



From stream to land: Ecosystem services provided by stream insects to agriculture

Julien Raitif, Manuel Plantegenest, Jean-Marc Roussel

► To cite this version:

Julien Raitif, Manuel Plantegenest, Jean-Marc Roussel. From stream to land: Ecosystem services provided by stream insects to agriculture. Agriculture, Ecosystems & Environment, 2019, 270-271, pp.32-40. 10.1016/j.agee.2018.10.013 . hal-02272263

HAL Id: hal-02272263

<https://institut-agro-rennes-angers.hal.science/hal-02272263>

Submitted on 27 Aug 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - ShareAlike 4.0 International License

Manuscript Number: AGEE19620R2

Title: From stream to land: ecosystem services provided by stream insects to agriculture

Article Type: Review Article

Keywords: aquatic subsidies; agroecosystems; winged aquatic insects; pollination; soil fertilization; biological control

Corresponding Author: Mr. Julien RAITIF,

Corresponding Author's Institution: INRA

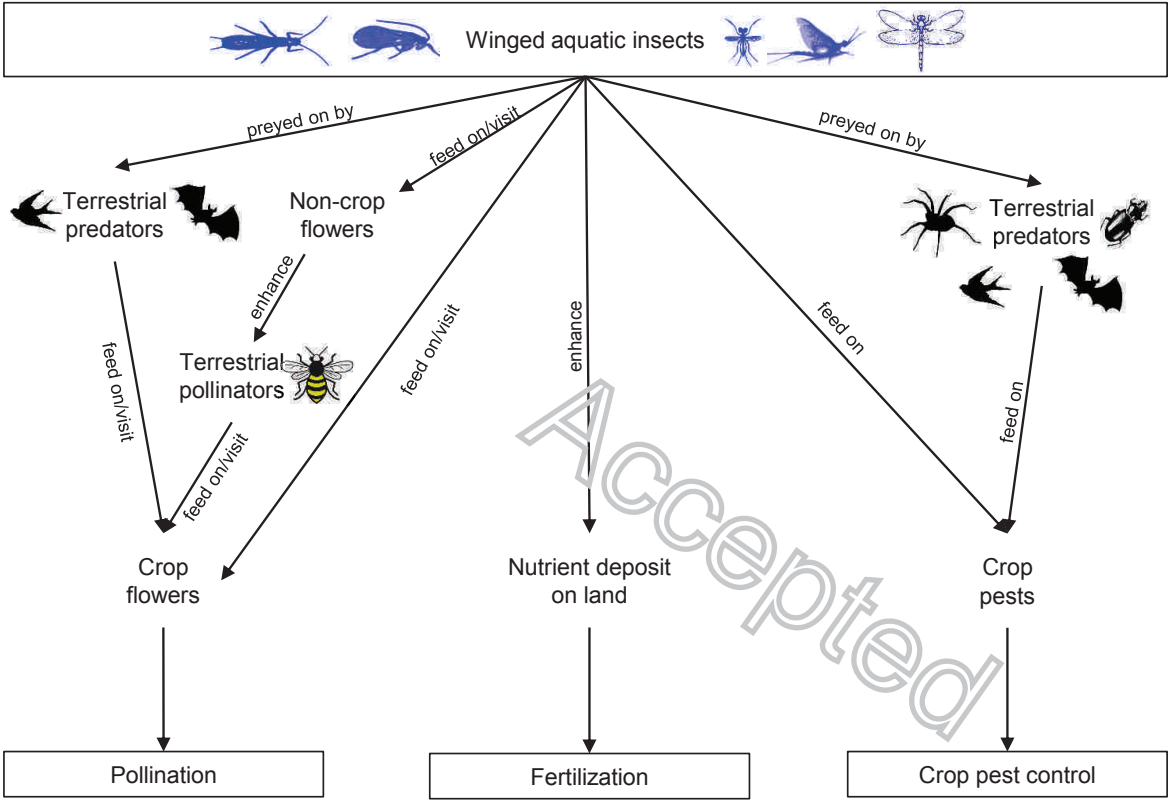
First Author: Julien RAITIF

Order of Authors: Julien RAITIF; Manuel Plantegenest; Jean-Marc Roussel

Manuscript Region of Origin: FRANCE

Abstract: The connection between aquatic and terrestrial habitats has increased scientific interest in ecological subsidies, focusing on how the transfer of matter and energy between adjacent ecosystems can modify the ecosystems functioning. Much attention has focused on subsidies associated with winged aquatic insects in pristine areas, but their existence and implications in agricultural landscapes are rarely considered. We reviewed current knowledge on the dominant types of winged stream insects involved in terrestrial ecosystem subsidizing and how agricultural practices can affect their communities. We compiled published data that illustrate the contribution of winged stream insects to ecological services in agroecosystems. Agricultural intensification has resulted in profound environmental modifications of streams and a decrease in large-bodied and sensitive taxa of Ephemera, Plecoptera and, to a lesser degree, Trichoptera orders, whereas more tolerant and small-bodied taxa of the Diptera order may increase. In return, these changes in stream invertebrate communities can modify the transfer of aquatic subsidies to agroecosystems. Winged stream insects can disperse up to 150 m from the stream bank, depending on species. They pollinate both wild and cultivated plants, fertilize the soil (depositing up to 12 mg N/m² per day) during emergence outbreaks and feed natural enemies of crop pests during crucial periods of the year. Promising evidence suggests that they can support the related ecosystem services (pollination, soil fertilization and crop pest control), indicating the need for further research. Another area of focus can include the influence of agricultural practices on the amount and type of emerging aquatic insects. Future research on aquatic subsidies in agricultural landscapes may provide new insights into the management and provision of ecosystem services to agriculture, while simultaneously ensuring the conservation of rich freshwater biodiversity for optimal ecosystem functioning.

Graphical Abstract



Graphical abstract: Potential ecosystem services supported by winged stream insects

Accepted

Highlights

- We review how agriculture affects winged insects emerging from streams
- Shifts in communities are observed, promoting small-bodied and more mobile taxa
- Changes in the transfer of aquatic subsidies to agroecosystems are reported
- Pollination, fertilization and biological control services could be altered

Accepted

From stream to land: ecosystem services provided by stream insects to agriculture

Raitif Julien^{1,2}, Manuel Plantegenest², Jean-Marc Roussel^{1,3}

¹ INRA, Agrocampus-Ouest, Ecology and Ecosystem Health, 65 rue de Saint-Brieuc, Rennes, France

² IGEPP, Institut de Génétique, Environnement et Protection des Plantes, Agrocampus Ouest, 65 rue de Saint Brieuc, Rennes, France

³ Management of aquatic ecosystems in agricultural watersheds, INRA, Agence Française pour la Biodiversité, Rennes, France

Abstract

The connection between aquatic and terrestrial habitats has increased scientific interest in ecological subsidies, focusing on how the transfer of matter and energy between adjacent ecosystems can modify the ecosystems functioning. Much attention has focused on subsidies associated with winged aquatic insects in pristine areas, but their existence and implications in agricultural landscapes are rarely considered. We reviewed current knowledge on the dominant types of winged stream insects involved in terrestrial ecosystem subsidizing and how agricultural practices can affect their communities. We compiled published data that illustrate the contribution of winged stream insects to ecological services in agroecosystems. Agricultural intensification has resulted in profound environmental modifications of streams and a decrease in large-bodied and sensitive taxa of Ephemera, Plecoptera and, to a lesser degree, Trichoptera orders, whereas more tolerant and small-bodied taxa of the Diptera order may increase. In return, these changes in stream invertebrate communities can modify the transfer of aquatic subsidies to agroecosystems. Winged stream insects can disperse up to 150 m from the stream bank, depending on species. They pollinate both wild and cultivated plants, fertilize the soil (depositing up to 12 mg N/m² per day) during emergence outbreaks and feed natural enemies of crop pests during crucial periods of the year. Promising evidence suggests that they can support the related ecosystem services (pollination, soil fertilization and crop pest control), indicating the need for further research. Another area of focus can include the influence of agricultural practices on the amount and type of emerging aquatic insects. Future research on aquatic subsidies in agricultural landscapes may provide new insights into the management and provision of ecosystem services to agriculture, while simultaneously ensuring the conservation of rich freshwater biodiversity for optimal ecosystem functioning.

