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REVIEW ARTICLE

Review of the importance of aquatic prey for riparian arthropod predators

Franziska Middendorf[a,*], Mirco Bundschuh[a,b], Bernhard Eitzinger[a], Martin H Entling[a], Jens Schirmel[a,c]

[a] *iES Landau, Institute for Environmental Sciences, University of Kaiserslautern-Landau (RPTU), Fortstraße 7, 76829, Landau, Germany*
[b] *Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Lennart Hjelms väg 9, SWE-75007, Uppsala, Sweden*
[c] *Eusserthal Ecosystem Research Station, University of Kaiserslautern-Landau (RPTU), Birkenthalstraße 13, 76857, Eusserthal, Germany*

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ABSTRACT

Aquatic-derived resources can be important subsidies for riparian consumers. We systematically reviewed variations in the use of aquatic prey by riparian predators and investigated whether changes and differences in the availability of emerging insects influence riparian arthropod predator communities. We found that aquatic subsidies present a major food source for several riparian arthropod predators. However, the role of aquatic prey in the diet varied between predator groups and hunting strategies. Riparian web-building spiders, especially horizontal web-builders such as *Tetragnatha*, showed the highest proportion of aquatic insects in their diet (70 %). However, free-hunting spiders and riparian beetles also benefited substantially from these subsidies. The use of aquatic prey decreased with increasing distance from the water, varied throughout the year in line with the emergence peaks, and was affected by habitat characteristics. Our review also shows that the abundance and biomass of riparian arthropod predators can be influenced by variations in the availability of aquatic subsidies. This was particularly evident for riparian web-building spiders, especially horizontal web-building spiders such as *Tetragnatha*. Despite the considerable research activity over the past two decades, we identified several research gaps and present opportunities for future studies. First, there is a clear geographical bias, with a marked lack of studies in the Southern Hemisphere and Asia, with the exception of Japan. Second, most studies have focused on a few families of mostly web-building spiders while only a few have considered spiders with different hunting modes (e.g., ambush hunters or free hunters on vegetation), carabids and other beetles. Third, most studies used stable isotope analysis (SIA) for prey analysis. Additional methods, such as polyunsaturated fatty acid (PUFA) analysis, molecular gut content analysis, or combinations of these methods with SIA, should give a clearer picture of the reliance of riparian arthropods on aquatic prey.

Introduction

Ecosystems are interconnected by flows of energy and nutrients in the form of subsidy fluxes. Interest in the importance of aquatic-derived resources for terrestrial systems has grown strongly over time (Baxter et al., 2005; Kraus et al., 2020; Schulz et al., 2015, 2024). Although the mass transfer of organic carbon from terrestrial to aquatic ecosystems is typically higher, the nutritional quality of the flux from water to land is superior (Marcarelli et al., 2011; Twining et al., 2016). In particular, the export of essential polyunsaturated fatty acids (PUFAs) – such as arachidonic acid (ARA 20:4n-6) or eicosatetraenoic acid (EPA, 20:5n-3) – from aquatic ecosystems is vital for physiological processes in terrestrial consumers (Martin-Creuzburg et al., 2017; Twining et al., 2019).

Terrestrial animals that directly benefit from aquatic subsidies include fish-eating mammals and birds such as bears (e.g., *Ursus arctos*; Levi et al., 2020), raccoon dogs (e.g., *Nyctereutes procyonoides*; Kauhala et al., 1998), kingfisher (e.g., *Alcedo atthis*; Nessi et al., 2021), and cormorants (e.g., *Phalacrocorax carbon*; Klimaszyk & Rzymski, 2016). In addition, aquatic insects – i.e. species with aquatic larvae and terrestrial adults such as biting and non-biting midges, stoneflies and caddisflies – are an important food source for bats (e.g. Daubenton's bat; Vaughan, 1997), birds (e.g., Swallows; Jackson & Fisher, 1986; McCarty, 1997) and lizards (e.g. *Sceloporus* sp.; Sabo & Power, 2002). Importantly, the quantity and quality of the resource flows between aquatic and terrestrial systems are highly dependent on river structure (Füreder et al., 2005; Vannote et al., 1980) and environmental conditions, such as nutrient enrichment (Davis et al., 2011; Galloway & Winder, 2015; Kelly et al., 2019). These cross-ecosystem fluxes are also determined by season

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* Corresponding author.
E-mail address: franziska.middendorf@rptu.de (F. Middendorf).

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(Ahlgren et al., 1997) as well as top-down (Collins et al., 2020) or bottom-up processes (Allen et al., 2012).

Arthropods play a key role among riparian consumers due to their high diversity and abundance. Several riparian arthropod predators, such as spiders (Arachnida), ground beetles (Coleoptera: Carabidae) and rove beetles (Coleoptera: Staphylinidae), feed on aquatic subsidies, particularly aquatic insects (Nash et al., 2023; Paetzold & Tockner, 2005). For example, the diet of riparian web-building spiders – such as species of the genus *Tetragnatha*, the most diverse genus of long-jawed orb weavers (Tetragnathidae) – may be dominated by prey of aquatic origin Bollinger et al. (2023); Gergs et al. (2014); Krell et al. (2015). Aquatic subsidies can affect the abundance, biomass, density and fitness of riparian arthropod predators: Burdon and Harding (2007) showed that the abundance of web-building spiders was positively associated with biomass of emerging stream insects, suggesting that low predator abundance are due to low emergence rates. Similarly, Uno (2016) found that body sizes and juvenile survival rates of spiders were negatively affected by reduced abundances of aquatic insects. Earlier studies found that species with different web orientations (horizontal, vertical, sheet) responded differently to aquatic subsidy availability (Kato et al., 2003). Given the numerous studies published since, it is worth investigating whether these findings still hold.

