3 Aquatic-terrestrial resource fluxes

This chapter focuses on how rivers and their surrounding landscapes are closely linked, and how resource fluxes between these systems are important for maintaining aquatic and terrestrial biodiversity. It includes a discussion of the export of biomass and specific nutrients, so-called omega-3 PUFAs, as a crucial ecosystem service provided by healthy aquatic systems. Management and restoration projects should take into account this lateral connectivity to improve the success of restoration measures.

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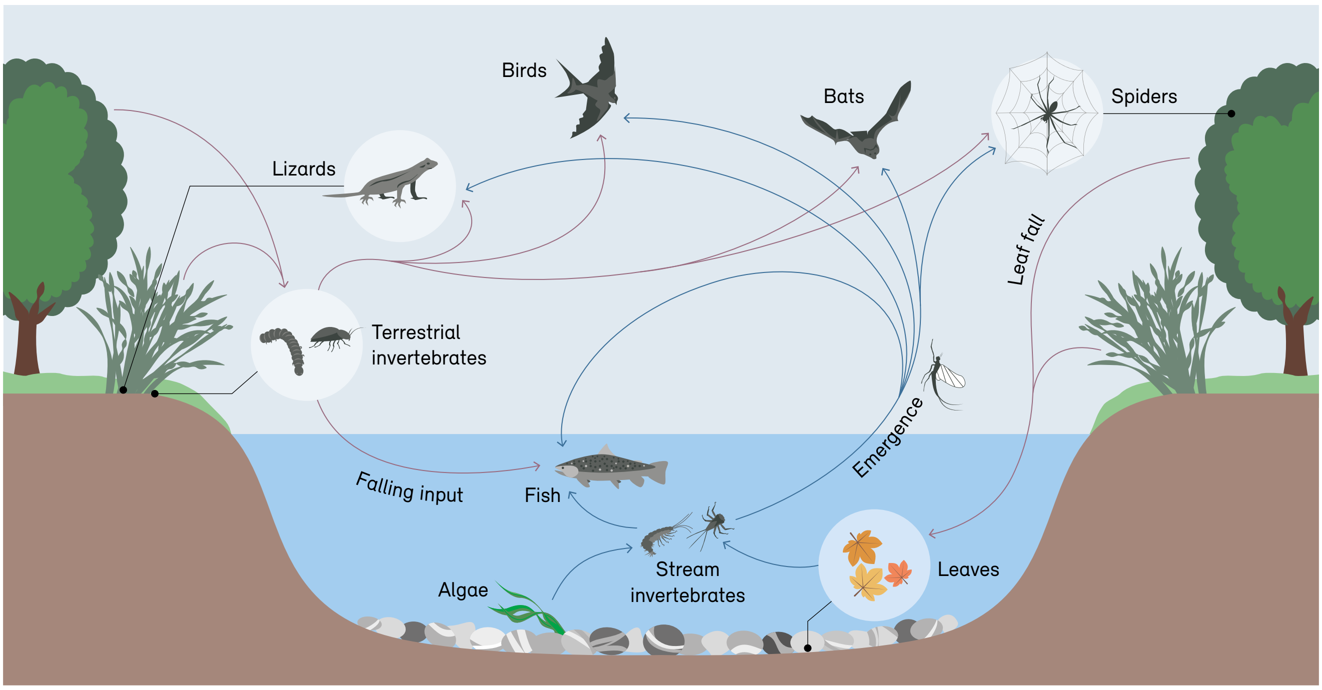
Rivers and the adjacent floodplains and riparian areas are interactive, open units connected along multiple pathways (Baxter *et al.* 2005). Here, we take a closer look into cross-boundary resource fluxes that involve, in this context, the exchange of organic resources (biomass and nutrients) between adjacent aquatic and terrestrial ecosystems (Fig. 12). Resource fluxes occur in both directions, e.g. via leaf litter input into streams and the emergence of aquatic insects into terrestrial systems, creating what Baxter *et al.* (2005) call a 'tangled web'. Such cross-boundary fluxes can play crucial roles in sustaining recipient systems.

3.1 Importance of cross-boundary fluxes from aquatic to terrestrial systems

The present chapter focuses on resource subsidies from aquatic to adjacent terrestrial ecosystems. Aquatic-derived resources provide an additional food source for riparian predators such as spiders, e.g. in the form of emerging aquatic insects. Many aquatic insects have life histories in which the larval stage is aquatic and the adult reproductive stage is terrestrial. The timing of aquatic subsidies reflects the life histories of local assemblages and leads to seasonal resource pulses. Aquatic insect emergence, especial-

Figure 12

Schematic of cross-boundary resource fluxes between a stream and the surrounding landscape.



Source: Baxter *et al.* (2005)

ly in spring, provides an important supplement for riparian predators at a time when terrestrial resources are low in abundance. Various studies have shown that riparian predators, such as spiders and birds, are seasonally dependent on aquatic resource subsidies (Iwata *et al.* 2003; Paetzold *et al.* 2005; Burdon and Harding 2008).

