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Julien Raitif, Manuel Plantegenest, Jean-Marc Roussel

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Corresponding Author: Mr. Julien RAITIF,

Corresponding Author's Institution: INRA

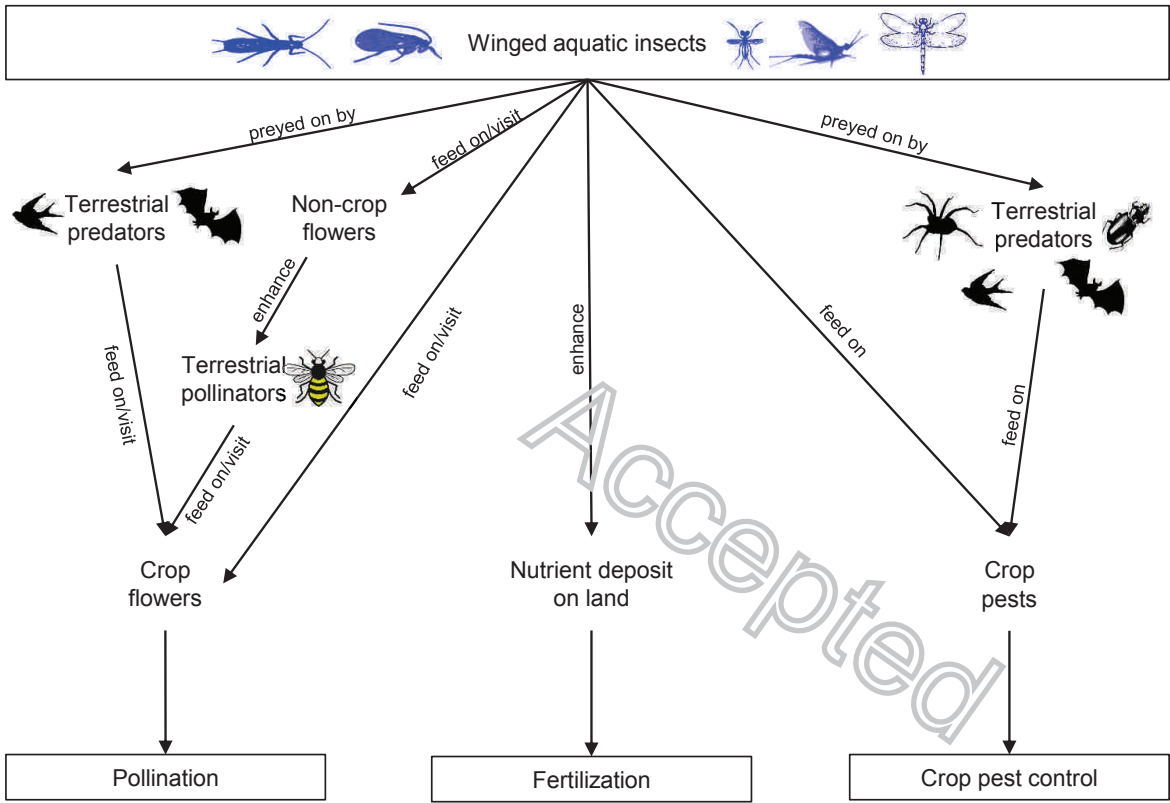
First Author: Julien RAITIF

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

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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

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

Accepted

1 *Abstract*

2 The connection between aquatic and terrestrial habitats has increased scientific interest in
3 ecological subsidies, focusing on how the transfer of matter and energy between adjacent
4 ecosystems can modify the ecosystems functioning. Much attention has focused on subsidies
5 associated with winged aquatic insects in pristine areas, but their existence and implications in
6 agricultural landscapes are rarely considered. We reviewed current knowledge on the
7 dominant types of winged stream insects involved in terrestrial ecosystem subsidizing and
8 how agricultural practices can affect their communities. We compiled published data that
9 illustrate the contribution of winged stream insects to ecological services in agroecosystems.
10 Agricultural intensification has resulted in profound environmental modifications of streams
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12 degree, Trichoptera orders, whereas more tolerant and small-bodied taxa of the Diptera order
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14 transfer of aquatic subsidies to agroecosystems. Winged stream insects can disperse up to 150
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20 influence of agricultural practices on the amount and type of emerging aquatic insects. Future
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22 management and provision of ecosystem services to agriculture, while simultaneously
23 ensuring the conservation of rich freshwater biodiversity for optimal ecosystem functioning.