Driven by the growing interest in this area, Lafage et al. (2019) conducted a meta-analysis of aquatic subsidy consumption by riparian arthropod predators based on 21 stable isotope analysis (SIA) studies and found that the aquatic subsidy usage was higher than expected. Our review expands on these findings by incorporating additional studies across diverse ecosystems and water body types, integrating non-SIA methods, and considering various spider hunting strategies. Our understanding of the variation in the usage of aquatic prey between different riparian arthropods and the consequences of changes and differences in the quality and quantity of emerging insects for riparian predators is still incomplete. This systematic review aims to fill these gaps by including studies that extend beyond SIA and by considering data on diet composition as illustrated by molecular gut content analysis and PUFA, as well as community data of riparian predator species. We addressed the following research questions: (i) Which riparian arthropod predator taxa and habitats were predominantly studied and in which geographical regions? (ii) Which approaches (e.g., SIA, molecular gut content, biomass, abundance) were used to study carnivore consumer-resources relationships for aquatic-derived resources? (iii) To what extent do aquatic subsidies contribute to the diet of riparian arthropod predators, and what internal (e.g., life stage, body size) and external (e.g., season, distance from the water) factors influence this? (iv) How can the availability and abundance of aquatic subsidies affect the abundance of riparian arthropod predators?

Literature search and data usage

We systematically searched the literature on the linkage between aquatic subsidies and riparian arthropod predators. We performed multiple searches without time restrictions in ISI Web of Science (https://www.webofscience.com/) and Google Scholar (https://scholar.google.de/), with the last search on 08 January 2025, using combinations of the following keywords: “terrestrial* arthropod*" OR "terrestrial* insect*" OR carabid* OR beetle* OR coleoptera* OR spider OR arachnid* OR "ground* dwelling" OR ”Opiliones” OR “harvestmen” OR “ant*” OR “Formicidae” AND "riparian* area*" OR stream* OR river* OR shore* OR "water* edge*" OR drift* OR flood* OR "wash* margin” AND "aquatic insect*" OR emergence* OR "aquatic* subsid*" OR drift* AND feeding* OR "food web*" OR diet* OR prey* OR predator*. The searches yielded 353 peer-reviewed studies, and the references in these publications were screened for additional potentially relevant literature (White, 2009). For our review, we focused on freshwater habitats that reported the use of aquatic subsidies by riparian arthropod predators. We included brackish waters because, similar to freshwater systems, they host aquatic insects, mainly chironomids, as potential prey for terrestrial arthropods (Fuentes et al., 2005; Parma & Krebs, 1977). Therefore, by screening titles and abstracts, we excluded studies that (I) studied only riparian herbivores or vertebrates, (II) investigated marine environments (except brackish), (III) studied only the pollution transfer from aquatic to terrestrial areas via aquatic subsidies, and (IV) analyzed the effects of terrestrial subsidies for aquatic consumers. A total of 109 studies were retained for this systematic literature review (see Appendix A Table 1). From these studies, we gathered information on the taxa of riparian arthropod predators and their prey studied, the methods used to identify the relation between riparian arthropod predators and aquatic subsidies (e.g., community analyses, SIA, gut content analyses), the study area (country), the waterbody studied (lentic, lotic or brackish) and the adjacent terrestrial habitats (e.g., forest, urban area, pasture). In some studies, more than one riparian arthropod predator taxon was observed, so the number of observations may exceed the number of studies.

Our qualitative review is based on all articles found ($N_{studies} = 109$). An exception is the presentation of the results related to the proportion of consumed aquatic subsidies by riparian arthropods (research question iii). To estimate the average proportions of consumed aquatic subsidies in the diet of riparian arthropod predators, only studies using SIA were used ($N_{studies} = 57$), because only these studies included proportions of consumed prey. Where sampling sites in these studies were arranged along lateral gradients from the shore to the adjacent terrestrial habitat, we only used data from the sampling site closest to the aquatic ecosystem. This limitation was made to allow for better comparability and because only a few observations were available at greater distances from waterbodies, but we have included distance information in the discussion. By measuring the ratios of stable isotopes such as nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$), SIA provides information on the trophic level of the consumer and the proportion of aquatic subsidy in the diet (Inger & Bearhop, 2008; Peterson & Fry, 1987; Post, 2002). However, the use of this method may over- or underestimate the aquatic prey based on the consumed carbon source of the prey or the challenge of determining the appropriate trophic discrimination factor (Mellbrand & Hambäck, 2010; Stephens et al., 2023). DNA-based gut content analysis is a powerful tool for understanding short-term dietary patterns by identifying recently consumed organisms down to species level. In particular, metabarcoding of gut content allows to characterize the collective prey community of single predator specimen. Yet, a correct quantification of ingested prey is hampered due to several methodological factors (e.g., primer bias Lamb et al., 2019) which is why most studies use frequency of prey occurrence across many predator individuals to measure prey proportions (e.g., Huszarik et al., 2024). While methods to quantify prey sources with DNA metabarcoding are being developed (Luo et al., 2023; Uiterwaal & DeLong, 2024), such information is not yet available for the diet of riparian predators. PUFA analysis provides short-term, high-resolution dietary information and tracks essential nutrients. As the PUFA content of aquatic organisms is higher than that of terrestrial organisms (which cannot synthesise them themselves), the occurrence of certain PUFAs in terrestrial consumers is a good proxy for aquatic sources (Hixson et al., 2015; Twining et al., 2016). Moreover, two studies have analyzed the gut content of riparian beetles by visual examination (Hering, 1998; Hering & Plachter, 1997). This method provides a direct indication of the midgut content, but it is very time-consuming and requires a high level of expertise in identifying insect fragments. However, calculating the actual amount of aquatic subsidies consumed remains a challenge (Heissenberger et al., 2010). It is not the aim of this literature review to compare the different methods; for further discussion, see Kuhrt et al. (2024) and Nielsen et al. (2018). Instead, we draw on findings from various studies to analyze prey use, acknowledging that different methods may yield varying results. Notably, we did not integrate results from different methods in our calculations, as numerical data from SIA were more prevalent than those from other approaches.

