



HAL
open science

From Stream to Bloom: Exploring the Potential Role of Aquatic Insects for Pollination in Wetland Environments

Cassandre Murail, Mathilde Baude, Benjamin Bergerot, Benoit Geslin,
Nicolas Legay, Irene Villalta, Sabine Greulich

► To cite this version:

Cassandre Murail, Mathilde Baude, Benjamin Bergerot, Benoit Geslin, Nicolas Legay, et al.. From Stream to Bloom: Exploring the Potential Role of Aquatic Insects for Pollination in Wetland Environments. *Journal of Applied Entomology*, 2024, 10.1111/jen.13359 . hal-04766797

HAL Id: hal-04766797

<https://hal.science/hal-04766797v1>

Submitted on 5 Nov 2024

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 - NoDerivatives 4.0
International License

REVIEW ARTICLE OPEN ACCESS

The Neglected Pollinators: Understanding the Importance of Lesser-Known Insect Taxa in Pollination

From Stream to Bloom: Exploring the Potential Role of Aquatic Insects for Pollination in Wetland Environments

Cassandre Murail¹  | Mathilde Baude^{2,3} | Benjamin Bergerot⁴ | Benoit Geslin^{4,5} | Nicolas Legay^{4,6}  | Irene Villalta⁷ | Sabine Greulich¹ 

¹Interdisciplinary Research Unit CItés, TERritoires, Environnement et Sociétés (CNRS UMR 7324 CITERES), University of Tours, Tours, France | ²University of Orleans, Chateau de la Source, Orleans Cedex 2, France | ³Sorbonne University, UPEC, University Paris Cité, CNRS, IRD, INRAE, Institute of Ecology and Environmental Sciences of Paris (iEESParis), Paris, France | ⁴Ecosystèmes, Biodiversité, Evolution (CNRS UMR 6553 ECOBIO), University of Rennes, Rennes, France | ⁵Institut Méditerranéen de la Biodiversité et d'Écologie marine et continentale (CNRS UMR 7263 IMBE), University of Aix-Marseille, Marseille, France | ⁶Institut National des Sciences Appliquées (CNRS 7324 INSA) Centre Val de Loire, Blois, France | ⁷Institut de Recherche Sur la Biologie de l'Insecte (CNRS UMR 7261 IRBI), University of Tours, Tours, France

Correspondence: Cassandre Murail (cassandre.murail-zimmermann@univ-tours.fr)

Received: 9 July 2024 | **Revised:** 23 September 2024 | **Accepted:** 2 October 2024

Funding: This study was funded by the French National Research Agency (ANR) under the STRANGE (Ecosystem Services provided by sTReams to AdjaceNt aGricultural tErrestrial ecosystems) project (ANR-23-CE03-0006).

Keywords: aquatic pollinators | aquatic subsidies | plant–pollinator interactions | riparian pollination | riparian vegetation | stream insects | winged aquatic insects

ABSTRACT

The substantial loss of insects we are experiencing today has been highlighted all over the world. There is a growing concern about the global decline of pollinators and its impact on terrestrial and agricultural ecosystems, but the focus of scientists towards bees remains the rule. Therefore, the role of other insect taxa in pollination is still overlooked. Our review focused on some of these neglected pollinating taxa, the winged aquatic insects, i.e., insects with an aquatic larval stage such as Ephemeroptera, Trichoptera, Plecoptera (ETP), Megaloptera and some aquatic Diptera. We first documented the visitors of aquatic and wetland flowering plants, anticipating a greater presence of aquatic insects on these plants compared to terrestrial pollinators. Secondly, we documented plant visits, pollen found in gut contents and pollen transfers performed by aquatic insects. Our results revealed a surprisingly low proportion of aquatic insects visiting both aquatic and wetland plants, suggesting a potential gap in the literature. The scarcity of articles dedicated to pollen transfer by aquatic insects also indicates that they are few considered in ecological studies. While the role of aquatic insects in pollination is not well documented in the literature, records of their flower visits and pollen found on them or in their gut contents do exist and are promising clues to consider them as effective pollinators. Future research is needed to provide new insights into the importance of winged aquatic insects for the reproductive success of plants, which could also be an argument for the importance of wetland conservation.