Keywords: aquatic subsidies; agroecosystems; winged aquatic insects; pollination; soil fertilization; biological control

26 1 Introduction

27 In recent decades, ecologists have explored the interactions between entities (*e.g.* individuals
28 or groups of individuals) previously considered isolated from each other. A growing body of
29 literature has substantially expanded the theoretical background from populations to
30 communities, focusing notably on the influence of landscape heterogeneity on community
31 structure (Holt 1997). More recently, the concept of meta-ecosystems has emerged (Loreau *et al.* 2003), which is based on the assertion that adjacent ecosystems in heterogeneous
32 landscapes exchange matter and energy. Although ecology has identified the existence of such
33 transfers, they were ignored until recently. In the 19th century, the entomologist John Gould
34 (1804-1881) observed birds preying on dragonflies (*in* Ballinger and Lake 2006), and in the
35 early 20th century it was acknowledged that energy could cross ecosystem boundaries
36 (Summerhayes and Elton 1923). In the late 1970s, Odum *et al.* (1979) highlighted that
37 allochthonous inputs from an ecosystem could modify the functioning of the adjacent
38 recipient ecosystem, initiating a promising field of research in ecology. A pioneer study by
39 Polis *et al.* (1997) provided a theoretical basis, stating that the significance of allochthonous
40 inputs, also referred to as “subsidies”, was expected to vary according to autochthonous food
41 abundance in the receiving ecosystem, *i.e.* its productivity. Predicting the effects of subsidies
42 remains complex and depends on the type of subsidy, the trophic levels involved and the
43 amount of resources provided to the receiving food web (Marczak *et al.* 2007). Multiple case
44 studies from a wide diversity of ecosystems provide clear evidence that food webs are fueled
45 by subsidies (*e.g.* Jackson and Fisher 1986; Gray 1989; Polis and Hurd 1995; Dreyer *et al.*
46 2012; Havik *et al.* 2014).

48 Interconnections between land and water are common in many ecosystems (Larsen *et al.*
49 2015), and the connection between aquatic and terrestrial habitats has prompted scientific
50 interest. Until recently, most literature described how physical laws determined the transfer of

subsidies to aquatic ecosystems. For instance, riparian tree leaves falling in the water sustain the detrital pathway in heterotrophic headwater streams (Vannote *et al.* 1980). At the watershed scale, fertilizer leakage across agricultural landscapes affects primary production and aquatic food webs, and ultimately has subtle effects on nutrient cycling in streams (Roussel *et al.* 2014). Conversely, deposition of nutrient-rich sediments from streams to valleys during flooding supported the emergence of agriculture in the Fertile Crescent during the Neolithic (Mazoyer and Roudart 2006). In estuaries and marine coastal areas, benthic food webs are largely fueled by terrestrial organic subsidies conveyed by rivers (Kostecki *et al.* 2010), while tidal surges and wind can transfer huge amounts of marine inputs to terrestrial habitats (Hyndes *et al.* 2014).

Based on the assumed prominent role of physical laws in subsidy transfers, aquatic ecosystems have long been considered as passive receivers of terrestrial subsidies. This paradigm was challenged when Polis *et al.* (1997) emphasized the role of living organisms in the reciprocal transfer from aquatic to terrestrial ecosystems. Examples exist of terrestrial and avian predators foraging in aquatic ecosystems, which ultimately fertilize terrestrial ecosystems (*e.g.* Havik *et al.* 2014). Additionally, arthropods metamorphosing from aquatic larvae to aerial adults are suitable candidates for reciprocal transfers of matter and energy from water to land (Schulz *et al.* 2015). They are common in all aquatic ecosystems, disperse towards land as winged adults, and are involved in nutrient cycling and the functioning of food webs (Baxter *et al.* 2005). Some studies have identified the important role of adult aquatic arthropods in the diet of terrestrial carabids (Hering and Plachter 1997), spiders (Paetzold *et al.* 2005), birds (Nakano and Murakami 2001) and lizards (Sabo and Power 2002). Recently, the meta-analysis by Bartels *et al.* (2012) highlighted that even though the mass of aquatic subsidies to land is lower than the reciprocal mass of terrestrial subsidies, their average contributions to the functioning of receiving food webs appeared to be similar.

Differences in the quality of subsidies could explain this unexpected result; aquatic insects are nutrient-rich, especially in nitrogen (N) and lipids, whereas freshwater receives mainly carbon-rich detrital organic matter (OM) from terrestrial plants.

Despite increasing evidence about the ecological importance of aquatic subsidies in terrestrial ecosystems, studies have focused mainly on forests and grasslands. Even though freshwater ecosystems are widespread in agricultural landscapes, the possible roles of aquatic subsidies are rarely considered. Depending on the aquatic species and its behavior as a winged adult in agroecosystems, they may support services to agriculture. This article aims to present the dominant types of winged aquatic insects involved in terrestrial ecosystem subsidizing and how agriculture can influence the magnitude of these subsidies through its impacts on aquatic communities. Our analysis focuses on streams due to their prevalence and extended interfaces with croplands and pastures. We chose to highlight the contribution of stream arthropods to three major ecosystem services to agriculture – pollination, fertilization and biocontrol – and to assess it from data available in the literature

2 *Effects of agriculture on stream insect communities*

The composition of stream insect communities varies among streams and from headwater tributaries to downstream sections, as a function of the habitats and food sources available (Vannote *et al.* 1980). In agricultural streams, most taxa with a winged adult stage are reported to belong to the following orders: Ephemeroptera, Plecoptera, Trichoptera (referred to as EPT) and Diptera. Inland dispersal of adult aquatic insects depends on their morphology and feeding and reproductive behaviors and thus differs greatly among orders (Muehlbauer *et al.* 2014). In the following sections, we emphasize how agricultural practices alter stream invertebrate composition and, in return, can modify the amount and quality of winged aquatic insects transferred to agroecosystems.

2.1 Organic matter, nutrients and pollution

The multiple energy pathways that flow in aquatic food webs, *i.e.* autotrophy and heterotrophy, depend on the availability of basal sources for primary consumers and higher-level predators through bottom-up effects. Heterotrophy dominates in narrow, light-limited headwater streams, where a significant portion of OM comes from riparian tree leaves, even though algae provide consumers with essential amino acids and fatty acids (Brett *et al.* 2017). The contribution of autotrophy likely increases downstream in larger, open water streams, where aquatic primary productivity increases (algae, macrophytes) before being hampered further downstream in more turbid water, where heterotrophy is enhanced by fine particles from terrestrial runoff (Vannote *et al.* 1980). Stream invertebrates, especially primary consumers, can be classified into functional groups according to the nature of OM they feed on. Along the upstream-downstream continuum, invertebrate communities tend to gradually shift from shredders and grazers in headwaters to filter-feeders and collector/gatherers in larger streams (Lancaster 2013).

Human activities that modify watershed vegetation and land cover influence the quantity and quality of basal carbon sources in streams. Lu *et al.* (2014) reported that land use significantly altered the nutritional value of OM (estimated from lipid concentration). Bellamy *et al.* (2017) highlighted how these changes in basal feeding sources due to agricultural pressure influenced aquatic macroinvertebrates differently according to their functional feeding group (FFG). Notably collector/gatherers (*Ephemera* mayflies) were more reliant on terrestrial and soil OM in agricultural landscape, a shift imputed to increased sedimentation. Deegan and Ganf (2008) showed how loss of riparian vegetation could significantly constrain shredder communities in Australian streams *via* the collapse of an adequate food source.

Anthropogenic inputs of nutrients from agricultural fertilizers have increased greatly over the past century in nearly all parts of the world (Galloway *et al.* 2008). Nutrient concentrations

have increased in streams, stimulating the autotrophic energy pathway. A large amount of literature illustrates how benthic invertebrate communities are subsequently altered *via* bottom-up transfers within aquatic food webs; however, multiple outcomes are reported. Davis *et al.* (2011) showed a two-fold increase in stream secondary production after 5 years of experimental addition of nutrients. They observed that larger Trichoptera emerged from the stream but were not more abundant. Cross *et al.* (2006) reported that benthic invertebrate biomass significantly increased after 2 years of enrichment of a headwater stream, but with a magnitude depending on the FFG. More recently, Raitif *et al.* (2018) studied 12 streams located in an intensive agricultural landscape. They reported that the proportion of agricultural land and ammonium concentration in water influenced significantly and positively the emerging drymass of Chironomidae while decreasing that of Ephemeroptera.

Intensification of agricultural practices has resulted in a large increase in pesticide use, which has been clearly identified as a major stressor for many aquatic species. They show contrasting susceptibility to pesticides, related in particular to life-cycle traits such as generation time and the presence of sensitive aquatic stages during pesticide exposure, as proposed by Liess and Von Der Ohe (2005). Analyzing the effect of agricultural pesticides on the taxa richness of stream invertebrates in 72 sites in Europe and Australia, Beketov *et al.* (2013) found a decrease up to 42% in family richness between uncontaminated and highly contaminated streams. Following the species-at-risk (SPEAR) method, which estimates the sensitivity of aquatic invertebrates to pesticide exposure, Plecoptera and Ephemeroptera are considered more sensitive taxa than Diptera and Trichoptera (Wogram and Liess 2001).

2.2 Water temperature, flow and substrate

Water temperature is a major driver of insect biology in freshwater ecosystems because it directly affects insect metabolism (Vannote and Sweeney 1980). Eurythermal species can develop under a wide range of temperatures, unlike stenothermal species (Ward and Stanford

1982). Several processes, in connection with air temperature and climate at a large continental scale, explain the variation in water temperature, as do local influences, including groundwater exchanges and shade (reviewed by Webb *et al.* 2008). Nagasaka and Nakamura (1999) estimated that agricultural intensification in Japan since 1945, especially clearing of riparian vegetation and river channelization (the widening and deepening of a river channel), had increased the maximum temperature of some rivers from 22°C to 28°C.

