edgar, 2010; Edgar & Flyvbjerg, 2015). Before collapsing, primers were removed using software Cutadapt (MARTIN, 2011). Then, ZOTUs were mapped back to the original trimmed reads using VSEARCH, and finally ZOTUs were assigned to prey taxa as explained below.

Data analysis

We summed the presence or absence of each prey taxon in each sample to end up with a frequency of occurrence (FOO) for each prey taxa. Additionally, all the frequencies were scaled to per cent of occurrence as explained in (Deagle *et al.*, 2019), creating a modified frequency of occurrence (MFO). We identified prey to the species level, where possible. The ZOTUs were initially identified using local BLAST against all COI sequences downloaded from BOLD and GenBank (Altschul *et al.*, 1990;

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[1] Washing the spiders several times in 99.6% ethanol during the collection, storage and preparation for extraction process was deemed to be appropriate sterilization.

Ratnasingham & Hebert, 2007). When species name was not available but match to the database was high, we used BIN codes from BOLD (Ratnasingham & Hebert, 2013). For details of the ZOTU's see Supplementary materials 1. To visualize the trophic interactions structures resolved by the molecular data, we used package BIPARTITE (Dormann *et al.*, 2008, 2009) implemented in program R (R Core Team, 2018). Semi-quantitative web was constructed using per cent of occurrence as explained above.

For further analysis, the cut-off threshold per ZOTU for the number of reads and 0.05% of the sample was set 0.05% of the total number of reads per spider, with a minimum threshold of 10 reads. A first multivariate analysis was performed to explore the variation in prey composition within the spider diet. The variation in the prey ZOTU composition within the diet of individual spiders was related to tree species combination, edge distance and spider size. A distance-based redundancy analysis (Euclidean distance) using the CAPSCALE function from the RDA package (Guo *et al.*, 2018) was applied. We performed an analysis of variance on the distance-based redundancy analysis with 1000 permutations (permanova) to quantify the variation in prey species composition explained by the different variables. Taxonomic units (prey species) were treated as binomial data (absence or presence) as the used metabarcoding technique does not allow a more quantitative approach.

Per spider, four diet-related response variables were calculated. Prey richness was taken to be the number of ZOTUs in the diet of each spider. For every single assigned prey item, its size (body length) was taken from literature (Supplementary materials 1). Prey size was taken to be the average prey size of taxonomic units preyed by each spider. Species with a body length over 1 cm are considered to be of highest gain (Venner & Casas, 2005). Prey richness of large prey was the number of taxonomic units with a body length of over 1 cm present in the diet of each spider. Prey size of large prey was the average prey size of taxonomic units larger than 1 cm present in the diet of each spider.

Four models were applied to the all diet-related response variables to explore different aspects of the data. M_{div} was the first model in which we tested for the effects of spider size, edge distance, tree diversity and the interacting effects of edge distance and tree diversity. The three other models were a set of models to compare to each other in order to understand the effects of spider size, edge distance and tree species composition (Kirwan *et al.*, 2009). The null model (M_{null}) includes only spider size and edge distance and assumes no effect of tree species composition. The additive model (M_{add}) includes, besides spider size and edge distance the relative basal area of each of the three focal tree species, and the intercept was forced through zero. This model assumes that tree species exert only additive identity effects. The pair-wise interaction model (M_{pair}) includes additionally the pair-wise interactions between the relative basal areas of the focal tree species. This model assumes not only additive effects, but also interacting effects between the tree species. The three composition models

(M_{null}, M_{add} and M_{pair}) were compared to each other to understand in which way the tree species composition impacted on the diet-related response variables. The model with the lowest AICc (obtained using the AICCMODAVG package by (Mazerolle, 2017) was considered the best. When differences in AICc between models were smaller than two, the simplest model was chosen based on parsimony. Spider size, edge distance and tree diversity were scaled around their mean in all models (Schielzeth, 2010).