Aquatic-derived resources not only represent an additional food source, but also contain an important nutrient in low supply in terrestrial ecosystems, the well-known omega-3 fatty acid EPA (Table 2). We find high concentrations of EPA in fish, making them a beneficial food source also for humans, and in other aquatic organisms like insects. In fact, aquatic ecosystems are considered a principal source of EPA (Hixson *et al.* 2015). EPA belongs to the group of

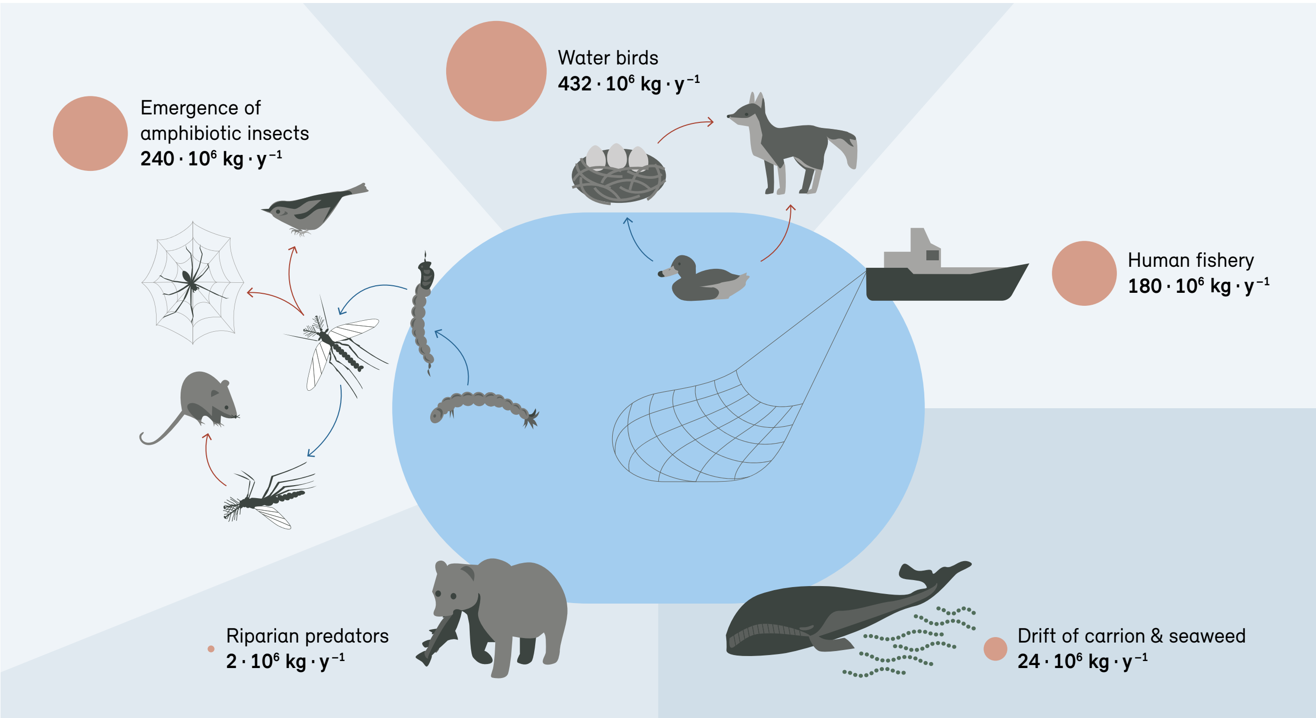
Table 2

Important omega-3 polyunsaturated fatty acids (PUFAs).

Abbreviation	Chemical formula	Name	Primary producers
ALA	C18:3n3	Alpha-linoleic acid	Produced by most algae and by some land plants, with especially high concentrations in some seeds and nuts (e.g. rapeseed, flaxseed, walnut)
SDA	C18:4n3	Stearidonic acid	Produced by many algae (e.g. many cryptophytes and some green algae) but by only a few higher plants (e.g. black currant and echium)
EPA	C20:5n3	Eicosapentaenoic acid	Produced by many algae (e.g. diatoms and cryptophytes) but not by higher plants (except some mosses); aquatic systems as principal source
DHA	C22:6n3	Docosahexaenoic acid	Produced mostly by marine algae (e.g. marine cryptophytes)

Figure 13

Estimated annual (y) export of EPA + DHA (see Table 2) via different pathways, illustrating the magnitude and importance of this ecosystem service provided by aquatic systems.



Source: Gladyshev *et al.* (2009)

polyunsaturated fatty acids (PUFAs; Table 2) that contain multiple double bonds, which only specific organism groups can produce. While several algal groups, e.g. diatoms, produce large amounts of EPA and it therefore accumulates in aquatic food chains, terrestrial plants, except for some mosses, completely lack this ability (Harwood 1996; Uttaro 2006; Hixson *et al.* 2015); this makes EPA-rich organisms (aquatic insects) a resource in high demand in terrestrial ecosystems. Preliminary estimates indicate that the quantity of PUFAs exported from aquatic systems can be substantial (Fig. 13), providing an important cross-boundary ecosystem service (Gladyshev *et al.* 2013).

But why are PUFAs so important? In animals, including humans, PUFAs are involved in many physiological processes. They are, for example, essential parts of our cell membranes, have important functions in our immune system, and play a role in signal transduction in the body (Stillwell and Wassall 2003; Stanley 2014; Schlotz *et al.* 2016). In short, PUFAs are essential for survival und need to be taken up with the diet. Although some organisms can convert other PUFAs to EPA, this process is generally inefficient, and EPA uptake via the diet is thus quite important. In support of this, studies on riparian predators have demonstrated, for example, a positive effect of aquatic-derived EPA fluxes on the development and breeding success of riparian birds, such as tree swallows (Twining *et al.* 2016, 2018), and on the immune system of riparian spiders (Fritz *et al.* 2017).