1 | Introduction

Decades of research have documented the significant loss of insects we face today (Van Klink et al. 2024). Seibold et al. (2019) reported a decline of up to 78% in arthropod abundance in

natural areas. Of particular concern are insect pollinators, which play an essential role in the support of both wild (Aguilar et al. 2006; Ollerton, Winfree, and Tarrant 2010) and cultivated plant communities (Klein et al. 2007; Garibaldi et al. 2014). But while interest in pollinators has grown considerably in recent

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2024 The Author(s). *Journal of Applied Entomology* published by Wiley-VCH GmbH.

years, attention is often limited to bees and their role in the reproductive success of cultivated plants (Smith and Saunders 2016; Valido, Rodríguez-Rodríguez, and Jordano 2019).

If the decline of both honeybees and wild bees is reaching spectacular levels (Blackburn 2012; Bianco, Cooper, and Fournier 2014), other insect taxa such as Lepidoptera, Coleoptera and Diptera are not less affected (e.g., more than half of the Syrphidae are threatened according to the IUCN 2022). Indeed, they also play an essential role as they can support pollination services in agricultural environments (Orford et al. 2016; Rader et al. 2015; Requier et al. 2023). Several studies have also shown that a greater diversity of pollinators increases the reproductive success of plants (Albrecht et al. 2012; Schurr et al. 2021), and therefore, a more advantageous pollination strategy should be based on as many different species as possible to ensure our food sovereignty. To explore this pollinator diversity, it is interesting to take a closer look at areas that are known to harbour incredibly rich biodiversity, such as aquatic and wetland areas (e.g., pond margins, rivers, streams, ditches and wet grasslands) (Williams et al. 2003; Dudgeon et al. 2006). Freshwater ecosystems not only shelter important flowering resources for pollinators (Zhang et al. 2022), they also host 9.5% of the Earth's described animal species, 60% of which are aquatic insects (Balian et al. 2008). Aquatic and semiaquatic insects can be found in all freshwater ecosystems (Lancaster and Downes 2013), representing almost 100,000 species divided into 12 orders (Dijkstra, Monaghan, and Pauls 2013). Among the aquatic arthropods (i.e., with a larval aquatic stage and a flying adult stage), the Ephemeroptera, Trichoptera, Plecoptera (abbreviated as ETP), Odonata and Megaloptera members are the most studied. Other orders such as Diptera, Lepidoptera or Hemiptera may also include aquatic species or families (Vallenduuk and Cuppen 2004; Dijkstra, Monaghan, and Pauls 2013). Concerning Diptera, to our knowledge, there is no exhaustive inventory of species with aquatic larvae, except for Chironomidae, Culicidae and some Syrphidae such as *Eristalis tenax* (Bertrand 1954; Speight 2011).

Recently, it has been recognised that aquatic insects have a fundamental role in aquatic-to-terrestrial subsidies, in part for their role in soil fertilisation by exporting nitrogen (Stenroth et al. 2015) or by the nutritional resource they represent for predators (Gergs et al. 2014). Studies showing their roles into terrestrial food webs continue to open up new perspectives on their importance in nonaquatic environments (Lafage et al. 2019). Little is known about the potential interactions between winged aquatic insects and flowering plants near watercourses; however, Raitif, Plantegenest, and Roussel (2019) have suggested that adult flying imago may provide specific ecosystem services, including pollination when they perch on flowers, which opens new perspectives to study them as pollinators. This role, so far rarely considered, would be all the more interesting since many aquatic insects are known to have particularly early emergence periods, which would be a real asset for the reproduction of early wild and cultivated plants (Raitif et al. 2022). Given their ubiquity, abundance and extreme diversity (Lancaster and Downes 2013), it seems thus surprising that aquatic insects do not play a role in pollination. At the same time, preliminary information on the feeding habits of specific winged aquatic insects suggests that they are likely to be involved in pollination. Indeed, although

nectar feeding was rarely observed, the mouthparts of certain Trichoptera (Lectrotarsidae, Kokiriidae and Stenopsychidae) are known to be adapted to ingest liquid food (Krenn, Plant, and Szucsich 2005). Similarly, within Plecoptera, adults of Systellognatha have reduced mouthparts and may ingest nectar, whereas adults of Euholognatha are considered to feed on flower pollen and nectar (Stewart et al. 2016). Ephemeroptera do not have mouthparts, but this does not mean they cannot be pollen carriers. Again, there is a notable gap in the literature on the precise diet of all imago aquatic insects. However, understanding whether their trophic regime includes pollen and/or nectar, similar to established pollinators, could be very informative about their role. In a global context of pollinator decline, it is essential to study the influence of other less studied but potentially effective pollinators, such as aquatic flying insects. Furthermore, it is important to emphasise the urgency of studying these insect taxa, as freshwater environments are particularly vulnerable to anthropogenic pressures (Del-Claro and Guillermo 2019; Reid et al. 2019).