To test whether compositional similarity in the diet within a plot, or spider size itself was impacted by edge distance, tree diversity or tree species composition all four models were also applied to spider size (unscaled), the plot-level Sørensen index (within-plot turnover of species composition in the diet) Spider size was excluded as an explanatory variable from these models. Finally, to test whether the levels of diet specialization within a plot varied, the four models were also applied to the plot-level coefficient of variation (CV) for prey richness and prey size. A scaled plot-level mean spider size was included as a variable, instead of individual-level spider size.

All analyses were performed in R, version 3.5.1 (R Core Team, 2018). All models, except the models with Sørensen index and coefficients of variation as a response variables, included plot ID as a random factor. This accounts for our data structure and the potential effect of plot ID. Models with overall prey size as response variable had a negative binomial distribution (log-link) with a variance increasing quadratically to the mean, applied through the GLMMTMB package (Brooks *et al.*, 2017). Models with the overall prey richness as response variable had a negative binomial distribution with constant variance using glm. Models with the richness of prey larger than 1 cm as response variable had a Poisson distribution. All other models had Gaussian distributions.

Results

The data analysis revealed *A. diadematus* as a versatile predator, with altogether 340 distinct prey species from 85 families in 8 orders and two classes (Figure 1). The HiSeq 4000 sequencing yielded 265 871 470 paired-end reads. After assigning these reads to unique dual-indexes used in this study, and after trimming and filtering, we ended up with 5765096 prey reads that could be mapped to the original samples. A total of 983 spiders were included in the molecular analysis, and 857 (87.2%) of these provided prey data after bioinformatic filtering including 298 prey species and were included in the subsequent analysis. The highest observed prey species richness within a single spider sample was 15 prey items. The most frequent prey detected was *Phaonia pallida* (N = 357), a forest-living muscid fly. The average prey size was 7.5 mm (SD ± 4.1), with only 39 prey species or genera larger than 1 cm. For a full list of prey taxa, and size data, see Supplementary materials 1.

Spider cephalothorax width ranged from 2.6 to 5.31 mm (average of 3.57 mm). Spider size decreased further from the edge; tree species identity had additive effects on spider size (Table 1-2, Figure S2 in supplementary material). Spider size was not impacted by tree diversity or the interaction between tree diversity and edge distance , but size was largest in monocultures of *Q. robur* and smallest in monocultures of *F. sylvatica* (Table 1-2, Figure S2 in supplementary material).

The multivariate analysis demonstrated that the composition of prey species in spider diets is highly variable (Figure 4). Although the constrained components of the ordination only explained 2,2% of the variation in composition, spider size (PERMANOVA, $F_{pseudo} = 4.41$, $p = 0.001$) and tree species combination (PERMANOVA, $F_{pseudo} = 2.65$, $p = 0.001$) strongly influenced prey species composition. However, all tree species compositions overlapped and showed large variation (Figure 4). Edge distance had no effect (PERMANOVA, $F_{pseudo} = 1.28$, $p = 0.127$). Compositional similarity of spider diet as measured by the Sørensen Index was not related to edge distance, tree diversity or tree species composition (Table 1-2, Table S1 in supplementary material).

The models including tree diversity (M_{div}) revealed that edge distance, tree diversity and the interaction between them had no impact on the four diet-related response variables: prey richness, prey size, richness of prey > 1cm and size of prey > 1cm (Table 1). In the best fitting composition models (Mnull, Madd, Mpair) edge distance had no impact on the diet-related response variables either (Table 2). Spider size was related to overall prey richness and prey size, only marginally to the size of prey larger than 1 cm and not at all to the richness of prey larger than 1 cm (Table 1, S1 in supplementary material). Large spiders consumed fewer prey species (Figure S4 in supplementary material), but also larger prey. The effect of identity of the tree species and their relative contribution to prey richness was absent, as M_{null} was the best fitting model (Table S1 in supplementary material). For prey size there were additive effects of tree identity (Table 2). Spiders in monocultures of *F. sylvatica* consumed the largest prey species, whilst spiders from *Q. robur* and *Q. rubra* monocultures had very similar sized prey (Table 2, Figure 2). Spiders inhabiting mixtures consumed prey size were the average size of the monoculture values of tree species included in the tree species composition.