Shifts in aquatic invertebrate community composition are frequently associated with an increase in stream temperatures, especially for stenothermal EPT families (Sponseller *et al.* 2001; Haidekker and Hering 2008). Sponseller *et al.* (2001) observed that aquatic macroinvertebrate diversity was negatively correlated with stream temperature, since eurythermal taxa such as chironomids dominate in warmer streams. A similar pattern was also reported by Kiffney *et al.* (2003) who found more chironomids in sites with narrow riparian vegetation, more light and higher water temperatures. However, when temperature stays inside the tolerance limits, warmer temperature can enhance the emerging drymass of Trichoptera and Ephemeroptera (Raitif *et al.* 2018).

The effect of increasing temperature after the clearing of riparian vegetation may be further exacerbated by global warming, which increases the threat to cold-stenothermal taxa. In their review of 297 sites in the western United States (U.S.), Poff *et al.* (2010) showed that the expected increase in temperature by the end of the 21st century could replace many cold-stenothermal taxa, especially those in the Plecoptera order, with eurythermal species of Diptera and Trichoptera, potentially resulting in profound consequences for stream ecology.

Habitat conditions in streams also influence invertebrate communities, especially hydraulic conditions and the type of substrate. For instance, floods and droughts exert pressures that select morphological, physiological or behavioral traits of aquatic insects in response to these perturbations (Bunn and Arthington 2002). Regulating river discharges, in connection with

hydroelectricity production, water supply or irrigation, can decrease aquatic insect diversity, especially by reducing habitat diversity, food availability and affecting thermal regime. Low taxa richness is often observed in regulated rivers, promoting chironomids and other flexible taxa such as certain Ephemerellidae at the expense of other sensitive mayflies (Heptageniidae) (Brittain and Saltveit 1989; Munn and Brusven 1991). At local scales, the succession of pool and riffle habitats hosts multiple assemblages of macroinvertebrates (Brown and Brussock 1991). Ephemeroptera and Trichoptera are generally more abundant in riffle habitats, whose larger substratum particles provide foraging sites for grazers and filter feeders in these orders. Conversely, burrowers and collector/gatherers of the Diptera order (*e.g.* chironomids) prevail in pools, where water velocity is low and the substratum is fine sediment (Logan and Brooker 1983). Channelization alters water flow and aquatic habitat heterogeneity. In a study along the Rio Grande River in New Mexico, U.S., Kennedy and Turner (2011) found that channelization reduced the density and diversity of aquatic macroinvertebrates and resulted in outbreaks of chironomids and a loss of mayflies. In most agricultural areas, river channels have been reshaped to facilitate crop irrigation and reduce flooding risks. The resulting loss in aquatic habitat heterogeneity induces a decrease in macroinvertebrate species abundance and diversity. Negishi *et al.* (2002) highlighted that the decrease in bottom invertebrate shelters in a channelized section of a stream endangers community recovery after flood episode, resulting in a lower density of macroinvertebrates than in natural sections. Altering stream morphology has a strong influence on the hyporheic zone, where most aquatic invertebrates seek refuge during hydrological disturbances (Dole-Olivier 2011).

The silting of streams, often observed in agricultural landscapes following clearing of terrestrial vegetation, can also influence aquatic macroinvertebrate assemblages greatly (Allan 2004). Excess sediment loads in stream beds, resulting from greater terrestrial surface runoff, clog vital habitats for many aquatic insects, which significantly reduces the relative

abundance of sensitive EPT taxa (Burdon *et al.* 2013). By altering food availability, they also constrain aquatic insects to different degrees as a function of their FFG. Several studies show that siltation decreases filter-feeding and grazer taxa density and diversity, especially EPT taxa (Lemly 1982, Wagenhoff *et al.* 2011). Conversely, collectors/gatherers that burrow in silt can benefit from fine sediments, especially chironomids (Lemly 1982, Rabení *et al.* 2005).

3 *Effects of agriculture on stream insect subsidies*

As illustrated in section 2, much evidence suggests that agricultural practices significantly influence stream invertebrate communities and that Diptera species, especially chironomids, often become dominant in agricultural landscapes at the expense of EPT species (Figure 1). Few reliable studies exist that extend this finding to winged adults, and the consequences of agricultural practices on the magnitude of stream insect subsidies are not yet clearly established. However, recent studies demonstrated that agriculture influences the magnitude of aquatic exports and their assimilation in the terrestrial food web.

3.1 *Modification of the flux of aquatic subsidies*

Greenwood and Booker (2016) highlighted that agricultural intensification in watersheds in New Zealand resulted in a significant increase in the density of stream larvae species that become terrestrial winged adults. The authors also showed a shift towards smaller invertebrates with greater adult dispersal abilities, suggesting potentially greater export of aquatic insects toward land. Similarly, Stenroth *et al.* (2015) showed that land use can influence the size of the assemblage of emerging insects, with small aquatic insects being more abundant in agricultural areas. However, they did not observe changes in the biomass of aquatic subsidies. In Sweden, Carlson *et al.* (2016) found more winged aquatic insects near agricultural streams than near forested streams, especially small Diptera taxa (Chironomidae). In France, Delettre and Morvan (2000) studied chironomid dispersal and concluded that it was

restricted to stream corridors with dense riparian vegetation, whereas long-distance flights over terrestrial landscapes were observed from more open agricultural streams. Raitif *et al.* (2018) highlighted the role of agriculture in the amount of insect biomass emerging from small streams, and they estimated that aquatic drymass deposit on lands could range between 0.9 and 4.5 kg ha⁻¹ year⁻¹ in the vicinity of these streams.

3.2 Cascading effects on terrestrial communities

Riparian predators are key organisms because they facilitate the transfer of aquatic secondary production to terrestrial food webs. The diet of certain arthropod species, including carabids, staphylinid beetles and spiders (Paetzold *et al.* 2005), as well as insectivorous birds (Iwata *et al.* 2003), may include a large proportion of emerging aquatic insects during part of the year. Some evidence suggests that the heterogeneity of stream and riparian habitats has a strong influence on riverine predators. Laeser *et al.* (2005) estimated that the abundance of spiders that feed on aquatic insects along streams decreased by 70% after riparian vegetation was removed and agricultural practices straightened the channel. This was attributed to the loss of suitable riparian habitat for web-weaving spiders and a potential decrease in aquatic insect emergence resulting from channelization. Iwata *et al.* (2003) also described the potential detrimental effect of channelization and demonstrated that the loss of meanders in stream channels decreased the abundance of aquatic insects and insectivorous birds that prey on them. Carlson *et al.* (2016) reported that abundance of adult aquatic insects decreased more rapidly away from stream banks in open agricultural streams than away from those of forest streams. These results suggest that riparian vegetation can significantly modify the flux of subsidies from aquatic to terrestrial ecosystems. Moreover, many riparian predators such as birds (Buchanan *et al.* 2006) or spiders (Nentwig 1980) are size selective when preying on aquatic insects. Stenroth *et al.* (2015) highlighted that a greater abundance of small-bodied insects (*e.g.* Nematocera) emerging from agricultural streams was associated with greater

abundance of riparian carabid beetles and linyphiid spiders. Therefore, the changes in aquatic and riparian habitats, along with agricultural practices, can modify functional links between aquatic and terrestrial food webs, and consequently the transfer efficiency of aquatic subsidies to land.

4 Stream insect subsidies and ecosystem services to agriculture

Despite the growing field of research on aquatic subsidies, implications of water-to-land transfers in adjacent agroecosystems and ecosystem services are rarely addressed. In particular, winged adults of aquatic arthropods may sustain regulating services, most likely pollination, soil fertilization and pest control. To explore the current knowledge on this issue, we based our analysis on studies that quantified the contribution of aquatic arthropods to terrestrial ecological processes related to ecosystem services, *i.e.* visiting flowers or feeding on nectar/pollen for pollination, dispersal of aquatic insect biomass for fertilization and the percentage of aquatic prey in the diets of natural enemies for pest control.

4.1 Pollination

Seventy percent of worldwide crops rely on animal pollination, and flower-visiting insects undoubtedly are the major pollinators (Klein *et al.* 2007). Insects also play a critical role in the conservation of wild flowers (Biesmeijer 2006). The global decline in insect pollinators (Potts *et al.* 2010), especially in agroecosystems, highlights the fundamental influence of non-crop habitats (Ricketts *et al.* 2008), especially riparian buffer strips (Cole *et al.* 2015), on pollination services. Although bees still receive the most public and scientific attention, the importance of wild non-bee pollinators has become increasingly recognized (Garibaldi *et al.* 2013, Rader *et al.* 2016). However, adult aquatic insects emerging from streams have been ignored as pollinators, even though they feed on nectar or pollen, or at least visit wild flowers or crops (Table 1). Confirmed pollinators include many species of adult Plecoptera that

depend on pollen as a primary energy source (Winterbourn 2005). Occasional feeding on nectar or pollen was observed for Trichoptera (Petersson and Hasselrot 1994) and aquatic Coleoptera (Hoe *et al.* 2017). Consumption of pollen or nectar by adults of Megaloptera had also been recorded (reviewed and observed in laboratory by Villagomez & Contreras-Ramos, 2017). Besides hoverflies, which are active pollinators (Hass *et al.* 2018), many Diptera families with an aquatic larval stage, such as Chironomidae, Empididae, and Ceratopogonidae, were observed to visit flowers (Table 1). Because these Diptera families are composed of both species with aquatic or terrestrial larval stage, further studies are needed to confirm that the adults that visit flowers actually emerge from water. Additionally, adult aquatic insects that pollinate or visit flowers increase flower diversity in riparian ecosystems and thus indirectly help to sustain the community of well-known pollinators such as bees or hoverflies that depend on this flower diversity (Cole *et al.* 2015). In a field experiment, Stewart *et al.* (2017) observed an increase in the quality and quantity of strawberries produced near a pond compared to those in a crop habitat. This correlates with a greater abundance of hoverflies (Syrphidae, Diptera), for which the larvae of many species are aquatic (Speight 2014). This is promising and suggests the need for similar experiments near streams to assess potential effects of stream insect communities on pollination of crops and wild flowers.