Even though effective pollination is difficult to demonstrate, a bibliographic survey of flowering plants that are visited by aquatic insects could give a first hint of their pollinator potential. We might expect them to be common in wetlands where they originate, because specific aquatic insects can reach extremely high abundances (e.g., Chironomidae can form swarms of up to several millions of individuals, Armitage, Cranston, and Pinder 1995). To address the shortcomings identified above, we have reviewed the visitors of specific aquatic and wetland flowering plants to enrich this information. In addition, our literature review also aims to explore all known interactions between winged aquatic insects and flowering plants, supported by the presence of specific plant and aquatic insect traits that contribute to the plant-pollinator relationship (Table S1). To that end, we address two questions:

- i. Who are the flower visitors of aquatic and wetland plants, and what proportion of them are aquatic insects? This question was addressed with a particular focus on the flora of mainland France.
- ii. Can aquatic insects pollinate flowers? This question was explored by inventorying the visits and pollen transfers realised by winged aquatic insects on a global scale.

2 | Materials and Methods

2.1 | Literature Search for the Inventory of Plant-Pollinator Interactions

All insect and plant species names are based on the last published Taxref taxonomic reference updated in January 2024 (version 17) (Gargominy et al. 2022).

2.1.1 | Selection of Aquatic and Wetland Flowering Plant Species

We first documented all insects visiting aquatic and wetland flowering plants (herbaceous species) in mainland France. Corsica was not included in our survey because of its high

number of endemic species. The selection of plant species was based on Baseflor (Julve 1998), a free, scientifically recognised database (Tichý et al. 2023; Dengler et al. 2023) that compiles phytosociological and plant ecological data for France and that includes both native and exotic species. We selected therein species with Ellenberg moisture indicator values (adapted to France by Julve) > 5, that is, meso-hygrophilous to intra-aquatic species. We withdrew species living in very specific environments like saline areas or clearly ornamental species with little presence outside gardens. This led to a total of 619 species. We then checked in the EUNIS (EUropean Nature Information System) habitat database for running waters, the littoral zone, and riparian and gallery woodland that no species cited as characteristic of these habitats was omitted.

2.1.2 | Selection of Winged Aquatic Insects

To document the visits of aquatic insects to flowers, we focused our research at a global scale on ETP, Megaloptera, Odonata and Diptera with an aquatic larval stage. The lack of ecological knowledge about Diptera larvae has led us to concentrate on Chironomidae and Culicidae. As Syrphidae are very common Diptera, we also added four *Eristalis* species whose larvae's aquatic status has been reported in the literature (Speight 2011): *Eristalis tenax*, *Eristalis arbustorum*, *Eristalis nemorum* and *Eristalis rupium*.

2.1.3 | Literature Review of Aquatic Insect Visitors

Keywords used in the *Web of Science* to summarise the insects visiting aquatic and wetland plants, and the visits made by aquatic insects are listed in Table 1. References of interest mentioned in articles not listed in our initial search were also included in our survey. The *Database of Pollinator Interactions (DoPI)*, Balfour et al. 2022) was finally used to complete the results, by checking the interactions given by the database for all the plant species or aquatic insects selected.

In addition to documenting aquatic insect visits to flowering plants available information on pollen loads (pollen grains per insect) and gut content of aquatic species were recorded to learn

more about their pollen consumption. Sampling periods were also examined to analyse whether any trends emerged between the abundance of aquatic insects found and a particular period of the year.

2.2 | Network Analysis

The R *bipartite* package (Dormann et al. 2009) was used to build binary networks based on insect occurrences (presence/absence) to illustrate the relationships between plants and pollinators reported in the literature. To observe whether any trends emerged, the indicators' *species degree* and *nested rank* were also computed. Species degree refers to the sum of links per species, while nested rank quantifies generality or specialisation by the rank of a species in a network matrix re-arranged for maximal nestedness. We used a normalised version of nested rank, ranging from 0 (most generalist) to 1 (most specialist).

Histograms were constructed using the *ggplot* package (Wickham 2016) to illustrate the variation in visitor frequency within orders.