Overview of studies

The use of aquatic subsidies by riparian arthropod predators was studied predominantly in the Northern Hemisphere, particularly in Europe (37.7 %) and North America (35.8 %), followed by Asia (16.0 %; Fig. 1A). Only a few studies were conducted in the Southern Hemisphere, including Australia, Brazil, New Zealand, and South Africa (Fig. 1A). Since 2000, the number of studies per year has steadily increased, while earlier publications appeared less frequent (Fig. 1B).

Representation of predator taxa, habitats and aquatic subsidies

Among the studies included in this systematic literature review, 78 specifically targeted spiders (Araneae) (Fig. 1A and 2A). Of these, 33 focused on web-building spiders, 15 on free-hunting spiders, and 30 either included both or did not provide identification beyond spiders. At the family level, Tetragnathidae ($N_{Studies} = 46$, all belonging to the genus *Tetragnatha*), Araneidae ($N_{Studies} = 28$), and Linyphiidae ($N_{Studies} = 22$) were the most studied web-building spiders, whereas Lycosidae ($N_{Studies} = 42$) and Pisauridae ($N_{Studies} = 11$) were the most studied free-hunting spiders (see Appendix A Table 2). Remaining studies often combined spiders with other taxa, such as carabid beetles (Coleoptera: Carabidae) or rove beetles (Coleoptera: Staphylinidae), or combined different beetle species (Fig. 2A). Only five studies exclusively investigated carabid beetles (Fig. 2A).

Most of the studies ($N_{Studies} = 66$) investigated riparian arthropod predators adjacent to lotic waters, ranging from large rivers, such as the Scioto River (Ohio, USA: 372 km length) (Alberts & Sullivan, 2016), to small streams such as the Buizin (France: 12 km length) (Barthélémy et al., 2022). Among these studies, 29 did not consider the river section as an influencing factor, and detailed information on the location of the study sites along the watercourses was often not provided. However, 23 studies focused on a specific river section (headwater: $N_{Studies} = 11$ middle reach $N_{Studies} = 12$), and 14 studies took place along the river course. The linkages between aquatic subsidies and riparian arthropod predators were studied much less frequently in lentic ($N_{Studies} = 13$) and brackish waters ($N_{Studies} = 3$). Three out of the four studies on brackish waters were conducted on the southern Swedish coast, adjacent to the Baltic Sea, and one in Florida (USA) at a brackish creek (Moon & Silva, 2013). Across all water body types, the most common adjacent terrestrial habitat studied was forest ($N_{Studies} = 45$), followed by grassland ($N_{Studies}= 10$). In addition, only seven of all the studies provided specific details on the distance from the wateŕs edge at which they sampled, while most others simply described the sampling sites as “close to the wateŕs edge”.

As our systematic review focused on arthropod predators, only animals were considered as aquatic subsidies. In most studies (83 %), the aquatic insects considered as food sources were not further analyzed, while Chironomidae were identified as aquatic prey in 10 % of the studies, followed by Ephemeroptera, Plecoptera and Diptera (7 %). In most cases, only live insects were interpreted as prey, while only four studies argued that dead washed-ashore insects are a potential food source.