The coefficient of variation (CV) for prey richness revealed that across tree diversity, tree species composition, edge distance and spider size, the level of specialization was the same, as none of the explanatory variables were significant (Table 1), and M_{null} was the best fitting composition model (Table S1 in supplementary material). The CV for prey size revealed that larger spiders were more consistent in their consumed prey size, independent of tree diversity or edge distance (Table 1). In terms of tree species composition, in monocultures of *Q. robur* spiders were least consistent in the consumed prey size and in monocultures of *F. sylvatica* spiders were most consistent (Table 2, Figure 3). Spiders inhabiting mixtures a level of consistency in prey size that was the average of the monoculture values of tree species included in the tree species composition (Table 1; Figure 3).

Richness of prey with the highest gain (prey larger than 1 cm) showed no effects of tree species identity; size of prey with the highest gain (prey larger than 1 cm) did show effects of tree species identity (Table 1-2). These large prey were proportionally most abundant in the diet of spiders from *F. sylvatica* monocultures. Prey body size was lowest in *F. sylvatica* - *Q. robur* mixtures, relative to their anticipated size in the respective monocultures (Table 2, Figure S5 in supplementary material).

Discussion

Trophic interactions between a spider and its prey were documented by metabarcoding methods. We were able to demonstrate the importance of both environmental conditions (tree diversity, tree species composition and edge effects) and intraspecific variation (body size) as determinants of prey species consumed in a generalist species. In terms of intraspecific variation, prey species richness in the spider diet decreased with spider size, but no significant changes in the richness or size of large prey species were found. Larger spiders were more consistent in the consumed prey species size than small spiders and selected larger prey species. Not all environmental conditions were relevant for spider diet. Tree species composition, rather than tree diversity, impacted diet. More specifically, spiders consistently consumed larger prey in monocultures of *F. sylvatica* than in other tree species compositions. We also found indirect effects of environmental variation on the trophic interactions between this generalist predator and its prey via changes in predator size: spiders were largest in monocultures of *Q. robur* and smallest in monocultures of *F. sylvatica,* but also larger closer to the forest edge.

In contrast to our expectations, we found larger spiders to consume slightly less prey species. Larger spiders did show, here, a tendency to be more selective in their foraging. In order to achieve their energy requirement (Brown *et al.*, 2004), the lower number of prey species consumed can be explained by either the consumption of fewer, but larger prey species or the consumption of more individuals of a fewer prey species. We cannot attribute the general prey size increases to the selection of the largest most energy efficient prey, as prey larger than one cm did not show a clear relationship with spider size. More-over, our approach does neither allow to perform more quantitative analyses on the relative abundances, consumed biomasses or intraspecific variation in prey size.

Unlike our expectation that plant diversity impacts insect diversity and trophic interactions (Price, 2002; Scherber *et al.*, 2010; Rzanny *et al.*, 2013), we did not find any effect of tree diversity on the richness or size of prey in the diet. The does not imply that plant diversity cannot have an impact on the diet of other predators. In one of the rare studies that focussed on trophic interactions of a generalist predator in relation to plant diversity, it was shown that the richness of consumed prey in carabid beetles did increase along an experimental grassland diversity gradient (Tiede *et al.*, 2016). The general expectation that the diet of a predator contains more prey in prey rich habitat, is based on ecological opportunism (Bison *et al.*, 2015). Essentially, a generalist predator's diet would reflect the diversity of prey available. However, this is contradicted by the idea that the availability of more prey species allows intraspecific specialization on species (Staudacher *et al.*, 2018). We found no support for increased specialization in more diverse forest, as the coefficient of variation in prey richness did not depend on tree diversity. It should, however, be made clear that the occurrence of ecological opportunism can neither be confirmed nor dismissed as both processes act at the individual level, and may be levelled out at the population-level.