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25 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.*
32 2003), which is based on the assertion that adjacent ecosystems in heterogeneous
33 landscapes exchange matter and energy. Although ecology has identified the existence of such
34 transfers, they were ignored until recently. In the 19th century, the entomologist John Gould
35 (1804-1881) observed birds preying on dragonflies (*in* Ballinger and Lake 2006), and in the
36 early 20th century it was acknowledged that energy could cross ecosystem boundaries
37 (Summerhayes and Elton 1923). In the late 1970s, Odum *et al.* (1979) highlighted that
38 allochthonous inputs from an ecosystem could modify the functioning of the adjacent
39 recipient ecosystem, initiating a promising field of research in ecology. A pioneer study by
40 Polis *et al.* (1997) provided a theoretical basis, stating that the significance of allochthonous
41 inputs, also referred to as “subsidies”, was expected to vary according to autochthonous food
42 abundance in the receiving ecosystem, *i.e.* its productivity. Predicting the effects of subsidies
43 remains complex and depends on the type of subsidy, the trophic levels involved and the
44 amount of resources provided to the receiving food web (Marczak *et al.* 2007). Multiple case
45 studies from a wide diversity of ecosystems provide clear evidence that food webs are fueled
46 by subsidies (*e.g.* Jackson and Fisher 1986; Gray 1989; Polis and Hurd 1995; Dreyer *et al.*
47 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

51 subsidies to aquatic ecosystems. For instance, riparian tree leaves falling in the water sustain
52 the detrital pathway in heterotrophic headwater streams (Vannote *et al.* 1980). At the
53 watershed scale, fertilizer leakage across agricultural landscapes affects primary production
54 and aquatic food webs, and ultimately has subtle effects on nutrient cycling in streams
55 (Roussel *et al.* 2014). Conversely, deposition of nutrient-rich sediments from streams to
56 valleys during flooding supported the emergence of agriculture in the Fertile Crescent during
57 the Neolithic (Mazoyer and Roudart 2006). In estuaries and marine coastal areas, benthic food
58 webs are largely fueled by terrestrial organic subsidies conveyed by rivers (Kostecki *et al.*
59 2010), while tidal surges and wind can transfer huge amounts of marine inputs to terrestrial
60 habitats (Hyndes *et al.* 2014).

61 Based on the assumed prominent role of physical laws in subsidy transfers, aquatic
62 ecosystems have long been considered as passive receivers of terrestrial subsidies. This
63 paradigm was challenged when Polis *et al.* (1997) emphasized the role of living organisms in
64 the reciprocal transfer from aquatic to terrestrial ecosystems. Examples exist of terrestrial and
65 avian predators foraging in aquatic ecosystems, which ultimately fertilize terrestrial
66 ecosystems (*e.g.* Havik *et al.* 2014). Additionally, arthropods metamorphosing from aquatic
67 larvae to aerial adults are suitable candidates for reciprocal transfers of matter and energy
68 from water to land (Schulz *et al.* 2015). They are common in all aquatic ecosystems, disperse
69 towards land as winged adults, and are involved in nutrient cycling and the functioning of
70 food webs (Baxter *et al.* 2005). Some studies have identified the important role of adult
71 aquatic arthropods in the diet of terrestrial carabids (Hering and Plachter 1997), spiders
72 (Paetzold *et al.* 2005), birds (Nakano and Murakami 2001) and lizards (Sabo and Power
73 2002). Recently, the meta-analysis by Bartels *et al.* (2012) highlighted that even though the
74 mass of aquatic subsidies to land is lower than the reciprocal mass of terrestrial subsidies,
75 their average contributions to the functioning of receiving food webs appeared to be similar.