Humans have altered most aquatic ecosystems and especially rivers and streams, in both morphology and water chemistry, thereby causing the 'dark side of subsidies' via the cross-boundary transfer of micropollutants and heavy metals (Kraus 2019). Healthy freshwaters clearly sustain the positive side of cross-boundary resource fluxes to adjacent terrestrial systems as an ecosystem service. The extent to which human activities impact aquatic resource subsidies, in terms of both quantity and quality, remains unknown. Some 25% of Swiss running waterways are in a poor eco-morphological state. Specifically, over 100,000 artificial barriers blocking sediment movement occur on Swiss rivers, critically degrading streambed conditions for biota (FOEN 2018), and river shoreline length has been substantially reduced by straightening and shoreline fortifications. Emerging aquatic insect and insectivore bird abundance are positively correlated with shoreline length (Iwata *et al.* 2003), meaning that less natural river networks with a shorter shoreline may be associated with reduced PUFA transfer. By modifying both rivers and adjacent riparian zones, human activities and infrastructures clearly influence the distribution and amount of cross-boundary resource exchange and flux (Laeser *et al.* 2005; Paetzold *et al.* 2011).

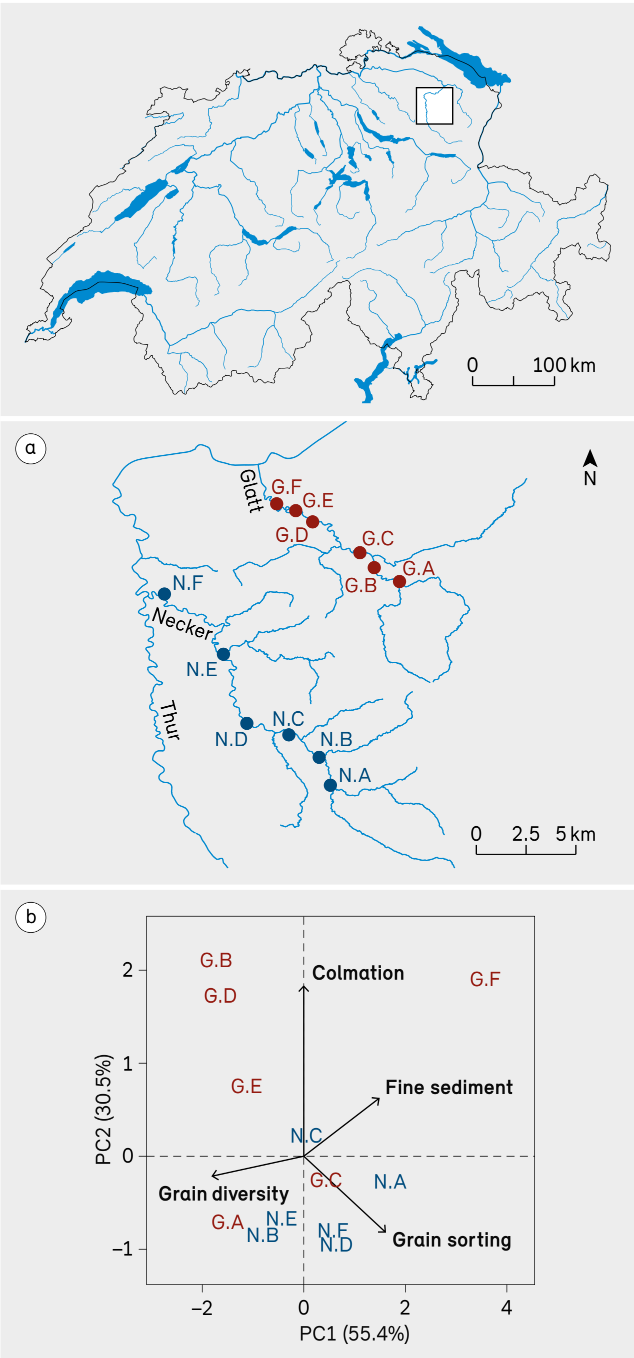
Despite the important ecological role of cross-boundary resource subsidies within the context of multi-dimensional riverscapes, they have been largely neglected in practical management. In future projects, restoration measures should therefore account for the lateral connectivity along rivers to incorporate cross-boundary resource fluxes.

3.2 Aquatic-terrestrial resource subsidy data from Switzerland

Here we present results about resource subsidies from aquatic to terrestrial systems along two contrasting rivers in Canton St Gallen (Fig. 14a). The Necker river (N) is a mostly unregulated river with a natural flow and sediment regime, whereas the adjacent Glatt river (G) is highly regulated, with multiple barriers that alter the flow and sediment regime. Land use also differs between the two catchments, with the Glatt having poorer water quality (higher nitrogen and phosphorus levels) than the Necker. We selected six sites along each river to assess aquatic resource subsidies to adjacent terrestrial ecosystems. We focused on emergent aquatic insects and the export of aquatic-derived PUFAs to two riparian predators (ground-dwelling and web-building spiders). Ground-dwelling spiders (ground spiders) are roaming predators in riparian areas, whereas web-building spiders (web spiders) are stationary predators, catching prey in their webs. Here, we address various aspects of resource subsidies along the two rivers.

Figure 14

(a) Map of sampling sites along the rivers Glatt (G) and Necker (N). (b) Principal component analysis (PCA) plot showing the difference in habitat properties between the two rivers. The axes represent dimensions 1 and 2 of the PCA, and the percentage of variance explained by each dimension is given. Sediment variables of colmation, grain (size) diversity, fine sediment (amount) and grain (size) sorting are represented as arrows.