Adult aquatic insects are an important part of the diet of riparian predators, such as birds and bats, some of which are active pollinators (Kunz *et al.* 2011, Whelan *et al.* 2008). For instance, species of Sylviidae (warblers) are frequently observed in riparian habitats feeding on insects and plants, and pollinating wild plants (Ford 1985; Whelan *et al.* 2008).

Conversely, Knight *et al.* (2005) observed that adult dragonflies that prey on wild bees could cause a significant decrease in plant pollination by decreasing the number of bees visiting flowers. Beyond this evidence, more studies are needed to better assess the magnitude of

direct (flower visits) and indirect effects (beneficial or detrimental effects on other pollinators) of aquatic insects on the pollination of wild plants and crops.

4.2 Soil fertilization

Rock weathering, atmospheric exchanges and the decomposition of OM provide essential elements for plant growth. In agricultural landscapes, soil fertility depends largely on external inputs. However, insect outbreaks can add large amounts of nutrients to the soil *via* their feces or cadavers (Hunter 2001). Studies of winged aquatic insects have concluded that a small percentage (3-9%) of their biomass ultimately returns to the stream (Jackson and Fisher 1986; Gray 1989). Deposition traps are rarely used to measure the biomass of stream-derived insects that fall to the ground per unit area (but see Stenroth *et al.* 2015); however, some authors have placed interception traps at multiple distances from streams (Table 2). The biomass of aquatic invertebrates trapped can be regarded as biomass deposition on the ground per unit area, and converted into N assuming that the dry mass of invertebrates contains 10% N (Fagan *et al.* 2003). These calculations show that stream-derived N deposition to land can vary during outbreaks from 1.5-12.5 mg.m⁻².d⁻¹ near the stream, depending on the study (Table 2). Deposition decreases as the distance from the stream increases, but still reaches 0.7-3.0 mg.m⁻².d⁻¹ 10-50 m away and up to 1.5 mg.m⁻².d⁻¹ 150 m away. Most published studies were conducted along forest streams, but the amount of aquatic subsidies is likely greater along agricultural streams, especially for small dipterans (chironomids) that disperse farther. From 200 studies of stream production, Finlay (2011) estimated that secondary production of macroinvertebrates is 7 times as great in human-impacted streams as in pristine streams. In Sweden, Carlson *et al.* (2016) found 10 times as many aquatic insects 1 m from, and 5 times as many 50 m from, small streams (<8 m wide) in agricultural landscapes compared to those in forests. Large rivers (>16 m wide) can export 4 times as many aquatic insects to land as smaller rivers (Gratton and Zanden 2009). Consequently, the amount of aquatic-derived N in

agroecosystems (Table 2) may be significantly underestimated. In comparison, this phenomenon may equal or even exceed current amounts of atmospheric N deposition in temperate regions (*i.e.* mean of 55 g N.ha⁻¹.d⁻¹, calculated from Krupa 2003), at least occasionally and near streams. Where agriculture is intensive and streams are highly productive, further research is required to estimate nutrient inputs per year and unit area of cropland that stream insects could transfer to agricultural landscapes.

4.3 Crop pest control

Biocontrol is commonly considered a relevant alternative to the use of chemicals. It relies on a wide diversity of natural enemies, including insects and spiders (Landis *et al.* 2000). A rich and abundant natural enemy community facilitates the control of pest outbreaks (Landis *et al.* 2000). The direct role of adult aquatic insects in pest control is rarely demonstrated; however, Yasumatsu *et al.* (1975) observed odonates in rice fields preying on several defoliators and stem borers. Many potential biocontrol agents prey on aquatic insects (Table 3), including spiders (Linyphiidae, Lycosidae, Salticidae, Thomisidae; Riechert and Lockley 1984) and carabids (Symondson *et al.* 2006). Because aquatic prey usually emerge in pulses in early spring for instance in temperate regions, they may be essential for sustaining natural enemy populations when crop pests are scarce and more likely to be controlled (Wissinger 1997). Riparian predators can shift from aquatic-derived prey in riparian habitats to crop pests later in spring or summer, following a process of seasonal predator spillover, as described for other adjacent ecosystems (French *et al.* 2001; Rand *et al.* 2006). For instance, bats and birds that actively feed on aquatic insects in riparian habitats were effective at reducing pest abundance and thus indirectly increasing crop yield, especially in tropical agroforestry (Maas *et al.* 2016). This cascading effect requires that the emergence and dispersal of aquatic insects matches the timing of riparian predator food needs when terrestrial subsidies are low. In their review, Larsen *et al.* (2015) highlighted that global environmental changes may threaten this

synchronicity, especially when the phenology and distribution of stream and riparian organisms are altered. This synchronicity could be threatened in agroecosystems in which the magnitude and quality of aquatic subsidies change greatly (see sections 2 & 3). Finally, alternative prey from aquatic ecosystems may distract natural enemies from pests and thus decrease the effectiveness of biocontrol (Symondson *et al.* 2006; Birkhofer *et al.* 2008). The considerable amount of aquatic biomass exported from large rivers (Gratton and Zanden 2009) probably has a significant effect on terrestrial food webs, including disruptions in biological control services. The multifaceted trophic interactions between stream invertebrate prey and terrestrial predators in agroecosystems require further studies to assess the influence on crop pest control.

5 Conclusion

Freshwater ecosystems have been traditionally viewed as passive receivers of terrestrial subsidies that result from agricultural practices on watersheds. However, consideration of the reciprocal subsidies supported by the emergence of adult aquatic insects could cause this simplistic assessment to be reevaluated. Intensification of agriculture resulted in massive use of chemical inputs and great changes to the landscape, which has decreased biodiversity and ecosystem functioning worldwide. In this context, it is critical to encourage a new model developed for sustainable agricultural practices that relies on the ecological processes that ecosystems provide. In this review, we highlighted promising scientific evidence that winged aquatic insects can support pollination, soil fertilization and the control of crop pests in agroecosystems. The influence of land-use and agricultural practices on the amount and type of emerging aquatic insects requires more thorough investigation. Studies of aquatic subsidies associated with the dispersal of stream insect communities in agricultural landscapes are essential for a comprehensive approach to the variety of ecosystem services provided in agroecosystems. Future research on aquatic subsidies in agricultural landscapes could

372 strengthen understanding of ecosystem services and their management, while simultaneously
373 meeting conservation goals for freshwater biodiversity to ensure optimal ecosystem
374 functioning.

375 *Acknowledgements*

376 This study received financial support from the EcoServ program of the French National
377 Institute for Agronomic Research (INRA) (for J.-M. Roussel) and from the French Ministry
378 for Research (Ph.D. grant, 2015-2018) (for J. Raitif).

Accepted

Table 1. Observed pollination or flower visits of aquatic insect taxa

Reference	Country	Aquatic insects involved ^a
Chartier et al., 2011	France, Spain	Diptera (Chironomidae, Psychodidae, Ceratopogonidae)
de Figueroa & Sánchez-Ortega, 2000	Spain	Plecoptera
Gilbert, 1981	England	Syrphidae (Diptera)
Hass et al., 2018	France, Germany, Spain, UK	Syrphidae (Diptera)
Hoe et al., 2017	Indonesia & Malaysia	Hydrophilidae (Coleoptera)
Kato et al., 1990	Japan	Diptera (Syrphidae, Empididae, Anthomyiidae, Tipulidae, Chironmidae), Hemiptera, Coleoptera (Curculionidae), Ephemeroptera, Trichoptera
Kevan, 1972	Canada	Diptera (Chironomidae, Culicidae, Dolichopodidae, Syrphidae)
Murza et al., 2006	Canada	Diptera (Chironomidae, Ceratopogonidae, Dolichopodidae)
Petersson & Hasselrot, 1994	Sweden	Trichoptera
Robson, 2008	Canada	Syrphidae, Stratiomyidae (Diptera)
Sato & Kato, 2017	Japan	Plecoptera

Thien et al., 1983	USA	Diptera (Chironomidae, Culicidae), Plecoptera, Trichoptera
Villagomez & Contreras-Ramos 2017	Laboratory	Megaloptera
Winterbourn, 2005	New-Zealand	Plecoptera

a: Dipterans cited as flower visitors in these studies were rarely identified to the species level. Since these studies were performed near streams or other water bodies, however, we assumed that the dipterans were mostly aquatic species.