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

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

90 2 *Effects of agriculture on stream insect communities*

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

100 2.1 Organic matter, nutrients and pollution

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

114 Human activities that modify watershed vegetation and land cover influence the quantity and
115 quality of basal carbon sources in streams. Lu *et al.* (2014) reported that land use significantly
116 altered the nutritional value of OM (estimated from lipid concentration). Bellamy *et al.* (2017)
117 highlighted how these changes in basal feeding sources due to agricultural pressure influenced
118 aquatic macroinvertebrates differently according to their functional feeding group (FFG).
119 Notably collector/gatherers (*Ephemera* mayflies) were more reliant on terrestrial and soil
120 OM in agricultural landscape, a shift imputed to increased sedimentation. Deegan and Ganf
121 (2008) showed how loss of riparian vegetation could significantly constrain shredder
122 communities in Australian streams *via* the collapse of an adequate food source.

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

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

136 Intensification of agricultural practices has resulted in a large increase in pesticide use, which
137 has been clearly identified as a major stressor for many aquatic species. They show
138 contrasting susceptibility to pesticides, related in particular to life-cycle traits such as
139 generation time and the presence of sensitive aquatic stages during pesticide exposure, as
140 proposed by Liess and Von Der Ohe (2005). Analyzing the effect of agricultural pesticides on
141 the taxa richness of stream invertebrates in 72 sites in Europe and Australia, Beketov *et al.*
142 (2013) found a decrease up to 42% in family richness between uncontaminated and highly
143 contaminated streams. Following the species-at-risk (SPEAR) method, which estimates the
144 sensitivity of aquatic invertebrates to pesticide exposure, Plecoptera and Ephemeroptera are
145 considered more sensitive taxa than Diptera and Trichoptera (Wogram and Liess 2001).

146 2.2 *Water temperature, flow and substrate*

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

150 1982). Several processes, in connection with air temperature and climate at a large continental
151 scale, explain the variation in water temperature, as do local influences, including
152 groundwater exchanges and shade (reviewed by Webb *et al.* 2008). Nagasaka and Nakamura
153 (1999) estimated that agricultural intensification in Japan since 1945, especially clearing of
154 riparian vegetation and river channelization (the widening and deepening of a river channel),
155 had increased the maximum temperature of some rivers from 22°C to 28°C.

156 Shifts in aquatic invertebrate community composition are frequently associated with an
157 increase in stream temperatures, especially for stenothermal EPT families (Sponseller *et al.*
158 2001; Haidekker and Hering 2008). Sponseller *et al.* (2001) observed that aquatic
159 macroinvertebrate diversity was negatively correlated with stream temperature, since
160 eurythermal taxa such as chironomids dominate in warmer streams. A similar pattern was also
161 reported by Kiffney *et al.* (2003) who found more chironomids in sites with narrow riparian
162 vegetation, more light and higher water temperatures. However, when temperature stays
163 inside the tolerance limits, warmer temperature can enhance the emerging drymass of
164 Trichoptera and Ephemeroptera (Raitif *et al.* 2018).

