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Flooding affects fluctuating asymmetry but not growth of a riparian orbweaving spider

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Abstract

1. Aquatic emerging insects play a critical role in riparian ecosystems by supporting terrestrial consumers, particularly generalist predators like spiders. Their emergence is highly sensitive to environmental changes such as river regulation and climate change.
2. While previous studies have demonstrated that fluctuations in aquatic insect subsidies influence spider abundance and diversity, little is known about how these changes affect spider morphology and physiology.
3. This study aimed to investigate how flooding affects both aquatic insect emergence and morphological responses of the web-building spider *Tetragnatha extensa* (Linnaeus, 1785).
4. We conducted an experiment using a riparian stream mesocosm facility, simulating four flooding events between May and September. Aquatic insects were sampled using emergence traps during all flooding events, while spiders were collected at the beginning and end of the experiment. To assess developmental stress, we measured spider head size and fluctuating asymmetry using landmarking and geometric morphometrics.
5. Spiders in flooded mesocosms exhibited ∼15% lower fluctuating asymmetry than those in controls, suggesting reduced developmental stress. This likely reflects the 45% higher emergence of chironomids, the main prey of *T. extensa*. These results indicate that spider developmental stability is responsive to prey availability and that geometric morphometrics is a sensitive tool for detecting such prey-mediated ecological effects.
6. Climate change, water use and river regulation, through altered flooding regimes, can disrupt cross-ecosystem fluxes by affecting the emergence of aquatic insects. Reduced prey availability may, in turn, impact spider physiology and propagate into

the riparian ecosystem through altered fitness, reproductive success and population dynamics of terrestrial consumers.

KEYWORDS
aquatic emerging insects, aquatic-terrestrial linkages, cascading effects, developmental stress, geometric-morphometric, physiology

INTRODUCTION

Aquatic and terrestrial ecosystems are interconnected by exchanging nutrients, organisms and energy (Bartels et al., 2012; Loreau et al., 2003). In freshwater systems, emerging aquatic insects are an important food source for terrestrial predators, including spiders (Middendorf et al., 2025; Paetzold et al., 2005). Climate change and altered hydrological regimes pose increasing threats to the dynamics of these fluxes (Häder & Barnes, 2019; Schulz et al., 2015). Frequent and unpredictable flooding events can affect insect emergence dynamics (Kennedy et al., 2016), altering aquatic insect availability for riparian spiders (Whiles & Goldowitz, 2001) and potentially impacting metabolism or activity level (Jensen et al., 2010; Koemel et al., 2019).

The emergence of chironomids is known to depend on various environmental factors, with changes in water flow, temperature and shoreline structure identified as major factors influencing emergence rates and timing (Vinnersten et al., 2014). Tronstad et al. (2010) demonstrated that chironomid larvae in inundated floodplains had higher growth rates benefiting from warmer water and higher food availability on flooded terrestrial areas, leading to faster emergence. As a key food source subsidizing many riparian predators, shifts in chironomid emergence can have cascading effects (Graf et al., 2017): Lower numbers of emerging insects have been linked with reduced abundance of riparian web-building spiders (Baxter et al., 2004), spiders' diet switch (Huszarik et al., 2024; Manfrin et al., 2017) or top-down effects on the riparian food web (Henschel et al., 2001).

Riparian web-building spiders such as *Tetragnatha* sp. strongly rely on aquatic insects as prey (Middendorf et al., 2025; Uno, 2016). Aquatic insect subsidies are highly nutritious due to their content of polyunsaturated fatty acids (PUFA) (Hixson et al., 2015). A diet rich in high-quality aquatic prey can improve growth (Pietz et al., 2023), reproductive success and increase overall fitness (Mestre & Bonte, 2012). An increase in these subsidies, particularly during critical life stages such as early growth, moulting or egg production (Wen et al., 2020), may enhance developmental stability in spiders. Developmental stability refers to an organism's ability to undergo normal growth and produce a consistent, symmetrical phenotype (Møller, 1997). Nutritional stress, pollution or other environmental pressures can alter developmental stability, leading to deviations from bilateral symmetry, known as fluctuating asymmetry (FA). Access to a high-quality diet could support healthier riparian predator populations and contribute to maintaining ecosystem functionality (Laws & Joern, 2013; Ohler et al., 2024). Conversely, reduced aquatic subsidies may force spiders to invest more energy into foraging, leaving fewer resources available for growth and the maintenance of developmental stability (Uetz et al., 2009). Such constraints can affect developmental stability and ultimately increase phenotypic asymmetry (Hendrickx et al., 2003).