Although effects of tree diversity were absent, environmental variation did have an impact on spider diet as we found clear effects of tree species identity. The two-species mixture of *Q. robur* and *F. sylvatica* held a different composition of species in the spiders' diet compared to the other tree species composition. This is also the mixture which has shown to support the richest group of herbivores within this study system. Yet, when focussing on prey richness or size in the diet, this tree species mixture does not stand out. Relative to spider size, spiders ate consistently large prey, and more and larger prey of high gain (> 1cm) in monocultures of *F. sylvatica* than in other tree species composition. Interestingly, monocultures of *F. sylvatica* also hold the smallest spiders. This dismisses the idea – at least for tree species composition – that as a result of more abundant and large prey sampling effort causes the relationship between spider size and prey richness and size. The larger average prey size in *F. sylvatica* plots cannot be related to an inability for spiders to capture and overpower large prey due their body size.

Alterations in diet due to changes in tree species composition can arise from differences in prey availability. Unfortunately, we do not have data on prey availability and can therefore not confidently conclude whether our findings are pure reflections of the prey availability. However, if spider diet did indeed reflect the prey availability, we would expect spider diet in forests with *Q. robur* to have the more species and being composed of larger prey, since *Q. robur* is known to harbour a more diverse arthropod community (Southwood *et al.*, 2004). We should not disregard the possibility that consumed prey size does not reflect prey availability in relation to tree species compositions, but that structural differences within the forest habitat might affect prey diversity as well. In our study area the cover of the shrub and herb layer is much lower in monocultures of *F. sylvatica* than in the other tree species compositions (De Groote *et al.*, 2017). In a sense, the complex and denser understories in the other tree species compositions have spatially a more fractal like structure, which is better utilized by smaller organisms (Morse *et al.*, 1985).

In contrast to the expected variation in prey availability and composition in relation to edge proximity, we found no changes in prey richness in relation to edge distance. However, a possible pattern could be masked by the occurrence of larger spiders in proximity of the forest edge. Neither larger spiders close to the edge, nor the absence of larger prey species consumed close to the edge fit the expectation that the warmer forest edges could favour smaller arthropods (Atkinson & Sibly, 1997; Kingsolver & Huey, 2008). However, another abiotic factor related to edges is that the wind is stronger in the forest edges (Schmidt *et al.*, 2017). Wind damages webs, which reduces the foraging efficiency and enforces costly web repairs (Tew *et al.*, 2015). This may select for larger spiders with higher silk production (Vollrath, 1999). It is possible that within this study a stronger effect is overlooked, as edge effects for both biotic and abiotic gradients are generally observed in first few meters from the edge (Murcia, 1995; Schmidt *et al*>, 2017; Smedt>*et al*>, 2018).

We used metabarcoding analyses at an unprecedented scale to assess the effects of both environmental variation and intraspecific variation in a complex ecosystem on the diet of a generalist arthropod predator. We showed that as a species, *A. diadematus* is undeniably a generalist, consuming many prey species and providing network complexity by its many trophic interactions. At an individual level, however, the prey spectrum of this generalist predator is substantially characterised by intraspecific spider size variation, in which large spiders forage on a smaller number of consistently larger prey species. Additionally, tree species composition affects both prey species richness and size. Edges had an indirect effect on spider diet by changes in spider size, and tree diversity had no effect. Therefore, we conclude that intraspecific size variation and tree species composition together define the spectrum of consumed prey of this generalist predator.

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Table 1 Summary of results for all M_{div} models. Except for the Sørensen index, Plot ID was added as a random factor in the models, but is not shown here. CV stands for coefficient of variation.