All figures and analyses were produced using R version 4.3.2.

3 | Results

3.1 | Visitors of Aquatic and Wetland Plants

The search for flower visitors gave results for 87 aquatic, semi-aquatic and hygrophilic plants in continental France, for a total of 148 articles (Table S2). Sampling periods were not always specified; however, in general, the surveys were conducted over several months, and most of them included June (65 articles), July (78 articles) and August (61 articles).

Of the 87 plant species, 26 were aquatic or semiaquatic, 14 were introduced, being 8 out of the 14 considered invasive. They were visited by 410 different insects identified at the species level and 79 identified at the genus level, belonging to 14 different orders (Figure 1). More than a thousand insect occurrences were recorded (1478). Aquatic insects were represented by 4 occurrences

TABLE 1 | Summary of queries used on *Web of Science*. Only the combinations that produced a result are shown.

Information	Queries
Insect visits to wetland and aquatic flowering plants	(<i>pollinat*</i> OR <i>pollen*</i>) AND (<i>ptarmica*</i> OR <i>aconitum*</i> OR <i>acorus*</i> OR <i>allium*</i> OR <i>Anacamptis*</i> OR <i>novi*</i> <i>belgii*</i> OR <i>Betonica*</i> OR <i>Bidens*</i> OR <i>Cardamine*</i> OR <i>Chamaenerion*</i> OR <i>Centaureum*</i> OR <i>Dactylorhiza*</i> OR <i>Eichhornia*</i> OR <i>Filipendula*</i> OR <i>Fritillaria*</i> OR <i>Ficaria* verna*</i> OR <i>Gentiana*</i> OR <i>Hesperis*</i> OR <i>rivale*</i> OR <i>Heracleum*</i> OR <i>Impatiens*</i> OR <i>Lotus*</i> OR <i>Lysimachia*</i> OR <i>Myosotis*</i> OR <i>Narthemcium*</i> OR <i>Rhinanthus*</i> OR <i>Ranunculus*</i> OR <i>Scrophularia*</i> OR <i>Urtica*</i> OR <i>Ludwigia*</i> OR <i>Pseudacorus*</i> OR <i>Pulmonaria*</i> OR <i>Platanthera*</i> OR <i>Stachys*</i> OR <i>myosotis*</i> OR <i>tetralix*</i> OR <i>Hyacinthoides*</i> OR <i>Utricula*</i> OR <i>Lythrum*</i> OR <i>lychnis*</i> OR <i>aquatica*</i> OR <i>nymphae*</i> OR <i>nelumbo*</i> OR <i>nuphar*</i> OR <i>crispus*</i> OR <i>Scutellaria*</i> OR <i>eupatorium*</i> OR <i>epilobium*</i> OR <i>palustr*</i> OR <i>Chamerion*</i> OR <i>Cardamine*</i> OR <i>Menyanthes*</i> OR <i>Symphyotrichum*</i> OR <i>sagittaria*</i> OR <i>silene* dioica*</i> OR <i>tazetta*</i> OR <i>paludosa*</i> OR <i>rivulare*</i> OR <i>veronica*</i> OR <i>Viburnum*</i> OR <i>Vaccinium*</i> OR <i>Viccia*</i>)
Visits by aquatic insects	(<i>Ephem*</i> OR <i>Trichop*</i> OR <i>Pleco*</i> OR <i>Megalo*</i> OR <i>Chirono*</i> OR <i>Odon*</i> OR <i>Culici*</i> OR <i>Eris* tenax*</i> OR <i>Eris* arbustorum*</i> OR <i>Eris* nemorum*</i> OR <i>Eris* rupium*</i>) AND (<i>pollinat*</i> OR <i>nect*</i> OR <i>pollen*</i>)