Geometric morphometrics can be a powerful tool to analyse developmental instability due to environmental stress (Graham et al., 2010; Leung et al., 2000; Scalici et al., 2018). It analyses body shape variations and has been widely applied in studies of sexual dimorphism, taxonomy and symmetry across various taxa, including spiders (Brandt et al., 2023; Fernández-Montraveta & Marugán-Lobón, 2017; Klingenberg, 2015; Spani et al., 2025). More recently, geometric morphometrics has been used to assess environmental stress responses to pesticide exposure in insects or bivalves (Gerard et al., 2018; Scalici et al., 2017; Scalici et al., 2020). Based on measurements of fluctuating asymmetry, geometric morphometrics can quantify small deviations from perfect bilateral symmetry. Fluctuating asymmetry can be interpreted as an indicator of developmental stress, reflecting altered physiology during growth that can be induced by adverse environmental states, such as chemical, physical or pathogen effects. Fluctuating asymmetry has been applied to ecological questions in arthropods, but the number of studies remains low, and responses can be variable because fluctuating asymmetry is affected by interactions between environmental stress and individual genetic expression (Graham et al., 2010). Chang et al. (2007) observed increased asymmetry in the wings and legs of damselflies exposed to pesticides or thermal stress during their larval development. Mauser et al. (2025) observed differences in wing asymmetry between damselflies with different mating success and exposed to different environmental conditions. Higher fluctuating asymmetry was found in isopods following dam construction, which disrupted natural flooding and led to drier soils and a major shift in vegetation (Vilisics et al., 2005). Carabid beetles collected in agricultural sites (olives and vineyard) showed higher fluctuating asymmetry than those collected from Mediterranean maquis and garrigue pristine habitats (Ivanković Tatalović et al., 2020). While geometric morphometrics in arachnology has primarily focused on species delimitation and taxonomic classification (Brandt et al., 2023; Kallal et al., 2019; Kallal & Wood, 2022), its application to studying environmental stress in spiders remains rare. Hendrickx et al. (2003), investigated reproductive performance and fluctuating asymmetry in spiders exposed to heavy metals and Uetz et al. (2009) detected higher fluctuating asymmetry in the tuft area of males that had faced a catastrophic flood. Compared to the often-used measurements of size or body mass (Wimp et al., 2021), fluctuating asymmetry offers a more integrative approach, detecting latent or chronic environmental impacts that may not be apparent through conventional morphological measurements (Parsons, 1992; Zakharov & Trofimov, 2022). Moreover, assessing the morphology and symmetry of specific body structures can provide direct insight into their developmental performance (Ivanković Tatalović et al., 2020) or reproduction (Danielson-François & Sullivan, 2021). While traditional fitness assessments often rely on size as a proxy, fluctuating asymmetry analysis offers more specific information as a sensitive marker of environmental stress (De Anna et al., 2013). This study aims to investigate how flooding regimes influence aquatic insect emergence and, consequently, the development of *Tetragnatha extensa*. Contrary to traditional studies that rely on size-based measures of fitness, we use geometric morphometrics and fluctuating asymmetry to assess the ecological responses of *T. extensa* to flooding regimes, via changes in prey availability and developmental stress.

To assess the cascading impact of flood on riparian spider size and fluctuating asymmetry, we induced 14 days of flood in replicated riparian mesocosms and compared to non-flooded controls. The flooding design was repeated in four subsequent flooding events between May and September. We collected *T. extensa* after the first and the fourth flooding event and measured the effect of flooding and potential varying availability of aquatic subsidies on *T. extensa* fluctuating asymmetry. *Tetragnatha extensa* adult females can be found between May and August (Bellmann, 2016). Therefore, individuals collected in May had largely completed their development before the experiment. In contrast, the immature individuals collected in September had developed within the mesocosms and experienced several moulting events during the experiment. We hypothesized that (1) flooding will increase the number of chironomids emerging from the flooded mesocosm and therefore prey availability for *T. extensa*. (2) We expect that at the end of the experiment, spiders from flooded mesocosms will exhibit larger head sizes compared to those from non-flooded mesocosms. We also expect that enhanced access to high-quality polyunsaturated fatty acids (PUFAs) from chironomids prey in flooded conditions will promote better developmental stability. Consequently, (3) we predict that spiders from flooded mesocosms will show lower fluctuating asymmetry than those from non-flooded mesocosms.

METHODS

Mesocosm facility description

The experiment was carried out at the Riparian Stream Mesocosm (RSM) facility in Landau, southwestern Germany (49°12′03.9″ N, 8°08′19.9″ E); the facility consists of 16 flow-through mesocosms (Manfrin et al., 2023), each designed to simulate a riparian ecosystem with both an artificial stream and an adjacent riparian zone (Figure 1a). The streams are approximately 0.73 ± 0.08 m wide and 15.15 ± 0.07 m long, with a 1% slope, while the grassland riparian area extends 3.74 ± 0.09 m along the left bank. A narrow maintenance pathway runs along the right bank (Figure 1b). To simulate a natural riverbed, each stream contains six alternating gravel bars.