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

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

175 hydroelectricity production, water supply or irrigation, can decrease aquatic insect diversity,
176 especially by reducing habitat diversity, food availability and affecting thermal regime. Low
177 taxa richness is often observed in regulated rivers, promoting chironomids and other flexible
178 taxa such as certain Ephemerelellidae at the expense of other sensitive mayflies (Heptageniidae)
179 (Brittain and Saltveit 1989; Munn and Brusven 1991). At local scales, the succession of pool
180 and riffle habitats hosts multiple assemblages of macroinvertebrates (Brown and Brussock
181 1991). Ephemeroptera and Trichoptera are generally more abundant in riffle habitats, whose
182 larger substratum particles provide foraging sites for grazers and filter feeders in these orders.
183 Conversely, burrowers and collector/gatherers of the Diptera order (*e.g.* chironomids) prevail
184 in pools, where water velocity is low and the substratum is fine sediment (Logan and Brooker
185 1983). Channelization alters water flow and aquatic habitat heterogeneity. In a study along the
186 Rio Grande River in New Mexico, U.S., Kennedy and Erner (2011) found that
187 channelization reduced the density and diversity of aquatic macroinvertebrates and resulted in
188 outbreaks of chironomids and a loss of mayflies. In most agricultural areas, river channels
189 have been reshaped to facilitate crop irrigation and reduce flooding risks. The resulting loss in
190 aquatic habitat heterogeneity induces a decrease in macroinvertebrate species abundance and
191 diversity. Negishi *et al.* (2002) highlighted that the decrease in bottom invertebrate shelters in
192 a channelized section of a stream endangers community recovery after flood episode,
193 resulting in a lower density of macroinvertebrates than in natural sections. Altering stream
194 morphology has a strong influence on the hyporheic zone, where most aquatic invertebrates
195 seek refuge during hydrological disturbances (Dole-Olivier 2011).

196 The silting of streams, often observed in agricultural landscapes following clearing of
197 terrestrial vegetation, can also influence aquatic macroinvertebrate assemblages greatly (Allan
198 2004). Excess sediment loads in stream beds, resulting from greater terrestrial surface runoff,
199 clog vital habitats for many aquatic insects, which significantly reduces the relative

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

205 3 *Effects of agriculture on stream insect subsidies*

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

213 3.1 *Modification of the flux of aquatic subsidies*

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

224 restricted to stream corridors with dense riparian vegetation, whereas long-distance flights
225 over terrestrial landscapes were observed from more open agricultural streams. Raitif *et al.*
226 (2018) highlighted the role of agriculture in the amount of insect biomass emerging from
227 small streams, and they estimated that aquatic drymass deposit on lands could range between
228 0.9 and 4.5 kg ha⁻¹ year⁻¹ in the vicinity of these streams.

229 3.2 *Cascading effects on terrestrial communities*

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

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

253 4 *Stream insect subsidies and ecosystem services to agriculture*

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

262 4.1 *Pollination*

263 Seventy percent of worldwide crops rely on animal pollination, and flower-visiting insects
264 undoubtedly are the major pollinators (Klein *et al.* 2007). Insects also play a critical role in
265 the conservation of wild flowers (Biesmeijer 2006). The global decline in insect pollinators
266 (Potts *et al.* 2010), especially in agroecosystems, highlights the fundamental influence of non-
267 crop habitats (Ricketts *et al.* 2008), especially riparian buffer strips (Cole *et al.* 2015), on
268 pollination services. Although bees still receive the most public and scientific attention, the
269 importance of wild non-bee pollinators has become increasingly recognized (Garibaldi *et al.*
270 2013, Rader *et al.* 2016). However, adult aquatic insects emerging from streams have been
271 ignored as pollinators, even though they feed on nectar or pollen, or at least visit wild flowers
272 or crops (Table 1). Confirmed pollinators include many species of adult Plecoptera that

273 depend on pollen as a primary energy source (Winterbourn 2005). Occasional feeding on
274 nectar or pollen was observed for Trichoptera (Pettersson and Hasselrot 1994) and aquatic
275 Coleoptera (Hoe *et al.* 2017). Consumption of pollen or nectar by adults of Megaloptera had
276 also been recorded (reviewed and observed in laboratory by Villagomez & Contreras-Ramos,
277 2017). Besides hoverflies, which are active pollinators (Hass *et al.* 2018), many Diptera
278 families with an aquatic larval stage, such as Chironomidae, Empididae, and
279 Ceratopogonidae, were observed to visit flowers (Table 1). Because these Diptera families are
280 composed of both species with aquatic or terrestrial larval stage, further studies are needed to
281 confirm that the adults that visit flowers actually emerge from water. Additionally, adult
282 aquatic insects that pollinate or visit flowers increase flower diversity in riparian ecosystems
283 and thus indirectly help to sustain the community of well-known pollinators such as bees or
284 hoverflies that depend on this flower diversity (Cole *et al.* 2015). In a field experiment,
285 Stewart *et al.* (2017) observed an increase in the quality and quantity of strawberries produced
286 near a pond compared to those in a crop habitat. This correlates with a greater abundance of
287 hoverflies (Syrphidae, Diptera), for which the larvae of many species are aquatic (Speight
288 2014). This is promising and suggests the need for similar experiments near streams to assess
289 potential effects of stream insect communities on pollination of crops and wild flowers.