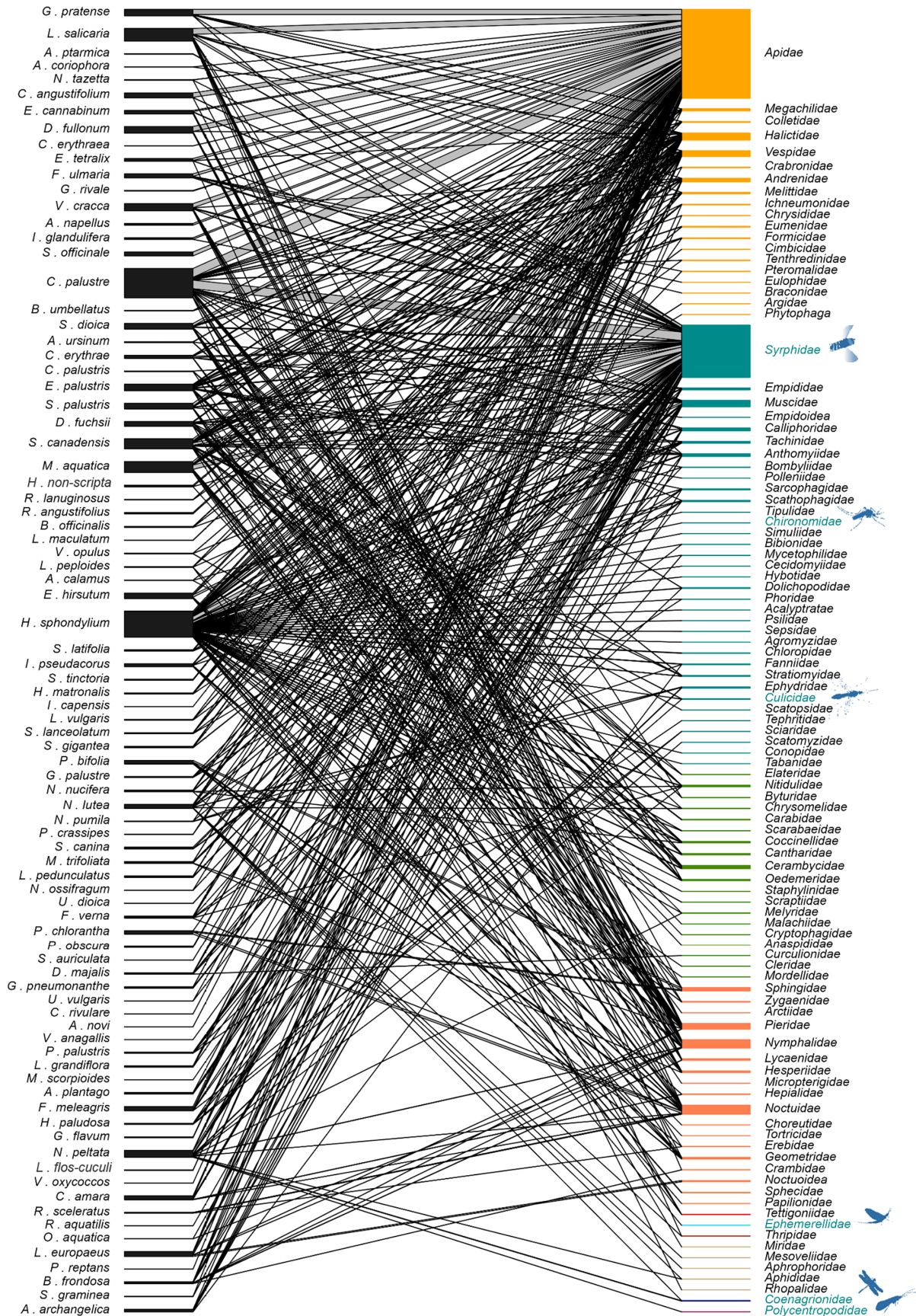


FIGURE 1 | Legend on next page.

FIGURE 1 | Bipartite network between insects and aquatic/wetland plants present in France. Left: Plant species. Right: Insect families coloured according to orders (Hymenoptera: Golden; Diptera: Bluish green; Coleoptera: Green; Lepidoptera: Orange; Orthoptera: Red; Ephemeroptera: Turquoise; Thysanoptera: Brown; Hemiptera: Beige; Odonata: Blue; Trichoptera: Purple). The four remaining orders (Plecoptera, Dermaptera, Mecoptera and Neuroptera) have not been documented to the family taxonomic level. Aquatic or semiaquatic families are indicated by blue figures. See Table S1 for the whole plant species names.

of ETP, 5 Odonata and 36 occurrences of Diptera from aquatic environments (1 Chironomidae, 4 Culicidae and 31 Syrphidae with aquatic larval stage) (Figure 2).