Water for the streams was continuously supplied from the nearby River Queich using pumps (BADU® Eco Flex, max. 40 m^3/h, 2.20 kW) at a flow rate of 4.2 ± 0.9 L/s (Rovelli et al., 2024). Each mesocosm was enclosed within a greenhouse-like structure covered with fine (1 mm) mesh gauze, preventing flying insects from entering or leaving the mesocosm as well as most ground-dwelling species (Figure 1a). During non-experimental periods (e.g., autumn to spring) the enclosures were removed, and the stream channels were left to dry, enabling natural colonization by plants and arthropods from the surrounding grassland.

To establish a natural macroinvertebrate community, we turned on the pumps one month before the start of the experiment. The pumps were equipped with a 6-mm filter that prevented large organisms such as fish and crayfish from entering our mesocosms but allowed for passive colonization of macroinvertebrates that passed through the filter to enter the mesocosms, ensuring emergence through the entire experiment. In addition, we actively introduced macroinvertebrates from the adjacent river Queich into the artificial streams after catching them with artificial substrates. A total of 80 wooden brooms (7 cm in diameter, 65 cm in length) were used as artificial substrates. The brooms were placed in a 100-m restored section of the river Queich for 16 days (from 19 April 2023 to 4 May 2023) to allow macroinvertebrate colonization. After broom collection, five brooms were randomly assigned to each mesocosm. All macroinvertebrates contained in the brooms were washed out and collected in trays. Unwanted material such as fish, crayfish, macrophytes and wood debris was removed before introducing the remaining organisms into each mesocosm stream. Although macroinvertebrates were not identified to lower taxonomic levels, the community was largely dominated by chironomid larvae and gammarids.

Flooding

For this experiment we used eight mesocosms. Four mesocosms were exposed to flooding for 14 days, and the other four were considered as controls and were never flooded during the experiment. The flooding was repeated in May, June, August and September 2023. Each flooding event was characterized by a slow increase of the water level inside the stream part until the inundation of 60% of the terrestrial area. The flood reached a maximum depth of 10 cm in the downstream section and gradually decreased toward the edges of the refuge area (Figure 1b), where only a few millimetres of water covered the soil surface.

Emerging insect collection

Aquatic emerging insects were sampled in both flooded and control mesocosms during defined periods surrounding each flooding event. In each mesocosm, emerging insects were collected using pyramidal emergence traps (Figure 1b), following the model of Cadmus et al. (2016), made from 20-mm PVC pipes, each with a 0.25-m^2 base, a height of 30 cm and covered with 500-μm mesh (Figure S1). A total