Accepted

Table 2. Published estimates of the dry mass of dispersing winged aquatic insects trapped at multiple distances from streams and their equivalent nitrogen (N) deposits during outbreaks

Reference	Country	Riparian habitat	Aquatic insects trapped	Experimental setup	Adult aquatic insect dry mass measured	Estimated N deposit ($mg.m^{-2}.d^{-1}$)
Jackson and Resh 1989	United States	Forest	Chironomidae, EPT	Sticky traps (0.26m ²)	At 5 m: 206 mg/trap	3.1
				26 days of capture	At 40 m: 152 mg/trap	2.3
				1 stream	At 150 m: 51 mg/trap	0.8
Henschel et al. 2001	Germany	Forest	Nematocera, Trichoptera	Sticky traps (0.01m ²)	Bank: 4.4 mg/trap	3.1
				14 days of capture	At 30 m: 1.0 mg/trap	0.7
				1 stream	At 60 m: 0.8 mg/trap	0.6
Lynch et al. 2002	Australia	Forest	Diptera, EPT	Sticky (0.106m ²) traps	Bank: 65 mg/m ² /day	6.5
				48 hours of capture	At 10 m: 30 mg/m ² /day	3.0
				4 streams	At 160 m: 15 mg/m ² /day	1.5
Kato et al. 2003	Japan	Forest	Not mentioned	Malaise traps (2.15 m ²)	Bank: 32 mg/trap/day	1.5
				7 days of capture, 1 stream		
Marczak and Richardson 2007	Canada	Forest	Diptera, EPT	Sticky traps (0.06 m ²)	At 2 m: 40 mg/trap	9.5
				7 days of capture, 2 streams		
Stenroth et al. 2015	Sweden	Forest & agriculture	Nematocera, Trichoptera, Plecoptera	Deposition (0.16 m ²) and interception (0.08 m ²) traps	Bank (max.): 1,250 mg/m ²	12.5
				10 days of capture, 10 streams	Bank (min.): 200 mg/m ²	2.0

See text for details of calculating N deposition, which should not be extrapolated beyond outbreak periods. EPT stands for Ephemeroptera, Plecoptera and Trichoptera.

Table 3. Percentage of aquatic prey in the diets of terrestrial arthropod predators that are potential natural enemies of crop pests

Reference	Country	Riparian habitats	Terrestrial natural enemies	Percentage aquatic prey (%)
Akamatsu et al. 2004	Japan	Forests and grasses	Spiders	54-92
Davis et al. 2011	United States	Forests	Spiders (Tetragnathidae, Araneidae, Linyphiidae)	12-100
Gergs et al. 2014	Germany	Forests	Spiders (Tetragnathidae, Lycodidae)	13-77
Henschel et al. 2001	Germany	Forests	Spiders (Tetragnathidae, Lycodidae, Linyphiidae)	24-53
			Cephalopods	11-20
			Others (Coleoptera)	0-29
Hering and Plachter, 1997	Germany	<i>Unspecified</i>	Coleoptera (Carabidae)	89
Paetzold et al. 2005	Switzerland and Italy	Forests	Coleoptera (Staphylinidae)	80
			Spiders (Lycosidae)	56
Sanzone et al. 2003	United States	Forests	Spiders (Araneidae, Tetragnathidae, Salticidae, Thomisidae, Lycosidae)	68-100
Stenroth et al. 2015	Sweden		Spiders (Lycosidae, Linyphiidae)	44-60
			Carabidae	43

References

- Akamatsu F, Toda H, Okino T (2004) Food source of riparian spiders analyzed by using stable isotope ratios. *Ecol Res* 19:655–662 . doi: 10.1111/j.1440-1703.2004.00680.x
- Allan, J. D. (2004). Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 35(1), 257–284. <https://doi.org/10.1146/annurev.ecolsys.35.120202.110122>
- Ballinger A, Lake PS (2006) Energy and nutrient fluxes from rivers and streams into terrestrial food webs. *Marine and Freshwater Research* 57:15 . doi: 10.1071/MF05154
- Baxter CV, Fausch KD, Carl Saunders W (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones: Prey subsidies link stream and riparian food webs. *Freshw Biol* 50:201–220 . doi: 10.1111/j.1365-2427.2004.01328.x
- Beketov MA, Kefford BJ, Schafer RB, Liess M (2013) Pesticides reduce regional biodiversity of stream invertebrates. *Proc Natl Acad Sci* 110:11039–11043 . doi: 10.1073/pnas.1305618110
- Bellamy AR, Bauer JE, Grotoli AG (2017) Influence of land use and lithology on sources and ages of nutritional resources for stream macroinvertebrates: a multi-isotopic approach. *Aquat Sci* 79:925–939 . doi: 10.1007/s00027-017-0542-3
- Biesmeijer JC (2006) Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science* 313:351–354. doi: 10.1126/science.1127863
- Birkhofer K, Wise DH, Scheu S (2008) Subsidy from the detrital food web, but not microhabitat complexity, affects the role of generalist predators in an aboveground herbivore food web. *Oikos* 117:494–500 . doi: 10.1111/j.0030-1299.2008.16361.x
- Brett MT, Bunn SE, Chandra S, Garloway A.W.E., Guo F, Kainz M J, ..., Wehr J.D. (2017) How important are terrestrial organic carbon inputs for secondary production in freshwater ecosystems? *Freshw Biol* 62:833–853 . doi: 10.1111/fwb.12909
- Brittain JE, Saltveit SJ (1989) A review of the effect of river regulation on mayflies (Ephemeroptera). *Regul Rivers Res Manag* 3:191–204 . doi: 10.1002/rrr.3450030119
- Brown AV, Brussock PP (1991) Comparisons of benthic invertebrates between riffles and pools. *Hydrobiologia* 220:99–108 . doi: 10.1007/BF00006542
- Buchanan, G. M., Grant, M. C., Sanderson, R. A., & Pearce-Higgins, J. W. (2006). The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management: Moorland bird diets. *Ibis*, 148(4), 615–628. <https://doi.org/10.1111/j.1474-919X.2006.00578.x>
- Bunn SE, Arthington AH (2002) Basic Principles and Ecological Consequences of Altered Flow Regimes for Aquatic Biodiversity. *Environ Manage* 30:492–507 . doi: 10.1007/s00267-002-2737-0

37 Burdon FJ, McIntosh AR, Harding JS (2013) Habitat loss drives threshold response of benthic
38 invertebrate communities to deposited sediment in agricultural streams. *Ecol Appl*
39 *Publ Ecol Soc Am* 23:1036–1047. doi: 10.1890/12-1190.1

40 Carlson PE, McKie BG, Sandin L, Johnson RK (2016) Strong land-use effects on the
41 dispersal patterns of adult stream insects: implications for transfers of aquatic
42 subsidies to terrestrial consumers. *Freshw Biol* 61:848–861 . doi: 10.1111/fwb.12745

43 Chartier M, Pélozuelo L, Gibernau M (2011) Do floral odor profiles geographically vary with
44 the degree of specificity for pollinators? Investigation in two sapromyophilous Arum
45 species (Araceae). *Ann Société Entomol Fr NS* 47:71–77. doi:
46 10.1080/00379271.2011.10697698

47 Cole, L. J., Brocklehurst, S., Robertson, D., Harrison, W., & McCracken, D. I. (2015).
48 Riparian buffer strips: Their role in the conservation of insect pollinators in intensive
49 grassland systems. *Agriculture, Ecosystems & Environment*, 211, 207–220.
50 <https://doi.org/10.1016/j.agee.2015.06.012>

51 Cross WF, Wallace JB, Rosemond AD, Eggert SL (2006) Whole-system nutrient enrichment
52 increases secondary production in a detritus-based ecosystem. *Ecology* 87:1556–1565
53 . doi: 10.1890/0012-9658(2006)87[1556:WNEISF]2.0.CO;2

54 Davis JM, Rosemond AD, Small GE (2011) Increasing donor ecosystem productivity
55 decreases terrestrial consumer reliance on a stream resource subsidy. *Oecologia*
56 167:821–834 . doi: 10.1007/s00442-011-2026-9

57 de Figueroa JMT, Sánchez-Ortega A (2000) Imaginal Feeding of Twelve Nemouroidean
58 Stonefly Species (Insecta, Plecoptera). *Ann Entomol Soc Am* 93:251–253. doi:
59 10.1603/0013-8746(2000)093[0251:IFOTNS]2.0.CO;2

60 Deegan BM, Ganf GG (2008) The loss of aquatic and riparian plant communities:
61 Implications for their consumers in a riverine food web. *Austral Ecol* 33:672–683 .
62 doi: 10.1111/j.1442-9993.2008.01834.x

63 Delettre YR, Morvan N (2000) Dispersal of adult aquatic Chironomidae (Diptera) in
64 agricultural landscapes. *Freshw Biol* 44:399–411 . doi: 10.1046/j.1365-
65 2427.2000.00578.x

66 Dole-Olivier M-J (2011) The hyporheic refuge hypothesis reconsidered: a review of
67 hydrological aspects. *Mar Freshw Res* 62:1281 . doi: 10.1071/MF11084