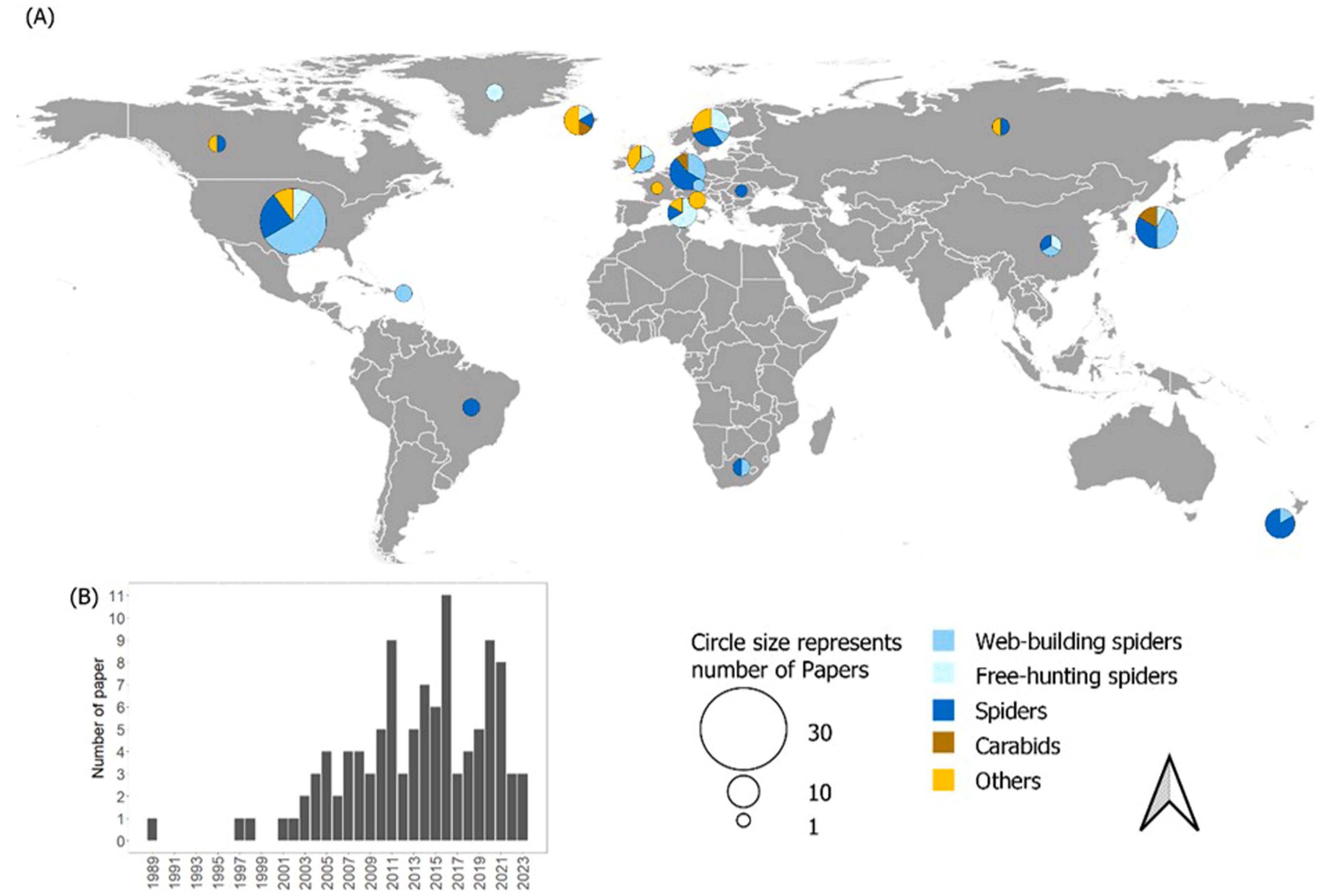

Fig. 1. (A) Spatial pattern of publications (circle size indicates number of studies) and studied organism groups (web-building spiders = exclusively investigating web-building spiders; free-hunting spiders = exclusively investigating free-hunting spiders; spiders = investigating spiders in general; carabids = exclusively investigating carabids; others = studies which did not fit in one of the other categories including roove beetles, harvestman, ants, common woodlouse and click beetles). (B) Number of publications per year between 1989 and 2023.

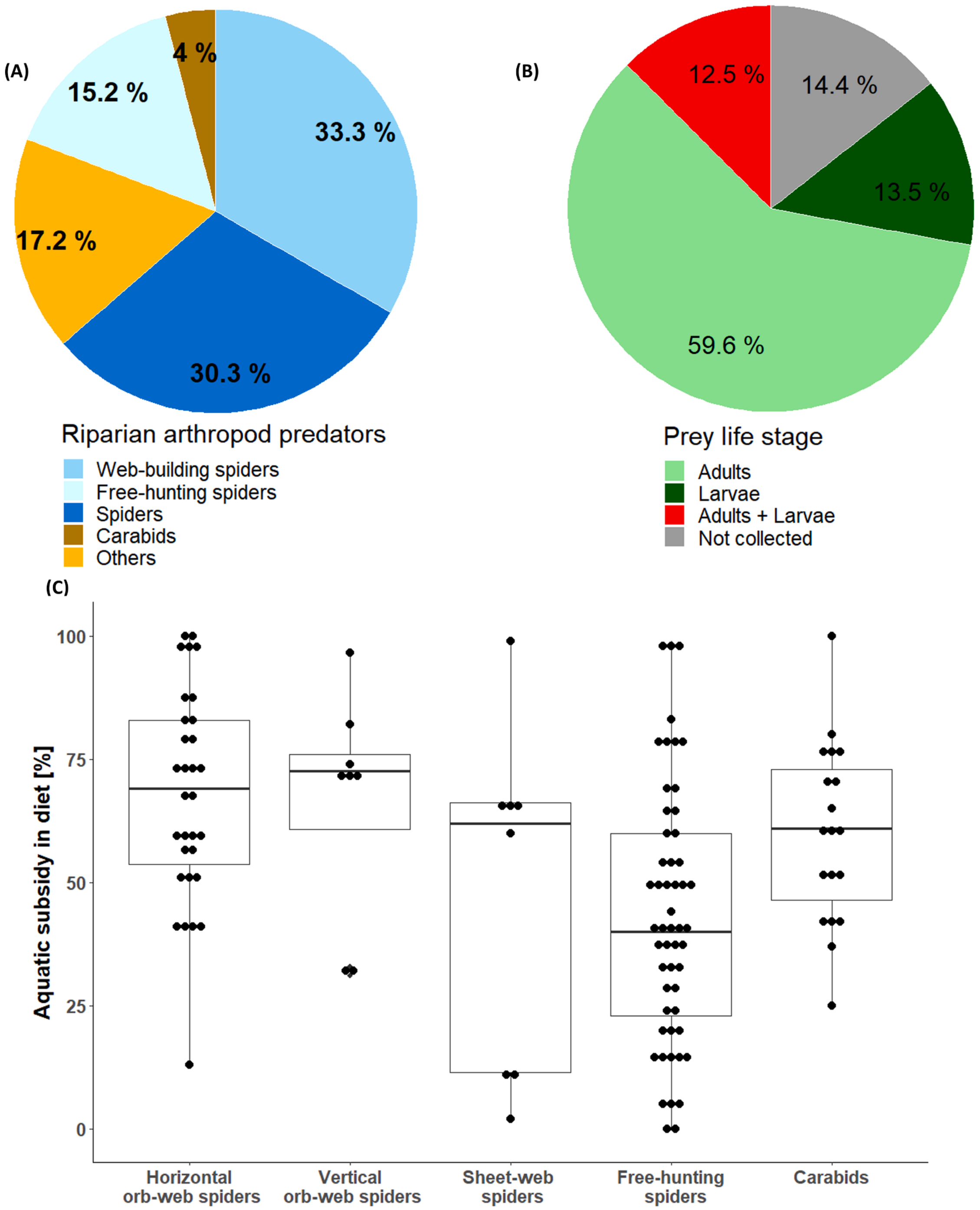

Fig. 2. Proportion of studies for (A) investigated riparian arthropod predator groups and (B) life stages of the sampled aquatic prey sources. (C) Proportion of consumed aquatic subsidies by horizontal orb-web spiders ($N_{studies} = 24$, $N_{observations} = 31$), vertical orb-web spiders ($N_{studies} = 7$, $N_{observations} = 8$), sheet-web spiders ($N_{studies} = 7$, $N_{observations} = 8$), free-hunting spider ($N_{studies} = 44$, $N_{observations} = 54$), carabids ($N_{studies} = 5$, $N_{observations} = 19$).