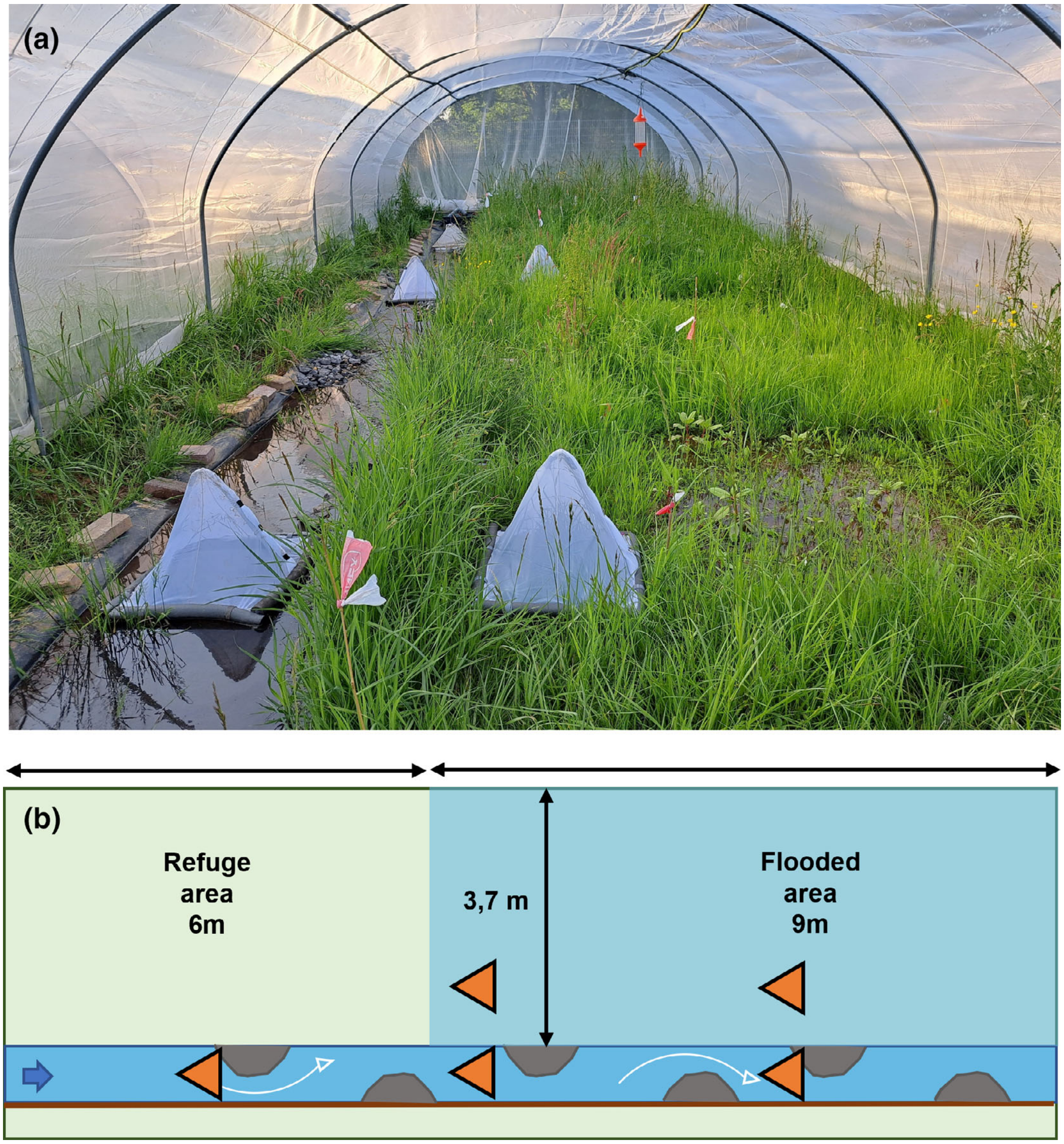

FIGURE 1 The Riparian Stream Mesocosm, Landau, Germany. (a) Inside view of one mesocosm equipped with greenhouse-like frame and covered by a 1 mm mesh gauze with emergence trap deployed (Picture by Stephane Mutel). (b) Schematic of one flooded mesocosm: stream (in blue), lateral bars (grey), adjacent riparian grassland with upstream 'refuge area' left unflooded (light green) and a 'downstream flooded area' (light blue); emergence traps position (orange triangles).

of five traps were deployed in each mesocosm. Three floating traps were positioned in the stream at upstream, middle and downstream positions, and two were placed on the terrestrial part, 1 m from the stream edge and parallel to the two most downstream traps (Figure 1b). To ensure consistent sampling across treatments, traps were deployed 3 days before the onset of each flooding event and remained in place until 4 days after its conclusion, regardless of whether the mesocosm was actually flooded. This resulted in a total of 21 days of sampling for each of the flooding events (Table S1). Outside of these defined sampling windows, no emergence traps were deployed. Traps were not equipped with catching bottles and preservative fluid but were emptied every 3 days using a mechanical pooter connected to a 150-mL Falcon tube. Captured insects were then immediately frozen at −20°C for preservation. Frozen insects were then counted and identified to family (Nilsson, 1997).

Spider collection, photography and landmarking

For imaging and landmarking, we analysed only female spiders from Flood 1 and Flood 4 to capture treatment extremes. Flood 1 spiders, already adults in May, served as controls, while Flood 4 spiders who developed under experimental conditions reflected cumulative flooding effects. Spiders from floods 2 and 3 were omitted due to logistical constraints and because the most pronounced effects were expected after Flood 4. *Tetragnatha extensa* females were handpicked along the stream edge, kept in individual containers for 24 h before being frozen at −20°C.

To obtain consistent images of the prosoma and to accurately capture its three-dimensional structure in two-dimensional photographs, spider legs were removed by cutting at the trochanter articulation to ensure the prosoma could rest flat on the sternum (Figure 2). The operation was conducted using micro scissors and tweezers. To improve stability and enhance the visibility of the lower part of the prosoma, the opisthosoma was removed prior to taking the photo. All images were captured with a stereomicroscope (Stemi 508, Carl Zeiss AG, Oberkochen, Germany, objective magnification: 0.63×, internal zoom set at 4.0×) using a ZEISS Axiocam 208c camera at a resolution of 2160 × 3840 pixels, resulting in a scale of 1.37 μm/px; exposure, colour range and white balance were adjusted individually to obtain best clarity and sharpness on each photograph.

To quantify fluctuating asymmetry (FA), we placed 16 landmarks on homologous points of the prosoma using the software tpsDig264 (version 2.32). The landmarking of the points was performed in a randomized order and by a single operator to prevent operator biases. Two central landmarks were positioned to define vertical symmetry (number 5 and 13, Figure 2), while the remaining seven pairs were set to capture the structural characteristics of the prosoma on both sides (Figure 2). After aligning all specimens to a common mean shape through a Generalized Procrustes Analysis (GPA), we quantified the FA component by comparing the coordinates of each left–right landmark pair, which provides a direct measure of how much the two sides deviate from perfect symmetry. The measurement error was assessed by randomly selecting 20 spiders from flood 1, capturing two images of each specimen, applying landmarks and performing a GPA followed by a bilateral symmetry analysis to quantify and compare variation, ensuring in this way that the measurement error was smaller than the variance. The Procrustes analysis of variance (ANOVA) revealed greater biological variation than landmarking error, confirming the reliability of our method for detecting potential treatment effects (Table S2).