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

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

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

299 4.2 Soil fertilization

300 Rock weathering, atmospheric exchanges and the decomposition of OM provide essential
301 elements for plant growth. In agricultural landscapes, soil fertility depends largely on external
302 inputs. However, insect outbreaks can add large amounts of nutrients to the soil *via* their feces
303 or cadavers (Hunter 2001). Studies of winged aquatic insects have concluded that a small
304 percentage (3-9%) of their biomass ultimately returns to the stream (Jackson and Fisher 1986;
305 Gray 1989). Deposition traps are rarely used to measure the biomass of stream-derived insects
306 that fall to the ground per unit area (but see Stenroth *et al.* 2015); however, some authors have
307 placed interception traps at multiple distances from streams (Table 2). The biomass of aquatic
308 invertebrates trapped can be regarded as biomass deposition on the ground per unit area, and
309 converted into N assuming that the dry mass of invertebrates contains 10% N (Fagan *et al.*
310 2003). These calculations show that stream-derived N deposition to land can vary during
311 outbreaks from 1.5-12.5 mg.m⁻².d⁻¹ near the stream, depending on the study (Table 2).
312 Deposition decreases as the distance from the stream increases, but still reaches 0.7-3.0
313 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
314 conducted along forest streams, but the amount of aquatic subsidies is likely greater along
315 agricultural streams, especially for small dipterans (chironomids) that disperse farther. From
316 200 studies of stream production, Finlay (2011) estimated that secondary production of
317 macroinvertebrates is 7 times as great in human-impacted streams as in pristine streams. In
318 Sweden, Carlson *et al.* (2016) found 10 times as many aquatic insects 1 m from, and 5 times
319 as many 50 m from, small streams (<8 m wide) in agricultural landscapes compared to those
320 in forests. Large rivers (>16 m wide) can export 4 times as many aquatic insects to land as
321 smaller rivers (Gratton and Zanden 2009). Consequently, the amount of aquatic-derived N in

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

328 4.3 Crop pest control

329 Biocontrol is commonly considered a relevant alternative to the use of chemicals. It relies on
330 a wide diversity of natural enemies, including insects and spiders (Landis *et al.* 2000). A rich
331 and abundant natural enemy community facilitates the control of pest outbreaks (Landis *et al.*
332 2000). The direct role of adult aquatic insects in pest control is rarely demonstrated; however,
333 Yasumatsu *et al.* (1975) observed odonates in rice fields preying on several defoliators and
334 stem borers. Many potential biocontrol agents prey on aquatic insects (Table 3), including
335 spiders (Linyphiidae, Lycosidae, Salticidae, Thomisidae; Riechert and Lockley 1984) and
336 carabids (Symondson *et al.* 2006). Because aquatic prey usually emerge in pulses in early
337 spring for instance in temperate regions, they may be essential for sustaining natural enemy
338 populations when crop pests are scarce and more likely to be controlled (Wissinger 1997).
339 Riparian predators can shift from aquatic-derived prey in riparian habitats to crop pests later
340 in spring or summer, following a process of seasonal predator spillover, as described for other
341 adjacent ecosystems (French *et al.* 2001; Rand *et al.* 2006). For instance, bats and birds that
342 actively feed on aquatic insects in riparian habitats were effective at reducing pest abundance
343 and thus indirectly increasing crop yield, especially in tropical agroforestry (Maas *et al.*
344 2016). This cascading effect requires that the emergence and dispersal of aquatic insects
345 matches the timing of riparian predator food needs when terrestrial subsidies are low. In their
346 review, Larsen *et al.* (2015) highlighted that global environmental changes may threaten this