		estimate	s.e.	z-value	p-value	
Spider size	Edge distance	-0.08	0.03	-2.74	0.009	**
	Tree diversity	0.01	0.03	0.38	0.705	
	Interaction	-0.003	0.03	-0.08	0.937	
Sørensen index	Edge distance	0.01	0.02	0.65	0.516	
	Tree diversity	0.01	0.02	0.48	0.635	
	Interaction	-0.01	0.02	-0.27	0.791	
Prey richness	Edge distance	-0.03	0.05	-0.60	0.550	
	Tree diversity	0.04	0.05	0.85	0.393	
	Spider size	-0.07	0.03	-2.48	0.013	
	Interaction	-0.01	0.05	-0.12	0.908	*
Prey size	Edge distance	-0.01	0.03	-0.21	0.808	
	Tree diversity	-0.02	0.03	-0.56	0.574	
	Spider size	0.06	0.02	3.37	<0.001	
	Interaction	-0.03	0.03	-1.01	0.311	***

		estimate	s.e.	z-value	p-value	
Prey richness > 1cm	Edge distance	-0.02	0.08	-0.28	0.777	
	Tree diversity	0.06	0.08	0.70	0.487	
	Spider size	0.06	0.05	1.27	0.204	
	Interaction	-0.01	0.09	-0.14	0.891	
Prey size > 1 cm	Edge distance	0.19	0.31	0.61	0.546	
	Tree diversity	0.03	0.31	0.08	0.933	
	Spider size	-0.33	0.19	-1.76	0.080	
	Interaction	0.001	0.34	0.01	0.996	.
CV of prey richness	Edge distance	-0.02	0.03	-0.51	0.610	
	Tree diversity	-0.01	0.03	-0.26	0.797	
	Spider size	-0.01	0.03	-0.17	0.869	
	Interaction	-0.01	0.04	-0.38	0.705	
CV of	Edge distance	-0.02	0.02	-1.01	0.316	
	Tree diversity	0.02	0.02	0.80	0.429	
	Spider size	-0.02	0.02	-0.84	0.406	
	Interaction	-0.01	0.02	-0.29	0.773	

Table 2 Summary of results for the best fitting models which test for tree species composition effects. CV stands for coefficient of variation.

		estimate	s.e.	z-value/t-value	p-value	
Spider size	Edge distance	-0.06	0.03	-2.27	0.028	*
	Rel. *F. sylvatica*	3.41	0.05	65.58	<0.001	***
	Rel. *Q. robur*	3.75	0.05	70.35	<0.001	***
	Rel. *Q. rubra*	3.55	0.05	69.38	<0.001	***
Sørensen index	Edge distance	0.01	0.02	0.72	0.475	
Prey richness	Edge distance	-0.03	0.05	-0.58	0.566	
	Spider size	-0.06	0.03	-2.47	0.014	*

		estimate	s.e.	z-value/t-value	p-value	
Prey richness > 1cm	Edge distance	-0.02	0.08	-0.26	0.795	
	Spider size	0.06	0.05	1.28	0.199	
Prey size > 1cm	Edge distance	0.17	0.31	0.57	0.570	
	Spider size	-0.29	0.19	-1.52	0.130	
	Rel. *F. sylvatica*	19.75	0.70	28.08	<0.001	***
	Rel. *Q. robur*	19.08	0.75	25.56	<0.001	***
	Rel. *Q. rubra*	18.56	0.80	23.07	<0.001	***
	Rel. *F. sylvatica* x Rel. *Q. robur*	-6.75	3.54	-1.91	0.065	.
	Rel. *F. sylvatica* x Rel. *Q. rubra*	3.87	3.79	1.02	0.313	
	Rel. *Q. robur* x Rel. *Q. rubra*	3.40	3.59	0.95	0.350	
CV of prey richness	Edge distance	-0.02	0.03	-0.49	0.630	
	Spider size	-0.01	0.03	-0.18	0.858	

Prey size	Edge distance	-0.01	0.03	-0.34	0.737	
	Spider size	0.07	0.02	3.80	<0.001	***
	Rel. *F. sylvatica*	2.17	0.05	41.68	<0.001	***
	Rel. *Q. robur*	1.91	0.05	34.92	<0.001	***
	Rel. *Q. rubra*	1.90	0.05	36.63	<0.001	***