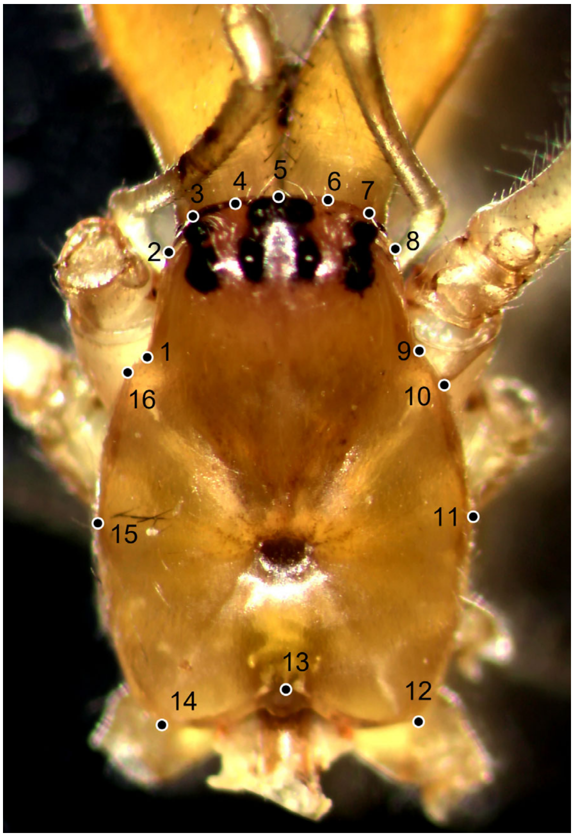

FIGURE 2 Dorsal view of *Tetragnatha extensa*'s prosoma landmarked on 16 homologous points (picture by Celia Thomas and Stephane Mutel).

Analysis

Chironomids represented 98% of the total insect emergence caught. For this reason, we focused our analysis exclusively on chironomids. For each mesocosm and flooding event, we summed the numbers of chironomids caught across the three emergence traps during the 21 days of sampling and standardized the values per day and square meter of sampling as Catch Per Unit Effort (CPUE, chironomids day^{-1} m^{-2}). We tested the effects of flooding event and flooding on the number of chironomids using a generalized linear model (GLM) with a Gamma distribution to account for the non-normal distribution of the residuals. The factors in the models included flooding event (flood 1, 2, 3 and 4), flooding (flood and no flood) and their interaction.

We analysed the landmark data using the 'geomorph' package in R (Adams & Otárola-Castillo, 2013; Baken et al., 2021). First, the tps files containing landmark coordinates were compiled into a geomorph data frame, incorporating specimen information. We then performed a GPA to align, scale and remove non-biological variation in shape due to size, orientation and positioning differences. We calculated Centroid Size as a proxy of head size (Curran, 2018) using the 'shapes' package (Dryden, 2023). Centroid size values (pixel) were then converted to head size (μm^2) by applying the scaling factor based on the magnification and resolution of the images. The FA score, an indicator of developmental instability, was calculated as the square root of the sum of the squared differences between the FA component and the mean shape as following the method described by Holzleitner and DeBruine (2020). Higher FA scores indicate greater asymmetry and, consequently, higher developmental instability.

To investigate the effect of flooding on the spider morphometry, we used GLMs on head size and on FA. The models included flooding (flood and no flood), flooding event (flood 1 and 4) and their interaction as fixed factors. Data distributions and homogeneity of variance were assessed using Shapiro–Wilk tests for normality and Levene's tests for variance homogeneity. Both variables (head size and FA) exhibited non-normal distributions of the residuals. While the assumption of homogeneity of variance was met by FA, it was not met for CS, nor for the interaction of flooding and flooding event and the individual factors. Hence, we chose to fit the GLM with a Gamma distribution for both variables after removing potential outliers identified using Rosner's test from the 'EnvStats' package (version 3.0.0, Millard, 2013); only one outlier was detected for FA and removed before model fitting. Because Flood 1 and Flood 4 spiders belong to different age classes, a smaller head size is ecologically expected in the Flood 4 individuals. We did not interpret the main effect of flood event on head size as biologically meaningful but retained the factor in the model to examine the interaction between flooding treatment and flooding event.

All statistical analyses were conducted using R (version 4.3.1; R Core Team, 2023), with a significance threshold set at $p < 0.05$. Model validation was performed using the DHARMa package (version 0.4.6, Hartig, 2022) by examining residual-fitted values plots to assess model assumptions. To test for the significance of the factors and their interaction, we performed an ANOVA on the fitted models using the 'Anova' function from the 'car' package (version 3.1-2; Fox & Weisberg, 2018). In case of significant interaction in our model, we used Estimated Marginal Means (EMMs) to perform pairwise comparisons between treatment groups as post hoc tests, using the 'emmeans' package (version 1.10.4, Lenth, 2024).