68 Dreyer J, Hoekman D, Gratton C (2012) Lake-derived midges increase abundance of
69 shoreline terrestrial arthropods via multiple trophic pathways. *Oikos* 121:252–258 .
70 doi: 10.1111/j.1600-0706.2011.19588.x

71 Fagan WF, Siemann E, Mitter C, Denno R.F., Huberty A.F., Woods H.A., Else J.J. (2003)
72 Nitrogen in Insects: Implications for Trophic Complexity and Species Diversification.
73 *Am Nat* 160:784–802 . doi: 10.1086/343879

74 Finlay JC (2011) Stream size and human influences on ecosystem production in river
75 networks. *Ecosphere* 2:1–21 . doi: 10.1890/ES11-00071.1

76 Ford HA (1985) Nectarivory and Pollination by Birds in Southern Australia and Europe.
77 *Oikos* 44:127 . doi: 10.2307/3544053

78 French BW, Elliott NC, Berberet RC, Burd JD (2001) Effects of Riparian and Grassland
79 Habitats on Ground Beetle (Coleoptera: Carabidae) Assemblages in Adjacent Wheat
80 Fields. *Environ Entomol* 30:225–234 . doi: 10.1603/0046-225X-30.2.225

81 Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai Z, Freney JR, ..., Sutton MA
82 (2008) Transformation of the Nitrogen Cycle: Recent Trends, Questions, and Potential
83 Solutions. *Science* 320:889–892 . doi: 10.1126/science.1136674

84 Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R.,
85 Cunningham, S. A., ... Klein, A. M. (2013). Wild Pollinators Enhance Fruit Set of
86 Crops Regardless of Honey Bee Abundance. *Science*, 339(6127), 1608–1611.
87 <https://doi.org/10.1126/science.1230200>

88 Gergs R, Koester M, Schulz RS, Schulz R (2014) Potential alteration of cross-ecosystem
89 resource subsidies by an invasive aquatic macroinvertebrate: implications for the
90 terrestrial food web. *Freshw Biol* 59:2645–2655 . doi: 10.1111/fwb.12463

91 Gilbert FS (1981) Foraging ecology of hoverflies: morphology of the mouthparts in relation to
92 feeding on nectar and pollen in some common urban species. *Ecol Entomol* 6:245–262
93 . doi: 10.1111/j.1365-2311.1981.tb00612.x

94 Gratton C, Zanden MJV (2009) Flux of aquatic insect productivity to land: comparison of
95 lentic and lotic ecosystems. *Ecology* 90:2689–2699 . doi: 10.1890/08-1546.1

96 Gray LJ (1989) Emergence Production and Export of Aquatic Insects from a Tallgrass Prairie
97 Stream. *Southwest Nat* 34:313 . doi: 10.2307/3672158

98 Greenwood MJ, Booker DJ (2016) Influence of hydrological regime and land cover on traits
99 and potential export capacity of adult aquatic insects from river channels. *Oecologia*
100 180:551–566 . doi: 10.1007/s00442-015-3462-8

101 Haidekker A, Hering D (2008) Relationship between benthic insects (Ephemeroptera,
102 Plecoptera, Coleoptera, Trichoptera) and temperature in small and medium-sized
103 streams in Germany: A multivariate study. *Aquat Ecol* 42:463–481 . doi:
104 10.1007/s10452-007-9097-z

105 Hass AL, Kormann UG, Tschardt T, et al (2018) Landscape configurational heterogeneity
106 by small-scale agriculture, not crop diversity, maintains pollinators and plant
107 reproduction in western Europe. *Proc R Soc B* 285:20172242. doi:
108 10.1098/rspb.2017.2242

109 Havik G, Catenazzi A, Holmgren M (2014) Seabird Nutrient Subsidies Benefit Non-Nitrogen
110 Fixing Trees and Alter Species Composition in South American Coastal Dry Forests.
111 *PLoS ONE* 9:e86381 . doi: 10.1371/journal.pone.0086381

112 Henschel JR, Mahsberg D, Stumpf H (2001) Allochthonous aquatic insects increase predation
113 and decrease herbivory in river shore food webs. *Oikos* 93:429–438 . doi:
114 10.1034/j.1600-0706.2001.930308.x

115 Hering D, Plachter H (1997) Riparian ground beetles (Coeloptera, Carabidae) preying on
 116 aquatic invertebrates: a feeding strategy in alpine floodplains. *Oecologia* 111:261–270
 117 . doi: 10.1007/s004420050234

118 Hoe YC, Gibernau M, Wong SY (2017) Diversity of pollination ecology in the
 119 *Schismatoglottis* Calyptrata Complex Clade (Araceae). *Plant Biol* 20:563–578. doi:
 120 10.1111/plb.12687

121 Holt RD (1997) From Metapopulation Dynamics to Community Structure. In:
 122 *Metapopulation Biology*. Elsevier, pp 149–164

123 Hunter MD (2001) Insect population dynamics meets ecosystem ecology: effects of herbivory
 124 on soil nutrient dynamics. *Agric For Entomol* 3:77–84 . doi: 10.1046/j.1461-
 125 9563.2001.00100.x

126 Hyndes GA, Nagelkerken I, McLeod RJ, Connolly RM, Lavery PS, Vanderklift MA (2014)
 127 Mechanisms and ecological role of carbon transfer within coastal seascapes: Carbon
 128 transfer within coastal seascapes. *Biol Rev* 89:232–254 . doi: 10.1111/brv.12055

129 Iwata T, Nakano S, Murakami M (2003) Stream Meanders Increase Insectivorous Bird
 130 Abundance in Riparian Deciduous Forests. *Ecography* 26:325–337. doi:
 131 10.1034/j.1600-0587.2003.03355.x

132 Jackson JK, Fisher SG (1986) Secondary Production, Emergence, and Export of Aquatic
 133 Insects of a Sonoran Desert Stream. *Ecology* 67:629 . doi: 10.2307/1937686

134 Jackson JK, Resh VH (1989) Distribution and Abundance of Adult Aquatic Insects in the
 135 Forest Adjacent to a Northern California Stream. *Environ Entomol* 18:278–283 . doi:
 136 10.1093/ee/18.2.278

137 Kato C, Iwata T, Nakano S, Kishi D (2003) Dynamics of aquatic insect flux affects
 138 distribution of riparian web-building spiders. *Oikos* 103:113–120 . doi:
 139 10.1034/j.1600-0706.2003.12477.x

140 Kato M, Kakutani T., Inoue T., Itino T. (1990) Insect-flower relationship in the primary beech
 141 forest of Ashu, Kyoto: an overview of the flowering phenology and the seasonal
 142 pattern from insect visits. *Contrib Biol Lab Kyoto Univ* 309–375

143 Kennedy TL, Turner TF (2011) River channelization reduces nutrient flow and
 144 macroinvertebrate diversity at the aquatic terrestrial transition zone. *Ecosphere* 2:art35
 145 . doi: 10.1890/ES11-00047.1

146 Kevan PG (1972) Insect Pollination of High Arctic Flowers. *J Ecol* 60:831 . doi:
 147 10.2307/2258569

148 Kiffney, P. M., Richardson, J. S., & Bull, J. P. (2003). Responses of periphyton and insects to
 149 experimental manipulation of riparian buffer width along forest streams. *Journal of*
 150 *Applied Ecology*, 40(6), 1060–1076. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2664.2003.00855.x)
 151 [2664.2003.00855.x](https://doi.org/10.1111/j.1365-2664.2003.00855.x)

152 Klein A-M, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C,
 153 Tscharnkte T (2007) Importance of pollinators in changing landscapes for world
 154 crops. *Proc R Soc B Biol Sci* 274:303–313 . doi: 10.1098/rspb.2006.3721

155 Knight TM, McCoy MW, Chase JM, McCoy KA, Holt RD (2005) Trophic cascades across
 156 ecosystems. *Nature* 437:880–883 . doi: 10.1038/nature03962

157 Kostecki C, Le Loc'h F, Roussel J-M, Desroy N, Huteau D, Riera P,...,Le Pape O (2010)
 158 Dynamics of an estuarine nursery ground: the spatio-temporal relationship between
 159 the river flow and the food web of the juvenile common sole (*Solea solea*, L.) as
 160 revealed by stable isotopes analysis. *J Sea Res* 64:54–60 . doi:
 161 10.1016/j.seares.2009.07.006

162 Krupa S. (2003) Effects of atmospheric ammonia (NH₃) on terrestrial vegetation: a review.
 163 *Environ Pollut* 124:179–221 . doi: 10.1016/S0269-7491(02)00434-7

164 Kunz TH, Torrez EB de, Bauer D, et al (2011) Ecosystem services provided by bats. *Ann N Y*
 165 *Acad Sci* 1223:1–38. doi: 10.1111/j.1749-6632.2011.06004.x

166 Laeser, S. R., Baxter, C. V., & Fausch, K. D. (2005). Riparian vegetation loss, stream
 167 channelization, and web-weaving spiders in northern Japan. *Ecological Research*,
 168 20(6), 646–651. <https://doi.org/10.1007/s11284-005-0084-3>