Source: Eawag

3.2.1 How does regulation influence environmental gradients along river networks?

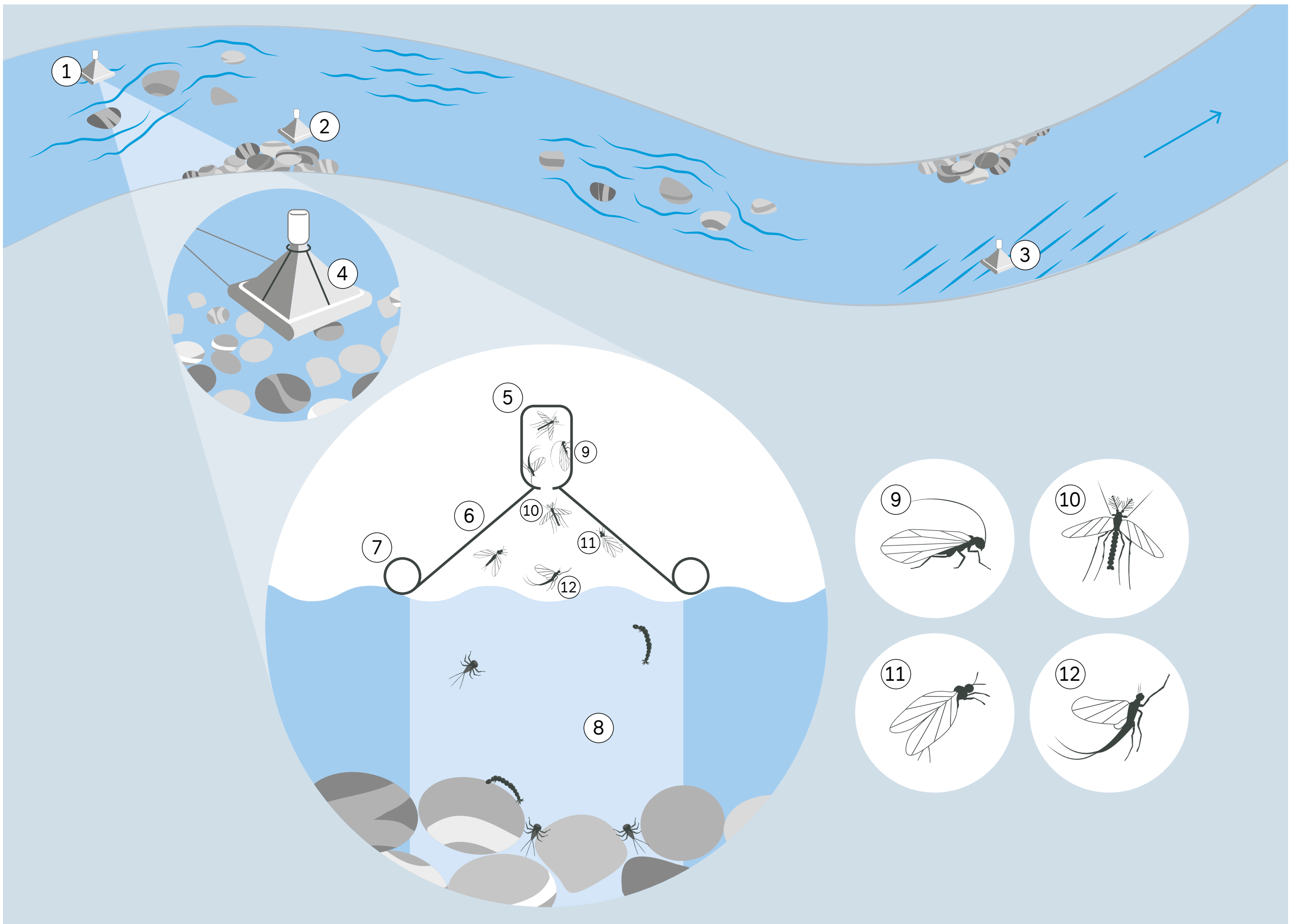
We evaluated various sediment characteristics, such as grain size distribution and internal colmation (see Chapter 7; Dubuis *et al.* 2023). We observed an increase in fine sediment and colmation at sites below structures (barriers) blocking bed movement. Along the Glatt river, the most upstream site (G.A) still had a natural sediment signature, but this changed rapidly downstream of the first structure (G.B). This change in habitat properties is shown in a principal component analysis (PCA) plot (Fig. 14b), where sites that are depicted close to each other have similar bed characteristics and arrows represent different reasons for a separation. G.A clusters with the more natural sites of the Necker river because it has less fine material, while G.B and the other Glatt sites are farther away because it has a higher degree of colmation.

3.2.2 How does stream degradation influence aquatic subsidies?

Flow regulation often causes habitat degradation in rivers, which typically translates to changes in the communities and abundances of macroinvertebrates in regulated waters relative to free-flowing watercourses. Consequently, the quality and quantity of resource subsidies transferred to adjacent riparian areas also differ. We compared insect biomass export along a bed degradation gradient in the Glatt and Necker rivers, using colmation as a proxy for bed degradation (see Fig. 15 for methods and Fig. 16 for results). No general decline in biomass export was observed with increasing colmation, but there was a change in community composition, with fewer emerging stoneflies in the Glatt than in the Necker river. While a peak in stonefly emergence in autumn, consisting of rather common stonefly species (*Leuctra* spp.), was visible to some extent at most sites along the Glatt river, the important peak in stonefly emergence in early spring was essentially missing along the Glatt river, with a low level of emergence occurring only at sites G.A and G.C (Fig. 16a). This early spring peak consisted of stonefly families that are more sensitive to environmental disturbances, such as an increased fine sediment load (Extence *et al.* 2013). This lack of stoneflies can have a large impact, as stoneflies express a different emergence behaviour than other aquatic insects, such as mayflies and caddisflies, which emerge in flight directly from the water column (Fig. 16b). In contrast, stoneflies crawl to shore before they emerge (Fig. 16c), thus representing an important cross-boundary pathway to ground-dwelling predators that is lost in streams without stoneflies (Fig. 17).