RESULTS

Aquatic emerging insects

The number of emerging chironomids was consistently higher in flooded mesocosms than in control mesocosms ($\chi^2 = 10.5$, df = 1, $p = 0.001$) across all flooding events, from May until September (Figure 3). We also observed a seasonal variation in emergence ($\chi^2 = 204.4$, df = 3, $p < 0.001$) with the highest numbers during May in flooded mesocosms. Chironomid CPUE decreased in June, reaching the lower value in August before rebounding in September (Figure 3). During the first flooding event, when emergence peaked, flooded mesocosms produced 27% more chironomids than the control mesocosms. In subsequent flooding events, emergence declined but flooded mesocosms still yielded 34% and 39% more chironomids than the controls during the second and third flooding events, respectively. During the fourth flooding event, emergence numbers rebounded, with 42% more chironomids emerging from the flooded mesocosms than from controls.

Head size and FA

After flood 1, we captured 78 female spiders, with 40 individuals from the control mesocosms and 38 individuals from the flooded ones. Similarly, after flood 4, 83 female spiders were captured, with 43 individuals from the control and 40 individuals from the flooded mesocosms.

Analysis of head size revealed a significant seasonal effect, with individuals from flood 1 displaying significantly larger heads compared to their immature offspring from flood 4 (Figure 4; $\chi^2 = 258.5$, df = 1, $p < 0.001$). However, there was no significant effect of the flooding ($\chi^2 = 0.12$, df = 1, $p = 0.7$) or the interaction of flooding and season on head size ($\chi^2 = 0.03$, df = 1, $p = 0.9$).

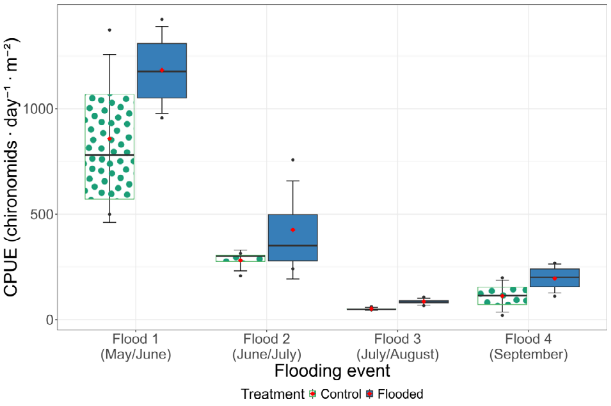

FIGURE 3 Number of chironomid individuals per square meter of trap surface (catch per unit effort [CPUE]) during each of the four flooding events according to flood exposure (control in green, 14 days flood in blue). Lower and upper box boundaries 25th and 75th percentiles, respectively. Lines inside the box represent the median, red dots the mean values, whiskers the standard deviation and black dots the outliers.

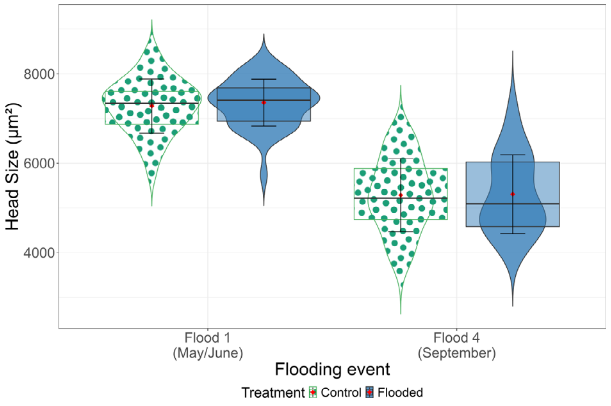

FIGURE 4 Head size of *Tetragnatha extensa* in control (green) versus flooded (blue) mesocosms after the first and fourth flood event (control flood 1: $n = 40$, control flood 4: $n = 43$, flooded flood 1: $n = 38$; flooded flood 4: $n = 40$). Lower and upper box boundaries 25th and 75th percentiles, respectively. Lines inside the box represent the median, red dots the mean values, whiskers the standard deviation.

The GLM on the FA revealed a significant flooding × flooding event interaction (Figure 5; $\chi^2 = 4.9$, df = 1, $p = 0.04$). We found that spiders collected after flood 4, that had developed under non-flooded conditions, showed 15% higher FA compared to those from the flooded mesocosms (df = 156, $t = 2.05$, $p = 0.04$).

DISCUSSION

The experiment showed that flooding of riparian grassland has an effect on the development of *T. extensa* spiders, influencing their

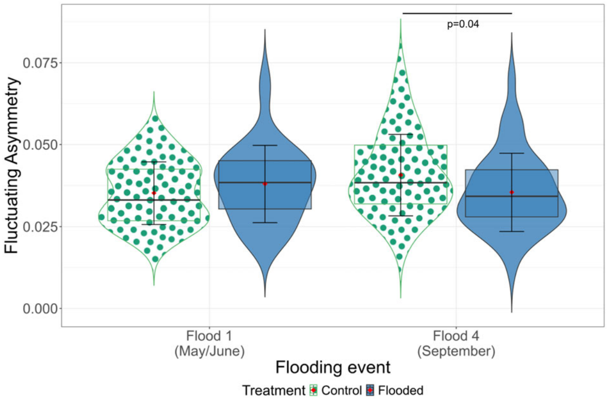

FIGURE 5 Fluctuating Asymmetry score in *Tetragnatha extensa*'s head in control (green) versus flooded (blue) mesocosms after the first and fourth flood event (control flood 1: $n = 40$, control flood 4: $n = 43$, flooded flood 1: $n = 38$; flooded flood 4: $n = 39$). Lower and upper box boundaries 25th and 75th percentiles, respectively. Lines inside the box represent the median, red dots the mean values, whiskers the standard deviation. The outlier was removed.