169 Lancaster J (2013) *Aquatic entomology*, 1st ed. Oxford University Press, Oxford

170 Landis DA, Wratten SD, Gurr GM (2000) Habitat Management to Conserve Natural Enemies
 171 of Arthropod Pests in Agriculture. *Ann Rev Entomol* 45:175–201 . doi:
 172 10.1146/annurev.ento.45.1.175

173 Larsen S, Muehlbauer JD, Marti E (2016) Resource subsidies between stream and terrestrial
 174 ecosystems under global change. *Global Change Biology* 22:2489–2504. doi:
 175 10.1111/gcb.13182

176 Lemly AD (1982) Modification of benthic insect communities in polluted streams: combined
 177 effects of sedimentation and nutrient enrichment. *Hydrobiologia* 87:229–245 . doi:
 178 10.1007/BF00007232

179 Liess M, Von Der Ohe PC (2005) Analysing effects of pesticides on invertebrate communities
 180 in streams. *Environ Toxicol Chem* 24:954 . doi: 10.1897/03-652.1

181 Logan P, Brooker M (1983) The macroinvertebrate faunas of riffles and pools. *Water Res*
 182 17:263–270 . doi: 10.1016/0043-1354(83)90179-3

183 Loreau M, Mouquet N, Holt RD (2003) Meta-ecosystems: a theoretical framework for a
 184 spatial ecosystem ecology. *Ecology Letters* 6:673–679. doi: 10.1046/j.1461-
 185 0248.2003.00483.x

186 Lu YH, Canuel EA, Bauer JE, Chambers RM (2014) Effects of watershed land use on sources
 187 and nutritional value of particulate organic matter in temperate headwater streams.
 188 *Aquat Sci* 76:419–436 . doi: 10.1007/s00027-014-0344-9

- 189 Lynch RJ, Bunn SE, Catterall CP (2002) Adult aquatic insects: Potential contributors to
190 riparian food webs in Australia's wet-dry tropics. *Austral Ecol* 27:515–526 . doi:
191 10.1046/j.1442-9993.2002.01208.x
- 192 Maas B, Karp DS, Bumrungsri S, et al (2016) Bird and bat predation services in tropical
193 forests and agroforestry landscapes: Ecosystem services provided by tropical birds and
194 bats. *Biological Reviews* 91:1081–1101. doi: 10.1111/brv.12211
- 195 Marczak LB, Richardson JS (2007) Spiders and subsidies: results from the riparian zone of a
196 coastal temperate rainforest. *J Anim Ecol* 76:687–694 . doi: 10.1111/j.1365-
197 2656.2007.01240.x
- 198 Marczak LB, Thompson RM, Richardson JS (2007) Meta-analysis: trophic level, habitat, and
199 productivity shape the food web effects of resource subsidies. *Ecology* 88:140–148.
200 doi: 10.1890/0012-9658(2007)88[140:MTLHAP]2.0.CO;2
- 201 Mazoyer M, Roudart L (2006) *A History of World Agriculture: From the Neolithic Age to the*
202 *Current Crisis*. NYU Press
- 203 Muehlbauer JD, Collins SF, Doyle MW, Tockner K (2014) How wide is a stream? Spatial
204 extent of the potential “stream signature” in terrestrial food webs using meta-analysis.
205 *Ecology* 95:44–55 . doi: 10.1890/12-1628.1
- 206 Munn MD, Brusven MA (1991) Benthic macroinvertebrate communities in nonregulated and
207 regulated waters of the clearwater river, Idaho, U.S.A. *Regul Rivers Res Manag* 6:1–
208 11 . doi: 10.1002/rrr.3450060102
- 209 Murza GL, Heaver JR, Davis AR (2006) Minor pollinator–prey conflict in the carnivorous
210 plant, *Drosera anglica*. *Plant Ecol* 184:43. doi: 10.1007/s11258-005-9050-y
- 211 Nagasaka A, Nakamura F (1999) The influences of land-use changes on hydrology and
212 riparian environment in a northern Japanese landscape. *Landsc Ecol* 14:543–556 . doi:
213 10.1023/A:1008164123102
- 214 Nakano S, Murakami M (2001) Reciprocal subsidies: Dynamic interdependence between
215 terrestrial and aquatic food webs. *Proc Natl Acad Sci U S A* 98:166–170. doi:
216 10.1073/pnas.98.1.166
- 217 Negishi JN, Inoue M, Nunokawa M (2002) Effects of channelisation on stream habitat in
218 relation to a spate and flow refugia for macroinvertebrates in northern Japan. *Freshw*
219 *Biol* 47:1515–1529 . doi: 10.1046/j.1365-2427.2002.00877.x
- 220 Nentwig, W. (1980). The selective prey of linyphiid-like spiders and of their space webs.
221 *Oecologia*, 45(2), 236–243. <https://doi.org/10.1007/BF00346464>
- 222 Odum EP, Finn JT, Franz EH (1979) Perturbation Theory and the Subsidy-Stress Gradient.
223 *BioScience* 29:349–352. doi: 10.2307/1307690
- 224 Paetzold A, Schubert CJ, Tockner K (2005) Aquatic Terrestrial Linkages Along a Braided-
225 River: Riparian Arthropods Feeding on Aquatic Insects. *Ecosystems* 8:748–759 . doi:
226 10.1007/s10021-005-0004-y

- 227 Petersson E, Hasselrot A t. (1994) Mating and nectar feeding in the psychomyiid caddis fly
228 *Tinodes waeneri*. *Aquat Insects* 16:177–187. doi: 10.1080/01650429409361553
- 229 Poff NL, Pyne MI, Bledsoe BP, Cuhaciyan C, Carlisle DM (2010) Developing linkages
230 between species traits and multiscaled environmental variation to explore vulnerability
231 of stream benthic communities to climate change. *J North Am Benthol Soc* 29:1441–
232 1458 . doi: 10.1899/10-030.1
- 233 Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web
234 ecology: the dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 289–
235 316. doi: <https://doi.org/10.1146/annurev.ecolsys.28.1.289>
- 236 Polis GA, Hurd SD (1995) Extraordinarily high spider densities on islands: flow of energy
237 from the marine to terrestrial food webs and the absence of predation. *Proc Natl Acad*
238 *Sci* 92:4382–4386
- 239 Potts SG, Biesmeijer JC, Kremen C, et al (2010) Global pollinator declines: trends, impacts
240 and drivers. *Trends Ecol Evol* 25:345–353. doi: 10.1016/j.tree.2010.01.007
- 241 Rabení CF, Doisy KE, Zweig LD (2005) Stream invertebrate community functional responses
242 to deposited sediment. *Aquat Sci* 67:395–402 . doi: 10.1007/s00027-005-0793-2
- 243 Rader R, Bartomeus I, Garibaldi LA, Garratt MPD, Howlett BG, Winfree R,..., Andersson
244 GKS (2016) Non-bee insects are important contributors to global crop pollination.
245 *Proc Natl Acad Sci* 113:146–151 . doi: 10.1073/pnas.1517092112
- 246 Raitif, J., Plantegenest, M., Agator, O., Piscart, C., & Roussel, J.-M. (2018). Seasonal and
247 spatial variations of stream insect emergence in an intensive agricultural landscape.
248 *Science of The Total Environment*, 644, 594–601.
249 <https://doi.org/10.1016/j.scitotenv.2018.07.021>
- 250 Rand TA, Tylianakis JM, Tscharnke T (2006) Spillover edge effects: the dispersal of
251 agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol*
252 *Lett* 9:603–614 . doi: 10.1111/j.1461-0248.2006.00911.x
- 253 Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski,
254 A., ... Viana, B. F. (2008). Landscape effects on crop pollination services: are there
255 general patterns? *Ecology Letters*, 11(5), 499–515. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2008.01157.x)
256 [0248.2008.01157.x](https://doi.org/10.1111/j.1461-0248.2008.01157.x)
- 257 Riechert SE, Lockley T (1984) Spiders as Biological Control Agents. *Annu Rev Entomol*
258 29:299–320 . doi: 10.1146/annurev.en.29.010184.001503
- 259 Robson DB (2008) The structure of the flower–insect visitor system in tall-grass prairie.
260 *Botany* 86:1266–1278 . doi: 10.1139/B08-083
- 261 Roussel J-M, Perrier C, Erkinaro J, Niemelä E, Cunjak RA, Huteau D, Riera P (2014) Stable
262 isotope analyses on archived fish scales reveal the long-term effect of nitrogen loads
263 on carbon cycling in rivers. *Glob Change Biol* 20:523–530 . doi: 10.1111/gcb.12293