347 synchronicity, especially when the phenology and distribution of stream and riparian
348 organisms are altered. This synchronicity could be threatened in agroecosystems in which the
349 magnitude and quality of aquatic subsidies change greatly (see sections 2 & 3). Finally,
350 alternative prey from aquatic ecosystems may distract natural enemies from pests and thus
351 decrease the effectiveness of biocontrol (Symondson *et al.* 2006; Birkhofer *et al.* 2008). The
352 considerable amount of aquatic biomass exported from large rivers (Gratton and Zanden
353 2009) probably has a significant effect on terrestrial food webs, including disruptions in
354 biological control services. The multifaceted trophic interactions between stream invertebrate
355 prey and terrestrial predators in agroecosystems require further studies to assess the influence
356 on crop pest control.

357 5 Conclusion

358 Freshwater ecosystems have been traditionally viewed as passive receivers of terrestrial
359 subsidies that result from agricultural practices on watersheds. However, consideration of the
360 reciprocal subsidies supported by the emergence of adult aquatic insects could cause this
361 simplistic assessment to be reevaluated. Intensification of agriculture resulted in massive use
362 of chemical inputs and great changes to the landscape, which has decreased biodiversity and
363 ecosystem functioning worldwide. In this context, it is critical to encourage a new model
364 developed for sustainable agricultural practices that relies on the ecological processes that
365 ecosystems provide. In this review, we highlighted promising scientific evidence that winged
366 aquatic insects can support pollination, soil fertilization and the control of crop pests in
367 agroecosystems. The influence of land-use and agricultural practices on the amount and type
368 of emerging aquatic insects requires more thorough investigation. Studies of aquatic subsidies
369 associated with the dispersal of stream insect communities in agricultural landscapes are
370 essential for a comprehensive approach to the variety of ecosystem services provided in
371 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 ($mg \cdot m^{-2} \cdot d^{-1}$)
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) 7 days of capture, 1 stream	Bank: 32 mg/trap/day	1.5
Marczak and Richardson 2007	Canada	Forest	Diptera, EPT	Sticky traps (0.06 m ²) 7 days of capture, 2 streams	At 2 m: 40 mg/trap	9.5
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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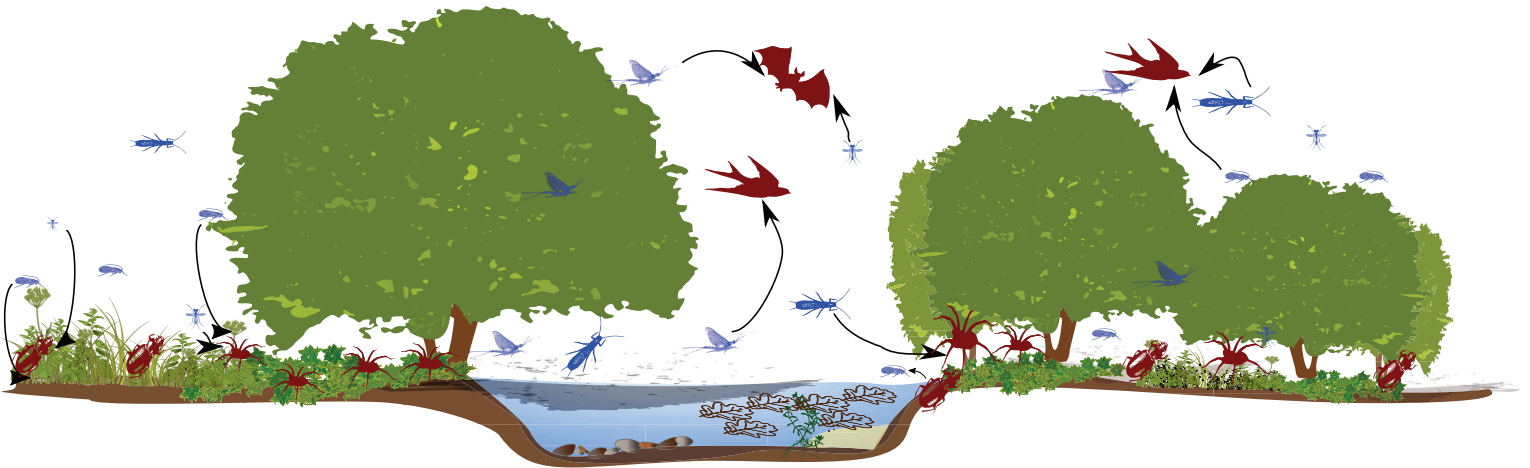
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Accepted