fluctuating asymmetry, but not their size. Following the first flooding event, there were no differences in either fluctuating asymmetry or size between spiders from flooded and non-flooded mesocosms. At the end of the season, after flood 4, individuals that had developed under flooded conditions exhibited higher symmetry, indicating improved developmental stability despite similar growth outcomes. Since flooding consistently led to higher chironomid emergence throughout the season compared to the controls, the increase in aquatic prey availability may have contributed to a higher diet quality and thus to a more stable spider development. At the same time, other effects of flooding, such as the creation of a more favourable microclimate with increased moisture and lower temperatures or shifts in terrestrial insect communities and predator–prey interactions, cannot be ruled out. Additionally, higher water levels may bring emerging aquatic insects into closer proximity to *Tetragnatha* webs spun on the riparian vegetation, potentially increasing prey capture success.

Our findings suggest that seasonal flooding events, when moderate, can enhance the availability of aquatic prey such as chironomids, which in turn may benefit terrestrial predators like spiders by improving foraging conditions (Henschel et al., 2001). Chironomids are well adapted to moderate environmental disturbances like flooding (Anderson & Ferrington, 2013; Dorić et al., 2023). Regular and moderate flooding events can create shallow habitats over terrestrial areas that warm more rapidly, potentially triggering earlier hatching or a more prolonged hatching period (Lytle, 2002). Our experimental set-up allowed drifting macroinvertebrates, such as Chironomidae larvae at various developmental stages, to enter throughout the experiment. We suggest that flooding in our system created more favourable conditions for larval survival and emergence by increasing water volume and surface area, prolonging retention time, reducing flow velocity and slightly raising temperatures (personal observations). Moreover, these hydromorphological conditions might have reduced larval drift out of the system, enhancing their retention. Thus, the increased emergence observed may result from both improved larval survival and altered drift dynamics under flooded conditions. Additionally, flooding increases the total water coverage over a given area, expanding the habitat available for aquatic insect emergence, thereby increasing the potential number of emerging insects for terrestrial predators. However, in our mesocosms, the expanded flooded terrestrial areas did not contribute substantially to chironomid emergence: only a few individuals (less than 0.5% of the total) emerged from these areas. While this suggests that most emergence occurred in the stream section, it is possible that the longer-term consequences of flooding could create more favourable conditions for chironomid larvae developing in wet soils. Our experimental design, with relatively short floods and intervals between flooding cycles, may have limited the opportunity for specialized chironomids to complete development and hatch (Frouz et al., 2003). In more natural settings, where longer periods elapse between floods, wetter soils could support enhanced larval growth and emergence, potentially sustaining aquatic insect flux over extended periods.

Prey availability and the presence of flooding did not affect spider head size. Despite lower emergence of aquatic insects in non-flooded mesocosms, spiders achieved similar growth, suggesting that either the reduced aquatic input was still sufficient or that spiders effectively supplemented their diet with terrestrial prey to maintain development (Radermacher et al., 2020; Takada et al., 2014). While previous studies have shown that prosoma size can reflect food limitation (Vollrath, 1988), our results indicate no significant difference in growth between spiders from control and flooded mesocosms. This suggests that overall food availability was sufficient in both cases. However, Pietz et al. (2023) demonstrated in a laboratory experiment that reduced intake of physiologically important fatty acids from the same ingested biomass reduced the growth of *T. extensa*. This suggests that in the control mesocosms the spiders may have compensated for the fatty acid deficit from aquatic insects by consuming more terrestrial prey in order to maintain the same growth rate. Nevertheless, variations in the composition and ratio of the spiders' diet of aquatic and terrestrial prey likely led to differences in the fatty acids ingested.