- 264 Sabo JL, Power ME (2002) River-watershed exchange : effects of riverine subsidies on
265 riparian lizards and their terrestrial prey. *Ecology* 83:1860–1869 . doi: 10.1890/0012-
266 9658(2002)083[1860:RWEEOR]2.0.CO;2
- 267 Sanzone DM, Meyer JL, Marti E, Gardiner EP, Tank JL, Grimm NB (2003) Carbon and
268 nitrogen transfer from a desert stream to riparian predators. *Oecologia* 134:238–250 .
269 doi: 10.1007/s00442-002-1113-3
- 270 Sato AAW, Kato M (2017) Pollination system of *Corylopsis gotoana* (Hamamelidaceae) and
271 its stonefly (Plecoptera) co-pollinator. *Plant Species Biol* 32:440–447. doi:
272 10.1111/1442-1984.12178
- 273 Schulz R, Bundschuh M, Gergs R, Brühl CA, Diehl D, Entling MH, Fahse L, Frör O,
274 Jungkunst HF, Lorke A, Schäfer RB, Schaumann GE, Schwenk K (2015) Review on
275 environmental alterations propagating from aquatic to terrestrial ecosystems. *Science*
276 of the Total Environment 538: 246–261
- 277 Speight (2014). Species accounts of European Syrphidae (Diptera). *Syrph the Net, the*
278 *Database of European Syrphidae*, 78, 321.
- 279 Sponseller RA, Benfield EF, Valett HM (2001) Relationships between land use, spatial scale
280 and stream macroinvertebrate communities. *Freshw Biol* 46:1409–1424 . doi:
281 10.1046/j.1365-2427.2001.00758.x
- 282 Summerhayes VS, Elton CS (1923) Contributions to the ecology of Spitsbergen and Bear
283 Island. *J Ecol* 11:216 . doi: 10.2307/2255864
- 284 Symondson WOC, Cesarini S, Dodd PW, Harner GL, Bruford MW, Glen DM,..., Harwood
285 JD (2006) Biodiversity vs. biocontrol: positive and negative effects of alternative prey
286 on control of slugs by carabid beetles. *Bull Entomol Res* 96:637–645 . doi:
287 10.1079/BER2006467
- 288 Thien LB, White DA, Yatsu LY (1983) The Reproductive Biology of a Relict-*Illicium*
289 *floridanum* Ellis. *Am J Bot* 70:719 . doi: 10.2307/2443126
- 290 Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The River
291 Continuum Concept. *Can J Fish Aquat Sci* 37:130–137 . doi: 10.1139/f80-017
- 292 Vannote RL, Sweeney BW (1980) Geographic Analysis of Thermal Equilibria: A Conceptual
293 Model for Evaluating the Effect of Natural and Modified Thermal Regimes on
294 Aquatic Insect Communities. *Am Nat* 115:667–695 . doi: 10.1086/283591
- 295 Villagomez F, Contreras-Ramos A (2017) First records of adult feeding in Megaloptera
296 (*Corydalidae*, *Corydalinae*) from Mexico and their possible relationship with the
297 increase in life span. *Zootaxa* 4341:287. doi: 10.11646/zootaxa.4341.2.11
- 298 Wagenhoff A, Townsend CR, Phillips N, Matthaei CD (2011) Subsidy-stress and multiple-
299 stressor effects along gradients of deposited fine sediment and dissolved nutrients in a
300 regional set of streams and rivers: Sediment and nutrients in streams. *Freshw Biol*
301 56:1916–1936 . doi: 10.1111/j.1365-2427.2011.02619.x

- 302 Ward JV, Stanford JA (1982) Thermal Responses in the Evolutionary Ecology of Aquatic
303 Insects. *Annu Rev Entomol* 27:97–117 . doi: 10.1146/annurev.en.27.010182.000525
- 304 Webb BW, Hannah DM, Moore RD, Brown RD, Nobilis F (2008) Recent advances in stream
305 and river temperature research. *Hydrol Process* 22:902–918 . doi: 10.1002/hyp.6994
- 306 Whelan CJ, Wenny DG, Marquis RJ (2008) Ecosystem Services Provided by Birds. *Ann N Y*
307 *Acad Sci* 1134:25–60 . doi: 10.1196/annals.1439.003
- 308 Winterbourn MJ (2005) Dispersal, feeding and parasitism of adult stoneflies (Plecoptera) at a
309 New Zealand forest stream. *Aquat Insects* 27:155–166. doi:
310 10.1080/01650420500062840
- 311 Wissinger SA (1997) Cyclic Colonization in Predictably Ephemeral Habitats: A Template for
312 Biological Control in Annual Crop Systems. *Biol Control* 10:4–15 . doi:
313 10.1006/bcon.1997.0543
- 314 Wogram J, Liess M (2001) Rank Ordering of Macroinvertebrate Species Sensitivity to Toxic
315 Compounds by Comparison with That of *Daphnia magna*. *Bull Environ Contam*
316 *Toxicol* 67:360–367 . doi: 10.1007/s001280133
- 317 Yasumatsu, Wongsiri, Navavichit, Tirawat (1975) Approaches toward an integrated control of
318 rice pests. Pt. 1: Survey of natural enemies of important rice pests in Thailand. Plant
319 protection service technical bulletin 24.

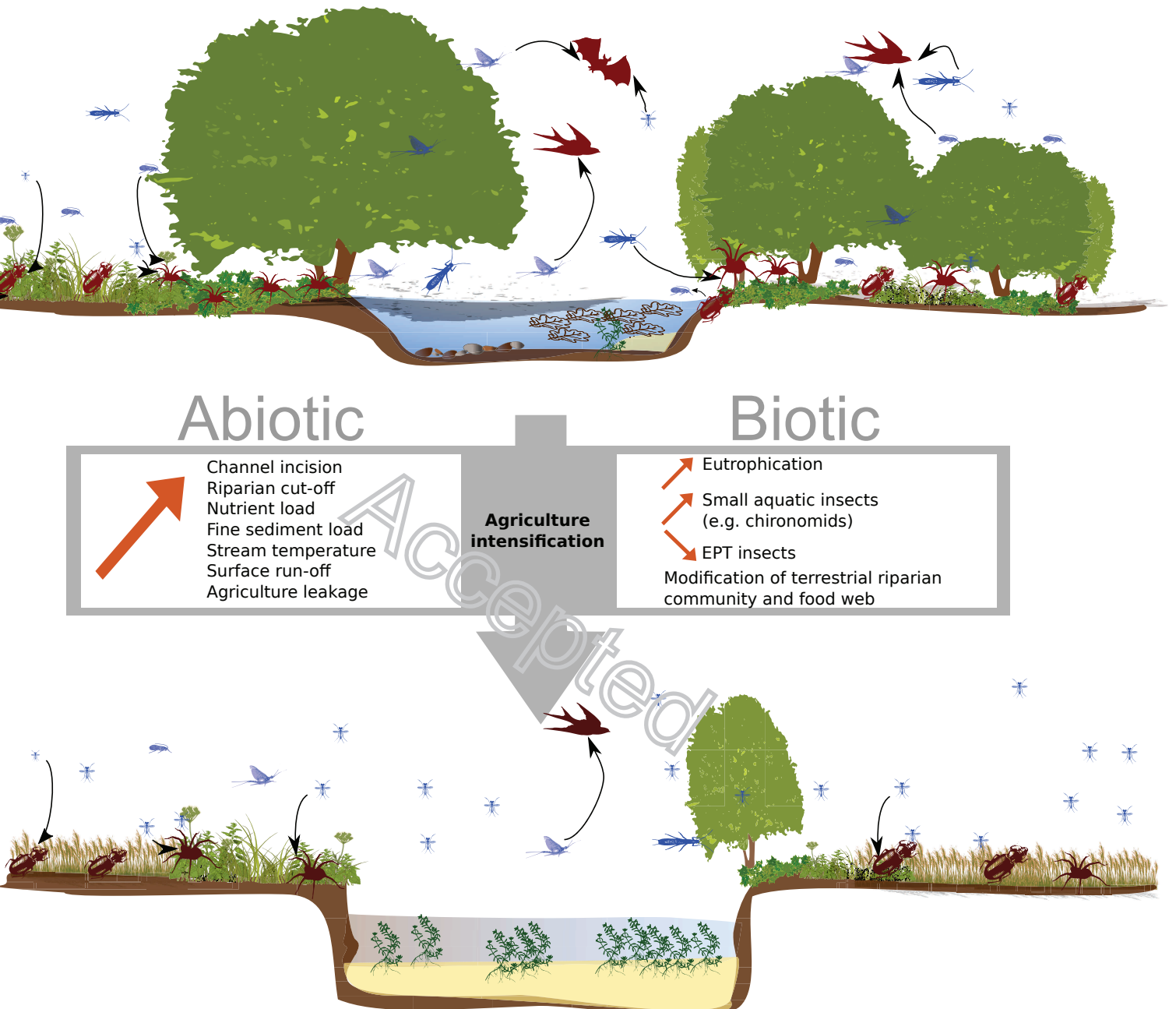


Fig. 1. Effect of agriculture intensification on stream insect community and aquatic subsidies. Aquatic insects (blue), terrestrial predators (red) and trophic links (black arrows) are indicated. Top: a stream with heterogeneous aquatic habitat (substrate, light, water temperature, food source, and hydraulic conditions), dense riparian vegetation and a rich community of winged adult aquatic insects. Trophic links between ecosystems involve many aquatic and terrestrial taxa. Bottom: agriculture intensification induces strong effect on abiotic parameters in the stream, leading to changes of aquatic communities. Community of winged stream insects is less diverse, notably with fewer sensitive taxa (Ephemeroptera and Plecoptera) and the dominance of smaller Chironomidae. Community of terrestrial predators (e.g. birds, bats, spiders) is also impacted.

Accepted