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

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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

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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

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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.

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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

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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.

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