Aquatic insects, such as chironomids, are richer in PUFAs than terrestrial insects (Hixson et al., 2015; Kowarik et al., 2021). PUFAs play a fundamental role in optimal growth and development, maintaining cell membrane function, hormone regulation and organism detoxification (Fritz et al., 2017), processes that are particularly sensitive during early developmental stages. In spiders, fluctuating asymmetry can be linked to developmental stress and be influenced by various factors, including food availability and quality or exposure to disturbances (Uetz et al., 2009). In our experiment, flooding increased aquatic insect availability, and spiders from flooded mesocosms showed lower asymmetry than those from non-flooded ones. Although we did not measure diet directly, greater access to PUFA-rich aquatic prey may have contributed to more stable development. Conversely, spiders in non-flooded mesocosms may have needed to forage more actively, increasing energetic demands, exposure to predators and reliance on lower-quality prey. Under such conditions, regulatory compounds required for maintaining symmetrical prosoma development may instead be diverted to other stress-mitigating functions, leading to small but detectable increases in fluctuating asymmetry. Experimental studies often show that strong stress can cause mortality before fluctuating asymmetry becomes measurable, whereas moderate stress allows subtle deviations to emerge (Symanski & Redak, 2021). The absolute differences we measured were minor and do not necessarily translate into direct measurable fitness consequences (e.g., head size). These minor deviations can nonetheless serve as sensitive markers of elevated developmental stress, reflecting subtle physiological or behavioural costs (De Coster et al., 2013). Similar patterns have been observed in other arthropods, such as grasshoppers stressed along an urbanization gradient (Rech et al., 2022). Since no comparative fluctuating asymmetry values are available from experimental studies that also measured fitness, our results do not allow us to conclude about fitness consequences. We encourage future studies to assess fitness consequences (e.g., mating success, egg clutch size, offspring survival) alongside asymmetry and size to test whether fluctuating asymmetry provides additional ecological insight beyond traditional size-based approaches.

As a result, floods may not only increase emergence but also shift the ratio of terrestrial to aquatic prey in spider diets (Henschel et al., 2001), impacting developmental stability. To our knowledge, no studies have directly linked dietary variation to fluctuating asymmetry in spiders, highlighting the need for future research in this direction as an indicator of nutritional stress.

Moulting is a critical phase in spiders' development, particularly sensitive to environmental conditions and nutritional quality, making it a key window where developmental instability, and thus fluctuating asymmetry, can arise. In our experiment, flooding may have impacted this specific aspect of spider ontogeny through two pathways: nutritional composition and moisture. Specific PUFAs have been linked to moulting efficiency and success as well as developmental stability (Wen et al., 2024), suggesting that shifts in prey composition could further influence fluctuating asymmetry. In addition, floods increased moisture, an essential parameter in spider moulting performance (DeVito & Formanowicz, 2003). Together, these factors suggest that flooding can influence fluctuating asymmetry not only by affecting aquatic prey availability but also by directly supporting the physiological demands of moulting.

The experiment highlights the critical role of aquatic subsidies in shaping riparian predator development. While river regulation has historically decreased flooding of riparian grassland, climate change will likely amplify drought stress while intensifying flood events at longer intervals, altering aquatic insect emergence dynamics. Predators relying on emergent aquatic insects may experience shifts in growth, symmetry and overall fitness, as well as a potential decoupling of prey availability during critical life stages. Such changes could alter food web dynamics through cascading effects, leading to shifts in predator diet, competition and prey selection. While we did not directly link fluctuating asymmetry to fitness response such as offspring production, our results show that asymmetry is sensitive to environmental variation that could not be detected with traditional size-based measurements. Although the study does not provide mechanistic conclusions, it provides a novel assessment of spider responses to dietary and hydrological stress, suggesting that changes in prey availability can influence developmental stability. Given that riparian zones are key ecosystems supporting biodiversity and trophic interactions, further research into both prey quantity and quality is crucial, as shifts in aquatic insect diversity and nutritional value could have an even greater impact on predator development and terrestrial food web dynamics.

AUTHOR CONTRIBUTIONS

Stephane Mutel: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; validation; writing – original draft; writing – review and editing; visualization. **Martin H. Entling:** Conceptualization; funding acquisition; supervision; validation; writing – review and editing. **Ken M. Mauser:** Conceptualization; formal analysis; validation; writing – review and editing. **Federica Spani:** Methodology; software; validation; writing – review and editing. **Celia Thomas:** Formal analysis; investigation; writing – review and editing. **Collins Ogbeide:** Resources; investigation; writing – review and editing. **Mirco Bundschuh:** Funding acquisition; supervision; writing – review and editing. **Franziska Fiolka:** Investigation; writing – review and editing. **Franziska Middendorf:** Investigation; writing – review and editing. **Ralf Schulz:** Funding acquisition; supervision; writing – review and editing. **Alessandro Manfrin:** Conceptualization; methodology; validation; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study (Mutel et al. 2025) are openly available in Zenodo at http://doi.org/10.5281/zenodo.17360335.

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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. Floating emergence trap made with PVC tube—50 cm × 50 cm base covered by foam isolation tubing (Picture: Pradeep Chintapalli).

Table S1. Calendar of the RSM 2023 experiment—flooding period in blue, emergence sampling period in light brown and *Tetragnatha extensa* handpicking in green (1 June and 23 September).

Table S2. Statistics of Procrustes ANOVA evaluating potential shape variations generated by landmarking errors on 20 random spider's prosoma from flood 1. The table reports the degrees of freedom (df), sum of squares (SS), mean square (MS), proportion of total variance (R^2), *F*-ratio (*F*), and *p*-value.

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