Figure 15

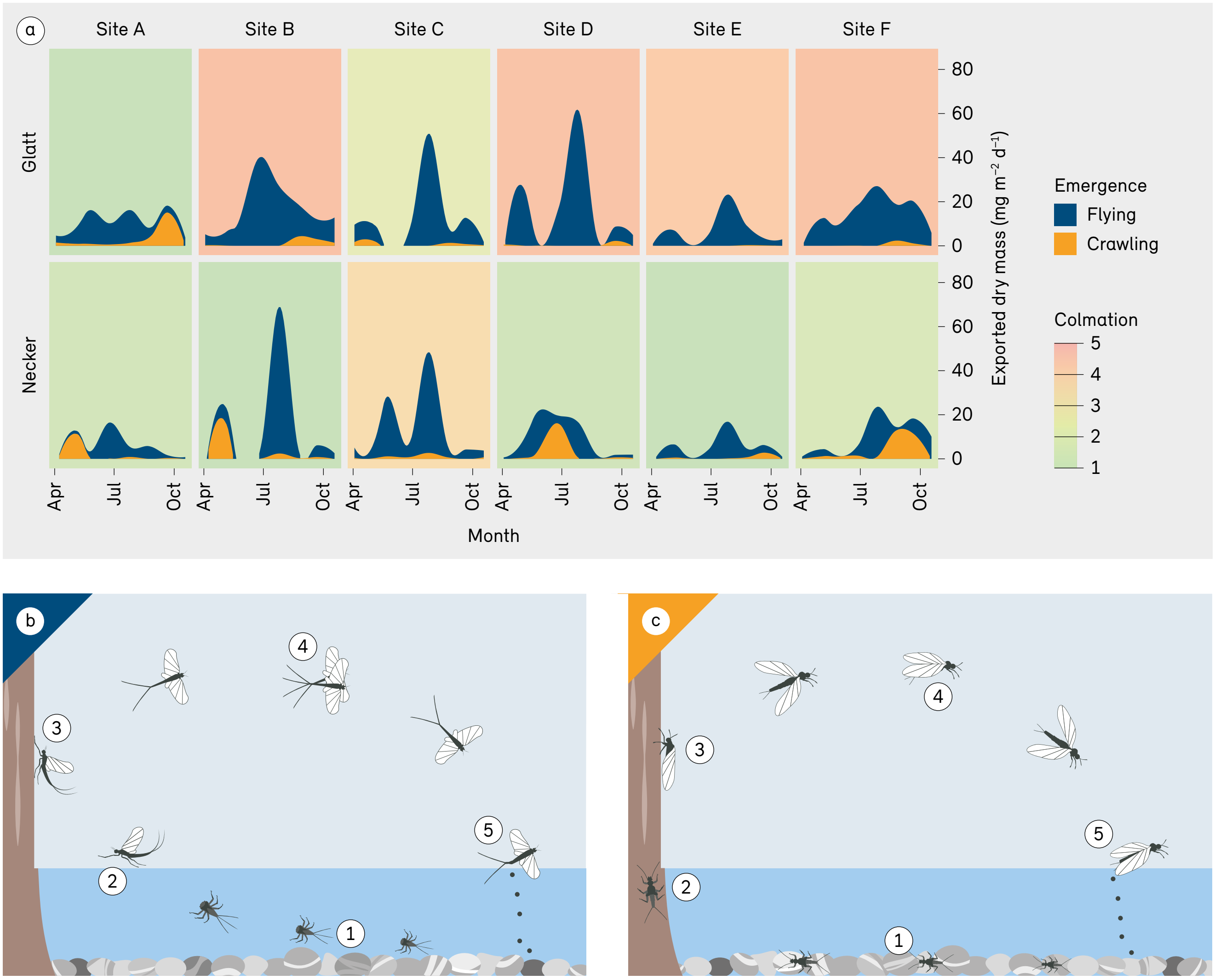
Method for estimating biomass export in the form of emergent aquatic insects. Three floating emergence traps were used per river reach (surface area 0.25 m²) to cover different habitat types: (1) riffle, (2) edge and (3) pool. (4) Emergence traps, consisting of (5) bottle for insect collection, (6) net cover (mesh size 100 µm), (7) styrofoam floaters, (8) area where emerging insects are collected. Collected insects (9) Trichoptera (caddisflies), (10) Diptera (midges), (11) Plecoptera (stoneflies), (12) Ephemeroptera (mayflies).