Approaches to study aquatic subsidies to riparian arthropod predators

The approaches to examine the use of aquatic subsidies by riparian arthropod predators can be divided into two main groups: (1) approaches to quantify the amount of aquatic prey in the diet of the target organism ($N_{studies} = 68$), and (2) approaches to analyze the abundance (including biomass, density or related measures) of the riparian arthropod predators as a response to the (altered) availability of the aquatic subsidies ($N_{studies} = 29$). Some studies examined other response variables such as feeding behavior or body condition. These studies will not be further discussed.

Various analytical methods have been used to study the diet of riparian arthropod predators (group 1). Stable isotope analysis is the most common method to quantify the proportion of aquatic and terrestrial food sources by analyzing the amount of nitrogen (^{15}N) and carbon (^{13}C) in riparian arthropod predators, sometimes in combination with PUFA ($N_{Studies} = 3$) or gut metabarcoding ($N_{Studies} = 1$). In addition, 10 studies used PUFA and two studies used DNA metabarcoding exclusively (Northam et al., 2012; Verschut et al., 2019). The relatively large number of SIA studies found in our review is due to the fact that this method was used much earlier than PUFA or molecular gut content analysis. Finally, two studies used microscopic gut content analysis of carabids (Hering, 1998; Hering & Plachter, 1997). Sampling of the potential aquatic prey is required for SIA and PUFA analyses to establish a baseline. A variety of methods were used, with sampling of emerging insects ($N_{Studies} = 75$) being the most common approach, followed by sampling of aquatic insect larvae ($N_{Studies} = 27$; Fig. 2B). Emerging insects were mainly collected using pyramidic floating emergence traps, sticky traps, or sweep nets. Aquatic larvae were mainly sampled with kick net techniques or Surber sampling (Surber, 1937). However, even when larvae were collected for SIA, the majority of studies considered only the flying adult stage as a potential food source for riparian arthropod predators (Paetzold et al., 2005; Raikow et al., 2011).

In studies of subsidy effects on predator abundance (group 2), predators were mostly collected by hand-picking ($N_{Studies} = 21$). Each of the remaining methods e.g., sweep netting, counting webs, and suction sampling using an adapted leaf vacuum, was used in less than four studies.

Aquatic insects in the diet of riparian arthropod predators

Variation of aquatic subsidies in the diet between riparian arthropod predator groups

Aquatic insects are high-quality food for riparian predators due to their PUFA composition (Pietz et al., 2023). In our literature review, we found that aquatic insects are often an important component of the diet of many riparian arthropod predators (Fig. 2C). While the SIA data collected from the literature showed a high variation in the intake of aquatic food sources both within and between predator groups, the mean intake of aquatic resources was higher in horizontal web-building spiders (70.0 % ± 19.1; $N_{studies} = 24$) compared to vertical web-building spiders (e.g., Araneidae; 66.5 % ± 21.4; $N_{studies} = 7$), sheet-web weavers (Linyphiidae; 47.1 % ± 21.4; $N = 7$), free-hunting spiders (e.g., Lycosidae 46.0 % ± 23) and carabids (60.0 % ± 17.9; $N_{studies} = 5$) (Fig. 2C). The high ingestion of aquatic prey by horizontal web-building spiders, as observed in our review, aligns with the findings of Gillespie (1987) and Tagwireyi and Sullivan (2014). These studies show that such spiders typically build their webs in overhanging vegetation near water, increasing their chances of capturing emerging aquatic insects.

The remarkably large variation in aquatic prey intake suggests interspecific differences in riparian arthropod predators and reflects the heterogeneity in sampling design, season, waterbodies, habitat types and geographical regions examined between studies. Importantly, prey choice is influenced not only by the availability of aquatic prey in the environment but also by the physical conditions of the predator species (e.g., life stage), as well as local and landscape-scale habitat and environmental conditions (e.g., waterbody size, riparian habitat type, surrounding land use and associated water pollution). Our review identified several factors that influence the proportion of aquatic prey in the diet of riparian arthropod predators, which are discussed in the following paragraphs.

Sex, life stage and body size

Our review demonstrates that prey selection in riparian spiders and beetles can be influenced by sex, life stage and body size. For example, males of the spider *Trichonephila clavata* (Nephilidae), which are substantially smaller than females (Chuang et al., 2023), feed relatively more on aquatic insects than females, even when the number of aquatic and terrestrial prey in the webs was constant (Akamatsu et al., 2007). Furthermore, juvenile wolf spiders have been shown to feed more on aquatic prey, while adults shift to terrestrial prey, even when aquatic prey such as chironomids are abundant (Verschut et al. 2019). This pattern may be explained by a more favorable predator-prey body size ratio, with aquatic prey often being smaller than terrestrial prey (Akamatsu & Toda, 2011). Similarly, smaller spiders are less efficient at capturing larger terrestrial prey due to their morphological characteristics and web structure (Collier et al., 2002). Consistent with this, smaller carabid beetles (e.g., *Bembidion* spp.) have been shown to feed more on aquatic subsidies (90 %) than larger carabids (e.g., *Nebria picicornis*; 51 %), despite sharing the same riparian habitat (Hering & Plachter, 1997). However, it should be noted that factors other than body size, such as agility, may contribute to the reduced aquatic uptake in larger beetles.