CV of prey size	Edge distance	-0.02	0.02	-1.25	0.266	
	Spider size	-0.04	0.02	-2.04	0.047	*
	Rel. *F. sylvatica*	0.20	0.04	5.02	<0.001	***
	Rel. *Q. robur*	0.38	0.04	8.89	<0.001	***
	Rel. *Q. rubra*	0.32	0.04	8.80	<0.001	***

Figures

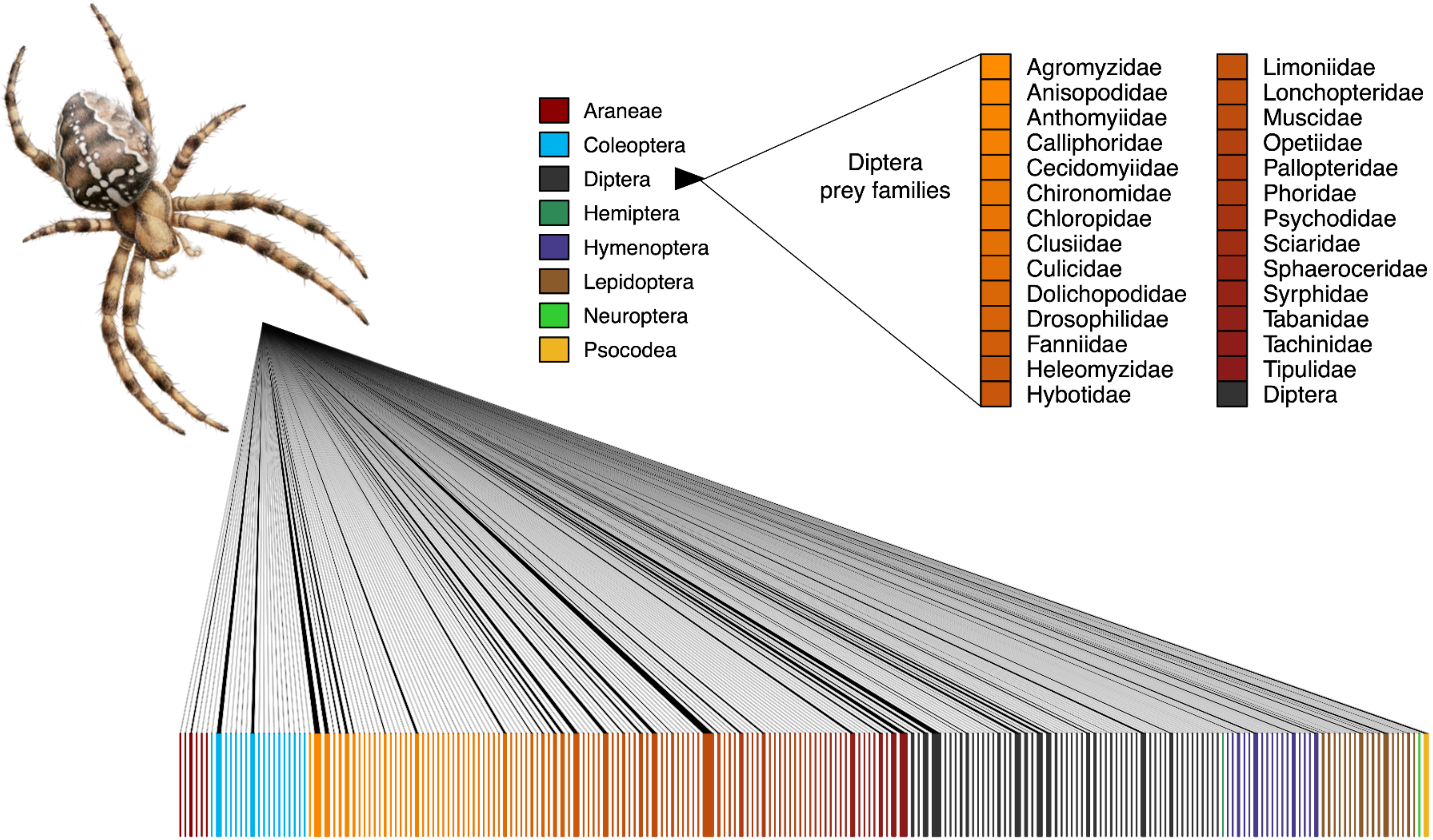

Figure 1 Visual representation of the taxonomic distribution and quantified strength of trophic links from *Araneus diadematus* to their prey. The blocks in the lower row represent prey species. A line connecting the predator with a prey represents detected predation events, and the thickness of the line represents the modified frequency of occurrences (MFO) of each predation record. See the “Data analysis” in the main text for details on the MFO..