Source: Eawag

Figure 16

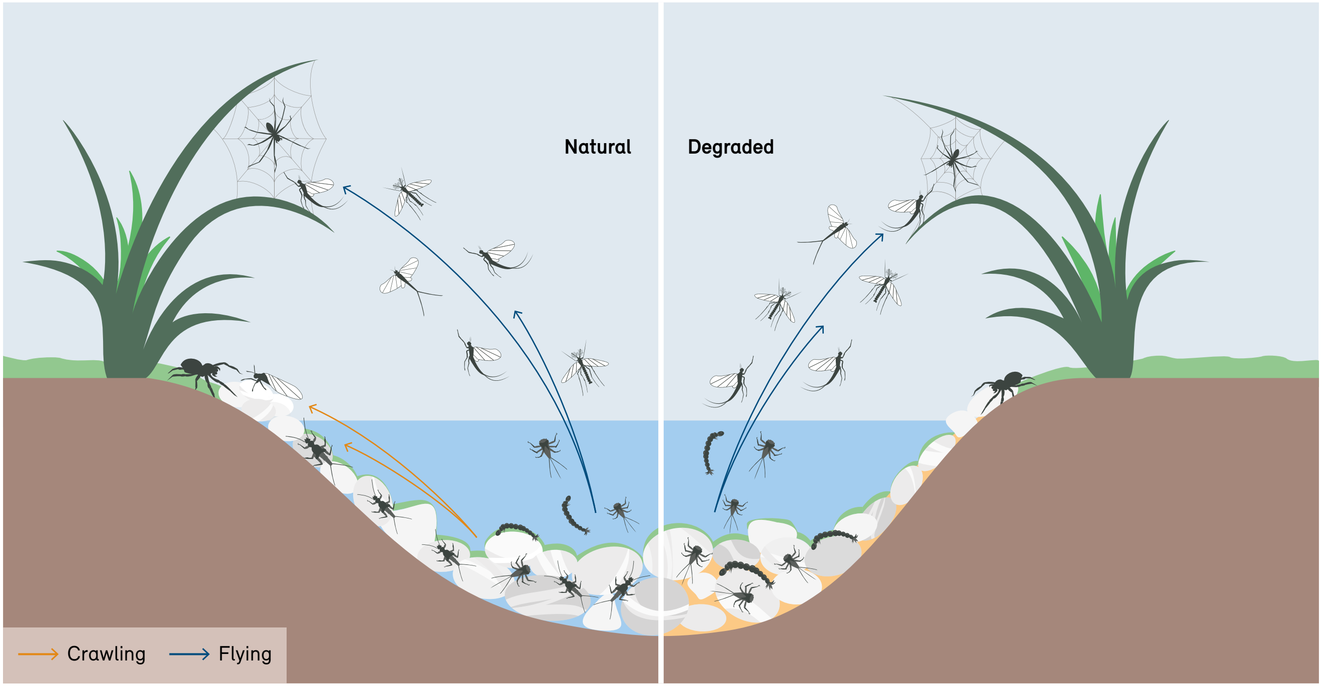
(a) Estimation of biomass export in the form of emergent crawling (e.g. stonefly) and flying (e.g. caddisfly, mayfly) aquatic insects along the Glatt river (top row) and the Necker river (bottom row). The sites (A–F) correspond to those shown on the map in Figure 14. (b and c) Illustration of the different emergence modes: (b) flying versus (c) crawling.



Source: (b) adapted from *http://www.delawareriverguide.net/insects/mayflycyc.html; (c) adapted from http://www.delawareriverguide.net/insects/stoneflycyc.html*

Figure 17

A potential consequence of stream degradation for the cross-ecosystem transfer of resource subsidies from aquatic ecosystems to riparian landscapes. The loss of stoneflies in degraded streams results in the loss of a resource pathway (yellow linkage) to adjacent riparian systems.



Source: Eawag

3.2.3 Do emergent insects transfer PUFAs and is there a difference between systems?

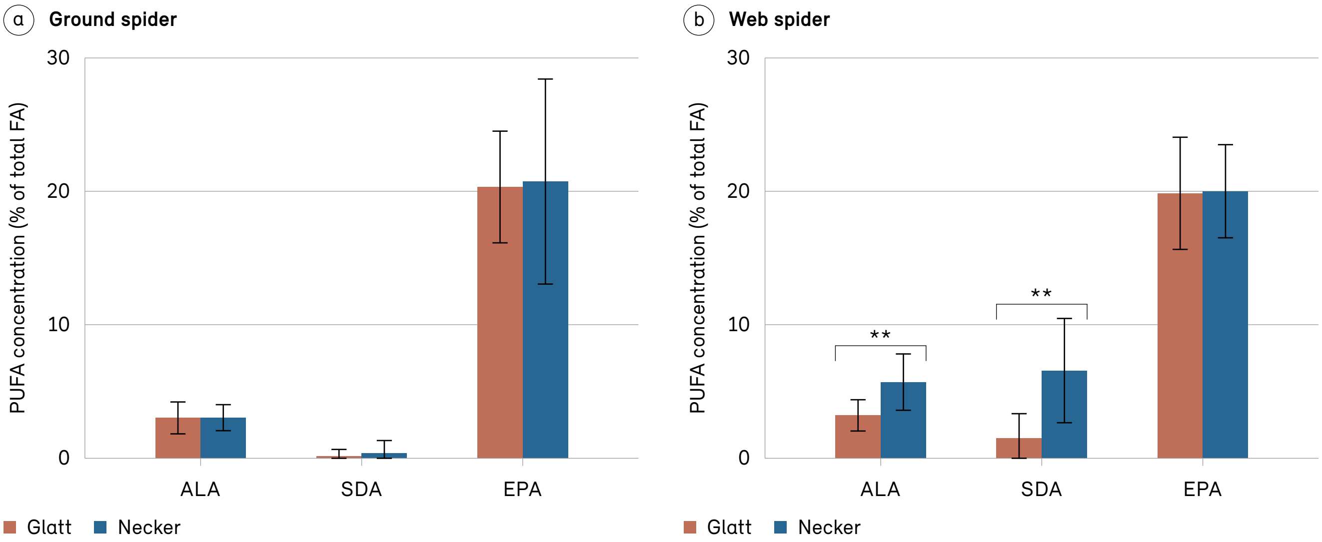
EPA and other PUFAs (i.e. ALA + SDA) predominantly found in aquatic environments were present in considerable concentrations in emergent insects (EPA: 15–25% of total fatty acids) and in riparian spiders along both the Glatt and the Necker river (Fig. 18). Web spiders and ground spiders had a similar ALA concentration (~4% of total fatty acids), and both had a very high EPA concentration (~15%) relative to other terrestrial organisms. SDA was higher in web spiders (1.4%) than in ground spiders (0.3%), indicating that predator type played a role in resource transfer.