Distance from the water

Across different groups of riparian arthropod predators, the proportion of aquatic subsidies in the diet of predators decreases with increasing distance from the water (e.g., Hering & Plachter, 1997; Lafage et al., 2019; Surber, 1937; Verschut et al., 2019). Three out of four studies on web-building spiders showed a clear decrease of aquatic subsidies in the diet with increasing distance, including lentic and lotic waters as well as brackish waters (Henschel et al., 2001; Mellbrand et al., 2011; Raikow et al., 2011). Similarly, the proportion of aquatic prey in the diet of free-hunting spiders decreased with increasing distance from the water (Briers et al., 2005; Fritz et al., 2017; Paetzold & Tockner, 2005) and carabid beetles sampled more than 50 m from the water's edge fed exclusively on terrestrial food sources (Paetzold & Tockner, 2005). It appears logical that this pattern occurs because the availability of aquatic insects decreases with increasing distance from the water's edge. In a meta-analysis, Muehlbauer et al. (2014) showed that aquatic prey activity was highly concentrated within 1.5 m of the waterbody, while only 10 % of the insect activity was found at a 500 m distance.

The reduced proportion of aquatic subsidies in the diet of predators with increasing distance from the water may also be due to lateral shifts in the composition of the predator community, with the abundance of riparian specialists decreasing with distance from the shoreline (Gallé & Schwéger, 2014; Scheidler, 1990). This is discussed in the chapter "Aquatic subsidies and the abundance riparian arthropod predators". However, a recent study found no difference in aquatic prey consumption between syntopic pairs of riparian specialist and generalist spiders (Bollinger et al. 2023).

Seasonal effects

The uptake of aquatic subsidies can vary with season (Chan et al., 2007; Gratton et al., 2008). However, it should be considered that this may interact with the ontogenetic stage of the predator and associated changes in dietary requirements (see above; Akamatsu et al., 2007). Nevertheless, a clear relationship between the seasonal peak of emergence and the number of aquatic insects in the diet was reported for web-building spiders (e.g., Chan et al., 2009; Chari et al., 2020; Kelly et al., 2015; Kowarik et al., 2021). For example, along tropical forest streams in China, the emergence of aquatic insects was lower in the dry season, resulting in 50 % fewer aquatic insects in the diet of web-building spiders (Chan et al., 2007, 2009). Furthermore, *Tetragnatha* spiders in Switzerland had the highest concentration of Eicosapentaenoic acid (EPA) – a long-chain fatty acid associated with aquatic sources (Hixson et al., 2015; Kowarik et al., 2021) – in spring, the season with the highest emergence of aquatic insects (Salvarina et al., 2017). Chironomids are often the most abundant emerging insects in aquatic habitats (Kautza & Sullivan, 2016). Indeed, feeding of web-building spiders on chironomid midges increases with prey density (Diesburg et al., 2021; Gergs et al., 2014). Similar to web-building spiders, the feeding behavior of free-hunting spiders has been shown to be altered by seasonal variation in the abundance of aquatic insects (Siebers et al., 2021; Verschut et al., 2019), with aquatic insects accounting for a higher proportion in the diet as the abundance of emerging aquatic insects increases. The diet of riparian carabids may be affected by seasonality in different ways, with some species showing temporal variation in the intake of aquatic subsidies, as described for spiders, while other carabids are highly dependent on aquatic insects throughout the season (Gratton et al., 2008; Terui et al., 2017). This may indicate that some carabid beetles actively hunt for aquatic insects, whereas other riparian carabids and spiders often are more generalist feeders whose diet is more dependent on what prey is available.

Size and trophic productivity of waterbodies

The primary productivity in river networks generally increases from headwaters (energized by the input of carbon particulate organic matter from adjacent terrestrial areas) towards the middle and lower reaches (Vannote et al., 1980). As a result, the biomass and transfer of aquatic insects to adjacent terrestrial habitats typically increases towards the highly productive middle and lower reaches (Vannote et al., 1980). The literature confirms that changes in the size and trophic productivity of waterbodies lead to changes in the availability of aquatic subsidies and consequently affect the proportion of aquatic insects in the diet of riparian arthropod predators ($N_{\text{studies}} = 7$). For example, high transfers of aquatic subsidies in middle and lower reaches increased the proportion of aquatic prey in the diet of web-building spiders (Chari et al., 2020). Consistent with this, Marker et al. (2023) reported a higher proportion of aquatic prey in riparian spiders from larger, more productive rivers compared to smaller, less productive streams. However, this pattern may also be influenced by the shoreline-to-water surface ratio, as lower ratios tend to facilitate higher aquatic subsidies (Gratton & Zanden 2009). Additionally, it must be noted that the isotope signal of aquatic insects in headwater regions is often more terrestrially driven (Kraus & Vonesh, 2012; Scharnweber et al., 2014), potentially weakening the aquatic signal in these areas. This complexity makes it more challenging to interpret the proportion of aquatic prey in riparian arthropod predators' diets in relation to waterbody size and productivity.