Abiotic

- Channel incision
- Riparian cut-off
- Nutrient load
- Fine sediment load
- Stream temperature
- Surface run-off
- Agriculture leakage

Biotic

- Eutrophication
- Small aquatic insects (e.g. chironomids)
- EPT insects
- Modification of terrestrial riparian community and food web

Agriculture intensification

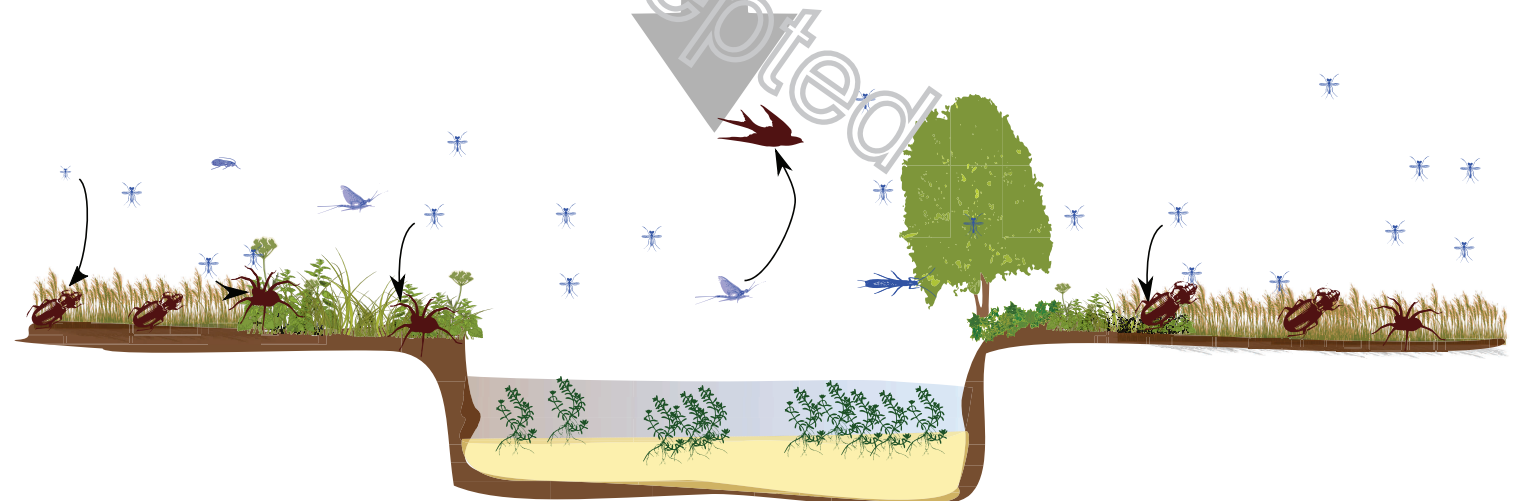


Fig. 1. Effect of agriculture intensification on stream insect community and aquatic subsidies. Aquatic insects (blue), terrestrial predators (red) and trophic links (black arrows) are indicated. Top: a stream with heterogeneous aquatic habitat (substrate, light, water temperature, food source, and hydraulic 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