We compared PUFA concentrations in riparian spiders between the two systems in spring. In ground spiders, we detected no significant differences. Web spiders, on the other hand, contained more SDA and ALA along the Necker river than along the Glatt river, although there was no significant difference in EPA concentration (Fig. 18). We also measured PUFA concentrations in emergent insects and periphyton scraped from rock surfaces and found similar patterns, especially for SDA. It appears that the difference between the systems already occurred at the base of the food chain, potentially because of different environmental conditions. We conclude that SDA production and transfer in particular were very limited along the Glatt river, while the nutritionally important EPA was transferred in comparable quantities.

A closer look at the EPA concentration in riparian spiders reveals some interesting patterns. First, the EPA concentration of riparian spiders was dependent on the distance from shore. At site N.F, where spiders were sampled at different distances from the shore, EPA concentration declined with increasing distance from the shore, with values already lower around 40–50 m from the channel, especially in ground spiders (Fig. 19a). Although differences were not significant due to relatively small sampling size, this pattern is in line with previous findings (Chari *et al.* 2020) and demonstrates that access to aquatic insects is important for EPA transfer and accumulation. Second, looking at seasonal changes, the EPA concentration in both spider types was highest in spring (Fig. 19b). This finding suggests that emergent aquatic insects are especially important for PUFA transfer into riparian zones in spring.

Figure 18

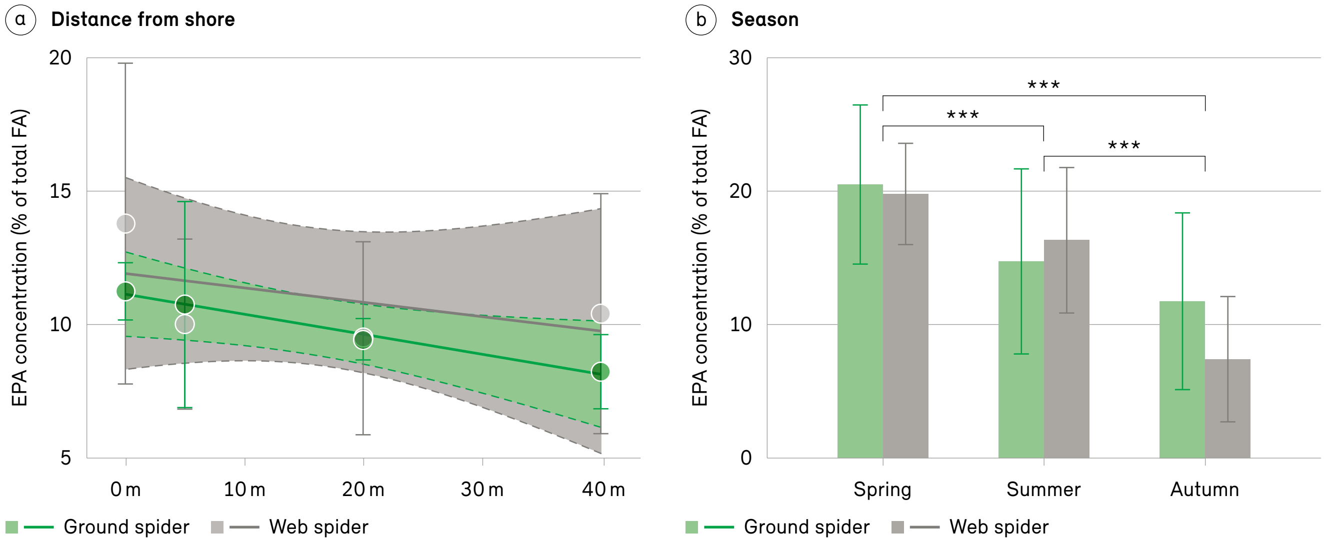
Mean (± SD) polyunsaturated fatty acid (PUFA: ALA, SDA and EPA; see Table 2) concentration, expressed as a percentage of the total fatty acid (FA) concentration in (a) riparian ground spiders and (b) web spiders in the Glatt and Necker rivers. Asterisks represent significant differences between the two river systems at p <0.01.



Source: Eawag

Figure 19

*(a) Mean (± SD) EPA concentration in riparian ground and web spiders (site N.F) at different distances from the river shore. The shaded areas represent 95% confidence intervals. (b) Seasonal differences in mean (± SD) EPA concentration in the two spider types, showing the importance of spring emergence. Asterisks represent significant differences between seasons (*** p <0.001).*