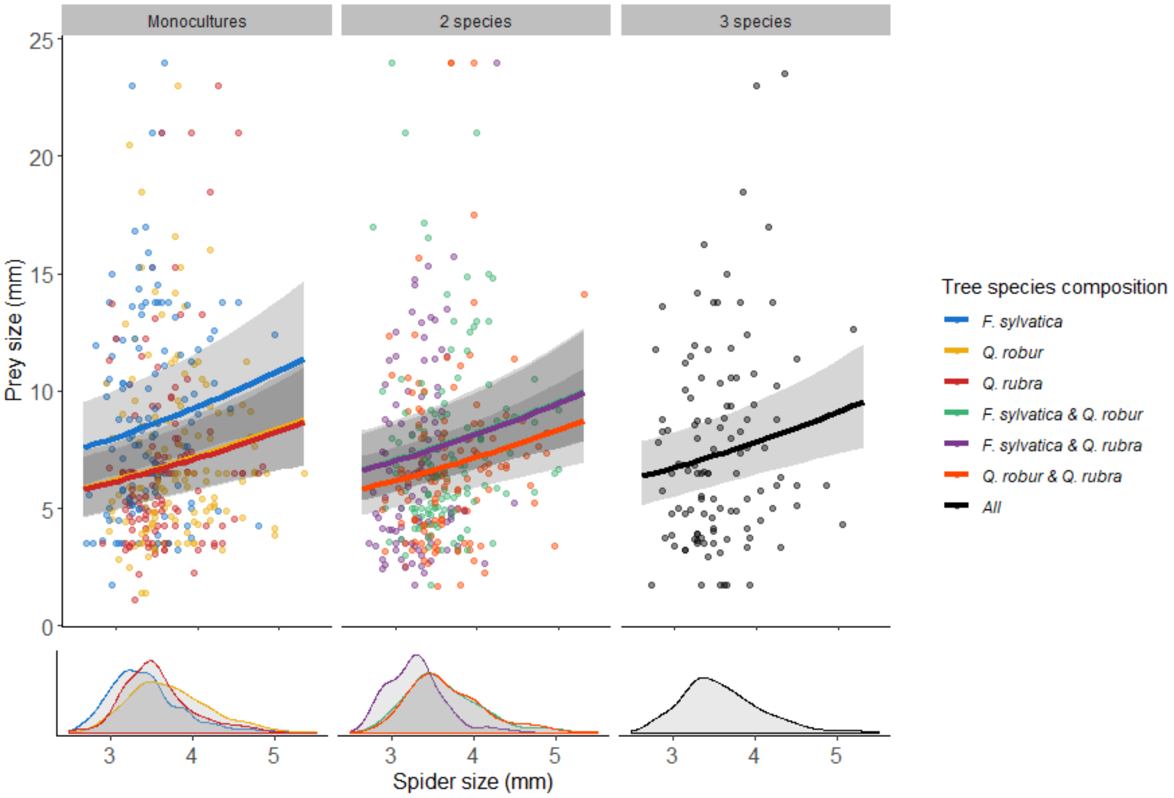

Figure 2 Relationship between the average prey size (mm) of the species caught and the spider's cephalothorax size (mm) per tree species composition. Data points are the individual spiders (N = 983). Lines with 95% CI are the estimated slopes based on model M_{add}. For estimation, edge distance was taken to be the overall average. Colours refer to the tree species composition. There is a positive relationship between average prey size and spider, and additive tree species composition effects, in which monocultures of *F. sylvatica* catch relatively larger prey species than the other monocultures. In mixtures, the prey size are averages of each individual monoculture contributing to the mixture. The lower part of the graph shows density plots of the spider size distribution within each tree species composition.