Riparian habitat, surrounding land-use and associated water pollution

Riparian habitat type and surrounding land use may influence the use of aquatic prey, although no consistent pattern has yet emerged within and across riparian arthropod predator groups. For web-building spiders, there are some indications that riparian forests may promote a more aquatic-based diet compared to open riparian habitats (Alberts & Sullivan, 2016; Ramberg et al., 2020). Spider communities in riparian forests are often diverse and include many web-building species that utilize aquatic prey (Jackson et al. 2016). Furthermore, the availability of alternative terrestrial prey may be higher in productive open grasslands (high primary productivity due to light and nutrient availability), making spiders in riparian forests more dependent on the presence of aquatic subsidies (Alberts & Sullivan, 2016). In contrast, Krell et al. (2015) observed higher proportions of aquatic prey in web-building spiders (Tetragnatidae) in grasslands (80–100 %) than in forests (40–60 %). Presumably, higher tree canopy cover in this study reduced the occurrence of emerging aquatic insects, as shown by Kautza and Sullivan (2015). However, Krell et al. (2015) also found only a small difference in the carbon stable isotope signature between aquatic and terrestrial insects in the forest areas, because aquatic insects may feed more on allochthonous food sources (leaf litter), which are more abundant in forest streams than in streams surrounded by open grassland. This may have underestimated the proportion of aquatic insects in the diet. An overestimation of the aquatic signal in riparian carabids due to the consumption of springtails feeding on aquatic algae was shown by Mellbrand and Hambäck (2010). This shows the limitations of SIA studies and highlights the importance of integrating additional methods (e.g., DNA-metabarcoding of gut content) for a better understanding of the origin of food sources. Furthermore, the use of PUFA could provide valuable insights into the quality of aquatic subsidies. For example, the FA quality of riparian *Tetragnatha* was shown to be higher in forested streams, even though the biomass of emerging insects was higher in agricultural surroundings. Consequently, shading and the stream pool quality appear to be more important determinants of FA quality than agricultural stressors (Ohler, 2024). In contrast to web-building spiders, free-hunting spiders and carabid beetles have been shown to rely more heavily on aquatic subsidies in open than in woody riparian habitats (Briers et al., 2005; Greenwood, 2014; Krell et al., 2015; Lafage et al. 2019; Siebers et al., 2021). Free-hunting spiders and carabid beetles are predominantly active on the ground, and higher abundances of soil-dwelling springtails, which are a high-quality food source, may explain the more terrestrial diet in forests (Krell et al. 2015). In addition, woody vegetation such as shrubs might act as a barrier for flying aquatic insects, restricting their availability in more distant areas around forest streams (Greenwood, 2014).

The surrounding land use, which strongly influences water pollution through the discharge of nutrients, pesticides and metals (Paetzold et al., 2011; Paul & Meyer, 2001; Tong & Chen, 2002), can also affect the diet of riparian arthropods. Water pollution can shift aquatic communities towards smaller insects (often chironomid midges) at the expense of larger species such as caddisflies, mayflies and stoneflies (Jones & Clark, 1987). Therefore, water pollution may explain the low use of aquatic subsidies by riparian web-building spiders in landscapes surrounded by agricultural or urban land use (Graf et al., 2020; Hunt et al., 2020). These aquatic communities may be less favorable for spiders, resulting in a more terrestrial diet of web-building spiders (Graf et al., 2020; Hunt et al., 2020). Thus, web-building spiders tend to have a higher proportion of aquatic insects in their diet in more natural riparian habitats and under more pristine conditions (Graf et al., 2020; Hunt et al., 2020; Kautza & Sullivan, 2016).

Invasive species

Invasive species can profoundly alter food web structure (David et al., 2017). Invasive aquatic predators can reduce the abundance of emerging aquatic insects, potentially affecting the diet of riparian predators. Jackson et al. (2016) found a 51 % trophic niche overlap between riparian web-building spiders and invasive trout, likely due to trout feeding on chironomid larvae (Kautza & Sullivan, 2016). In contrast, the overlap between spiders and native trout was only 5 %, suggesting greater competition for the same food between invasive fish and web-building spiders. Similar results were shown for the invasive amphipod *Dikerogammarus villosus* (Amphipoda: Gammaridae), which reduced the proportion of aquatic insects in the diet of *Tetragnatha* spiders from 60 % to 10 % (Gergs et al., 2014). However, niche overlap between invasive and native species need not necessarily result in competition, especially if prey is not a limiting factor, such as mass emergence events of midges (Corbet, 1964). In addition, invasive aquatic species could potentially provide an additional prey source for riparian arthropod predators – as has been shown, for example, for ibis feeding on invasive apple snails (Bertolero & Navarro, 2018) – but we did not find any such study with our search. However, due to the limited number of studies, it is too early to draw general conclusions about the influence of invasive aquatic species on the diet of riparian arthropod predators.

Aquatic subsidies and the abundance of riparian arthropod predators

Investigating the relationship between aquatic subsidies and riparian predator communities is challenging due to several confounding or interacting variables. For example, habitat structure and land use may influence the emergence rate of aquatic insects, which in turn may affect the population size of riparian predators (Krell et al., 2015). At the same time, habitat structure and land use can also directly influence riparian spiders (Alberts & Sullivan, 2016; Graf et al., 2019; Hunt et al., 2020). Nevertheless, our literature review suggests that variation in the availability of aquatic subsidies may indeed influence the abundance of riparian arthropod predators.