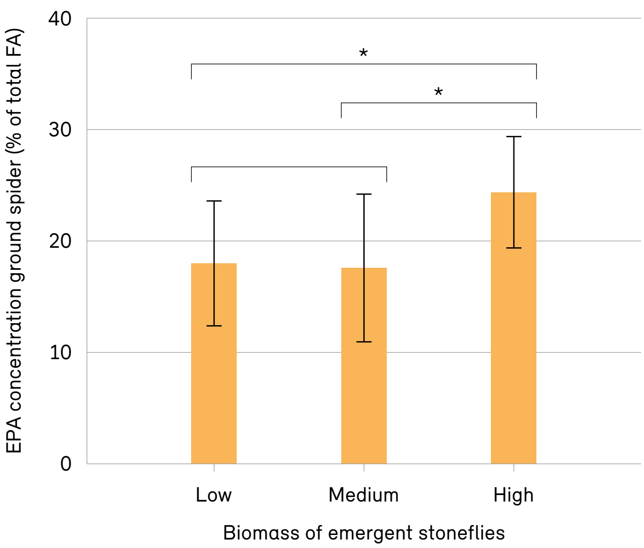


Source: Eawag

We found no significant difference in the total EPA export/transfer between the natural Necker river and the more degraded Glatt river. However, the difference in macroinvertebrate composition between streams, with reduced stonefly emergence in the Glatt (see Section 3.2.2), altered EPA availability for different kinds of riparian predators. While web spiders were largely unaffected, the EPA concentration in riparian ground spiders was lower in degraded sites with reduced stonefly emergence in spring (Fig. 20). As mentioned above, stoneflies have a specific 'emergence mode' involving crawling to shore. This behaviour makes them easy prey for ground-dwelling predators, while other insects that emerge by flight are much harder to catch. As the EPA concentration in ground spiders is linked with immune function (Fritz *et al.* 2017), less access to EPA, in this case resulting from reduced stonefly emergence, may have negative consequences on predator survival. Importantly, stonefly decline is a general problem in degraded streams; it weakens aquatic-terrestrial linkages, not only for riparian spiders but potentially also for other ground-dwelling riparian predators, such as lizards and beetles.

Figure 20

EPA concentration of riparian ground spiders in spring in relation to emergent stonefly biomass. Categories of stonefly biomass: low = dry mass <0.25 mg m^{-2} day^{-1}, medium ≤1 mg m^{-2} day^{-1}, high = dry mass >1 mg m^{-2} day^{-1}. Asterisks represent significant differences at $p < 0.05$.



Source: Eawag

3.3 Management implications

We show that both emergent aquatic insects and riparian spiders contain considerable concentrations of EPA and are thus a central link that promotes EPA transfer into terrestrial systems. Waterbodies, which provide aquatic subsidies, and riparian zones, which form the main habitat of riparian spiders, need to be in good ecological condition to sustain healthy populations. In riparian zones in particular, web spider density depends on riparian vegetation such as shrubs and trees (Laeser *et al.* 2005), and the PUFA concentration in spiders is higher if a riparian buffer zone is present (Ramberg *et al.* 2020). Conservation of the riverine zone, including a healthy watercourse, is therefore crucial for the maintenance of cross-boundary resource fluxes.

Research on Cross-boundary linkages provides a chance to inform and engage different stakeholders in riparian management projects, as suggested by Muehlbauer *et al.* (2019). Discussions of restoration projects should take a more holistic perspective, considering terrestrial and aquatic ecosystems in combination. For example, a bird conservation project might have low value if nearby waterbodies are in poor condition and cannot provide needed aquatic resource subsidies such as PUFAs. In this case, PUFA export should be considered a crucial ecosystem service. In this context, it is especially important to stop the general decline in stoneflies, which form a distinct export pathway easily accessible to ground-dwelling riparian predators. Stoneflies cannot live in streams with a poor ecological state, and thus this pathway and resource flux across ecosystem boundaries is lost in degraded riverscapes.

Box 6: In practice – Fostering key connections between a watercourse and its surrounding terrestrial area

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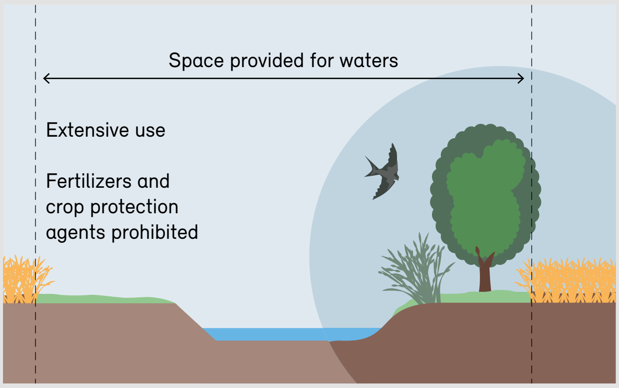
The Swiss Cantons and municipalities are currently defining the 'space provided for waters' in their spatial planning framework (Fig. 21). In this context, the space required for flood protection and for the protection of water bodies and aquatic organisms from agricultural pollution are important topics. However, most discussions revolve around the loss of usable agricultural land. The benefit that a near-natural shoreline can provide for the adjacent agricultural land is, in contrast, rarely discussed. Near-natural and heterogeneous banks harbour a diverse community of algae, aquatic plants and animals, which, as the presented study nicely demonstrates, produce important substances that are distributed far beyond the watercourses via emerging insects. This benefits not only the spiders studied here but also many other organisms, which in turn hunt for 'pests' in agricultural areas, thus benefitting humans.

We should seize the opportunity presented by this spatial planning definition and allow rivers to form diverse shorelines, create habitats for emerging insects, and grow richly structured shoreline vegetation with diverse habitats for spiders, birds and hedgehogs, which can benefit from aquatic insects as a food supply. Finally, we should appreciate the role that these organisms play in the natural pest control of crops.

Figure 21

An example of the 'space provided for waters', a widely used definition of the riverine zone by resource managers.



Source: AWA (2020)