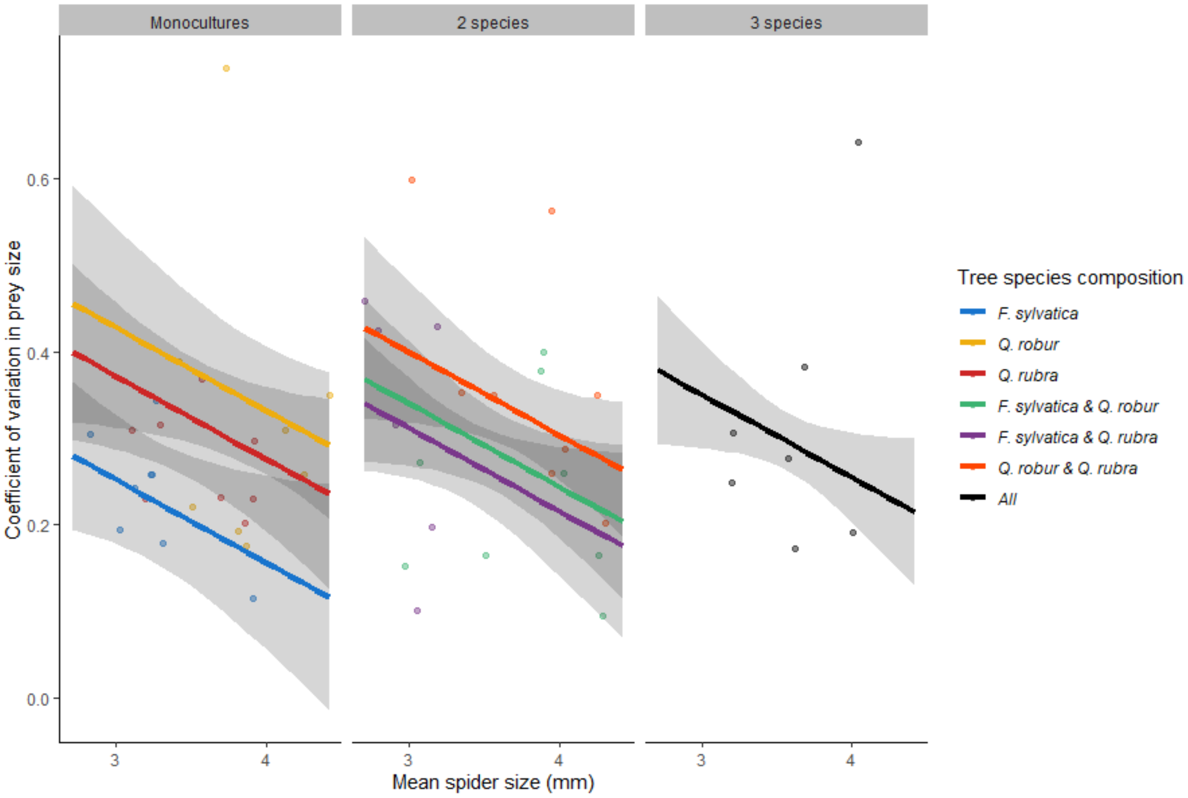

Figure 3. Relationship between the coefficient of variation (CV) for prey size per plot and the mean spider's cephalothorax size (mm) per plot. Data points are the individual plots (N = 53). Lines with 95% CI are the estimated slopes based on model M_{add}. For estimation, edge distance was taken to be the overall average. Colours refer to the tree species composition. In plots with larger spiders, there is a stronger stability in prey size (lower CV). Additive tree species composition effects are present. The strongest stability in prey size is found in monocultures of *F. sylvatica*, and the lowest stability in monoculture of *Q. robur*. In mixtures, the CV is an average of the CV of each individual monoculture contributing to the mixture.

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