We have found evidence that the abundance of riparian web-building spiders is positively related to the availability of aquatic subsidies in running waters (e.g., Kato et al., 2003; Wesner, 2012). As a result, natural or anthropogenically driven reductions (e.g., increased metal content (Kraus et al., 2014)) in rivers, in aquatic insects are often reported to have a negative impact on the abundance of web-building spiders. Such a pattern has been found in studies analyzing spider abundance at different distances from the water along lateral transects. For example, Burdon and Harding (2007) reported that the web abundance (as a proxy for spider abundance) in a forest decreased with increasing distance from the water edge, while the forest structure did not change along this lateral gradient. Consequently, this could be related to the reduced availability of aquatic insects with increasing distance from the shoreline (Muehlbauer et al., 2014). However, the reduced abundance of web-building spiders could also reflect the shift from riparian forest to inland forest, together with a change in the associated spider species composition. Henschel et al. (2001) contradict this by attributing the loss of spider biomass with increasing distance from the water to a reduced density of aquatic insects. Densities were 4.5–7.5 times lower 30–60 m from the shore compared to areas directly adjacent to the shore. However, physiological constraints, such as desiccation tolerance - which varies among spider species (Nentwig et al., 2025) - may also influence abundance patterns along the gradient from the moist riparian zone to the drier terrestrial area. Additionally, some studies show a positive relationship between seasonal peaks in the emergence rate and the abundance of web-building spiders (Kato et al., 2003; Wojan et al., 2014). However, seasonal variation of spider abundance is also driven by their life cycle, making it difficult to draw conclusions about the causal relationship with emergence. In general, riparian consumers in temperate regions show a greater dependence on periodic emergence fluxes than in the tropics, because of the greater climate-driven seasonal variation in emergence in temperate regions compared to the tropics (Nash et al., 2023). The abundance of web-building spiders (Tetragnathidae and Linyphiidae) has also been shown to reflect the variation in emergence rates between river sections of varying geomorphology and productivity (Iwata, 2007) and in response to invasive aquatic species. For example, the presence of the invasive rainbow trout in a Japanese river was associated with a 35 % reduction in emerging aquatic insects, which in turn reduced the abundance of *Tetragnatha* spiders by 65 % (Baxter et al., 2004).

Unlike web-building spiders, the abundance of free-hunting spiders often appears to be unaffected by changes in aquatic emergence rates, or patterns are not uniform (Recalde et al., 2016). In line with that, no changes in the abundance of *Pardosa glacialis* and other free-hunting spiders were observed with distance to ponds in Greenland (Culler et al., 2021) or the Baltic Sea (Mellbrand et al., 2010). In contrast, Yuen and Dudgeon (2015) found that the abundance and biomass of free-hunting spiders are higher directly adjacent to running waters than at further distances. Obviously, distance effects on riparian free-hunting spiders related to the availability of aquatic subsidies seem to be context-dependent and may vary with factors such as climate, type of water bodies, and habitat structure.

Effects of aquatic subsidies on the abundance of riparian beetles have rarely been studied, and the results are mixed. Hering and Plachter (1997) found no relationship between food availability and *Bembidion* density along a river. In a field experiment on gravel bars along a river, beetle abundance and richness were also not related to aquatic subsidies, but rather differed between wet and dry plots (Henshall et al., 2011), suggesting a stronger habitat effect on carabids than the availability of aquatic resources. In contrast, a similar field experiment found that beetle abundance was higher in plots with additional aquatic subsidies (Paetzold et al., 2006). Both studies were conducted on gravel banks along rivers and manipulated the amount of aquatic subsidies for riparian consumers. The contrasting results could be explained by differences in patch size, patch distance from the water and, most importantly, in the amount of aquatic subsidies added. Henshall et al. (2011) added 5 mg of dry weight of chironomids in a 4 m^2 plot, while Paetzold et al. (2006) added 50–100 mg of aquatic subsidies to 1 m^2, representing a multiple times higher subsidy concentration. In a study where salmon carcasses were added to riparian patches, the abundance of staphylinids in particular responded positively to the added aquatic subsidy. However, this effect was dependent on local habitat conditions and stronger in a vegetated (four times higher abundance than in the control) than in an unvegetated patch (Collins & Baxter, 2014).

Conclusion

Our literature review confirms that aquatic subsidies, mainly aquatic insects, are an important food source for riparian arthropod predators. At the same time, the role of aquatic prey is highly variable between and within arthropod predator groups, and is strongly dependent on the physical conditions of predators, river structure, habitat and environmental conditions. Riparian web-building spiders, especially horizontal web-builders such as *Tetragnatha*, showed the highest reliance on aquatic prey, but also free-hunting spiders and riparian beetles can make strong use of these inflows. The literature also shows that the abundance of riparian arthropod predators can be influenced by the availability of aquatic inflows. In particular, the abundance of web-building spiders was positively related to the abundance of emerging insects. Despite considerable research activity over the last two decades, there remain several research gaps and opportunities for future studies:

- There is a clear geographical bias, with a lack of studies in the southern hemisphere and Asia, except Japan. Future studies should attempt to fill these gaps. This is particularly interesting as the aquatic prey source may vary between ecozones, as has recently been shown for tropical and temperate forests (Nash et al., 2023).
- Most studies have focused on web-building spiders (mainly *Tetragnatha* spp.), while only a few studies have considered spiders with different hunting modes (e.g., ambush hunters or free hunters on vegetation), carabids and other beetles. Other riparian arthropod predators such as rove beetles, harvestmen (Opiliones) or ants (Formicidae) are severely underrepresented. Future studies should therefore investigate the potential importance of aquatic prey subsidies for riparian arthropod predators other than spiders and carabid beetles. Similarly, potential aquatic subsidies other than emerging aquatic insects should be considered, as ground-dwelling riparian predators also use dead organisms washed ashore (Hering & Plachter, 1997). We are not aware of any study analyzing aquatic prey subsidies in the diet of canopy-dwelling predators, reflecting the general lack of studies in this vegetation layer (Albacete et al., 2020).
- To analyze the proportion of aquatic insects in the diet of predators, most studies used SIA. However, differences in stable isotope signatures between freshwater and adjacent terrestrial ecosystems are often small, limiting the reliability of mixing models (Krell et al., 2015; Phillips et al., 2014). Thus, additional DNA-based prey analysis could give a clearer impression of the variety of food consumed (Verschut et al., 2019), while PUFA would add valuable information on the food quality (Ohler, 2024).

By identifying these research gaps, we hope to stimulate future research efforts that will ultimately strengthen our understanding of aquatic-terrestrial meta-ecosystems.

Data availability statement

Data is presented in supplementary material.

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CRediT authorship contribution statement

Franziska Middendorf: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mirco Bundschuh:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Bernhard Eitzinger:** Writing – review & editing, Supervision, Conceptualization. **Martin H Entling:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Jens Schirmel:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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