Honeybees aside, the most frequent visitors were all from the *Bombus* genus. The plant *Heracleum sphondylium* was the most visited with 120 different insect species visits and highly generalist according to the nested rank (0). Although Hymenoptera was the most represented order, Diptera was second with a strong presence of hoverflies. The aquatic Syrphidae *Eristalis tenax* is the most generalist aquatic insect of the review (nested rank: 0.02), followed by *E. nemorum* (0.03) and *E. arbustorum* (0.05).

Water lilies (*Nymphaoides peltata* and *Nuphar lutea*) were the most visited plants by aquatic insects (Odonata, Trichoptera and Diptera) followed by *Cirsium palustre*, but only visited by aquatic Syrphidae, being also the second most generalist flowering plant of all (nested rank = 0.01) just after *Heracleum sphondylium* (0).

3.2 | Aquatic Insects Visiting Flowers

Our worldwide aquatic insect survey identified 76 articles and returned 37 insect taxa that were identified at the species level and 5 insect taxa identified at the genus level. They were divided into seven orders, visiting 102 plant taxa identified at the species level and 20 at the genus level. Of the plant species visited by aquatic insects, 7 were aquatic or semi-aquatic according to the selected Ellenberg's indicator moisture values, 52 were specific to wetlands and 43 were terrestrial plants (Figure 3, Table S3). Most of the surveyed aquatic insects were Diptera (220 occurrences), followed by Plecoptera (17), Trichoptera (7), Megaloptera (5), Odonata (5) and Ephemeroptera (2).

Sampling periods were not always specified, but Ephemeroptera, Trichoptera and Megaloptera were mostly found in the beginning of the summer (six occurrences in June and six in July), while Plecoptera were found all along the year with a slight peak in May (four occurrences), and Diptera were found most in summer (33 occurrences in July, 28 in June and 21 in August).

Of the 76 selected articles, 22 also documented effective pollen transfers by microscopic analysis (Table S4). The pollen loads (mean number of pollen grains attached to the insect) were estimated in 13 articles for five different species, other aquatic insects having only traces of pollen attached to their body parts (Table 2).

In the literature documenting gut contents, six articles mentioned pollen found in the gut contents of six different families of Plecoptera, one Diptera and one Megaloptera. They were mainly from trees, especially pines (Table 3).

The first most generalist species were all Diptera according to the nested rank. The lowest values were found for *Eristalis tenax* (0), which was found to visit 75 different plant species, and *E. nemorum* (0.03), visiting 41 of them.

4 | Discussion

Our results undoubtedly reflect a lack of aquatic insects in the literature. Two hypotheses could explain this absence: Either they are not able to pollinate flowering plants due to morphological or behavioural constraints, or they are not considered by researchers while studying pollination. Through a thorough analysis of our results, we will evaluate both options and try to understand why there are so few aquatic insects in pollination studies.

4.1 | A Low Representation of Aquatic Insects

Our review first documented the visits made by 14 different insect orders to 87 aquatic and wetland flowering plant species. Most of the insect orders found have few representatives, while the main visitors are highly dominated by Hymenoptera, followed by Diptera, then Lepidoptera and finally Coleoptera. Our results also underline the importance of wetlands for providing resources to common pollinators, as shown by the plant species *Heracleum sphondylium* that is highly visited by *Bombus* sp., or the plant species *Lysimachia vulgaris* supporting the monoleptic bee *Macropis europaea* (Hoffmann 2005; Triponez et al. 2015). Strange though, of the 148 articles we reviewed, only 22 of them mentioned aquatic insects, which is surprisingly low regarding the type of documented habitats.

To gain a deeper understanding of visits made by aquatic insects, the second step of our review examined the records of aquatic insect visitations on a global scale documented by 76 articles. Most of them focused on the four targeted Syrphidae species. Excluding this family, only 18 relevant articles were found. Including articles that focus on the importance of pollinators other than bees, aquatic insects other than *Eristalis* sp. are barely mentioned, nor is their aquatic ecology at the larval stage (Rader et al. 2020).

The first hypothesis that could explain the absence of aquatic insects is their inability to pollinate. This assumption would be rather surprising for two reasons. First, the biomass of emerging aquatic insects can reach 1200–2500 kg ha⁻¹ year⁻¹ in lakes (Gratton and Vander Zanden 2009; Del-Claro and Guillermo 2019). In agricultural landscapes, 12.5 kg ha⁻¹ year⁻¹ of aquatic insects also emerge from streams and fall to the ground within 10 m of the stream (Raitif et al. 2022). Secondly, aquatic insects are represented by nearly 100,000 species belonging to

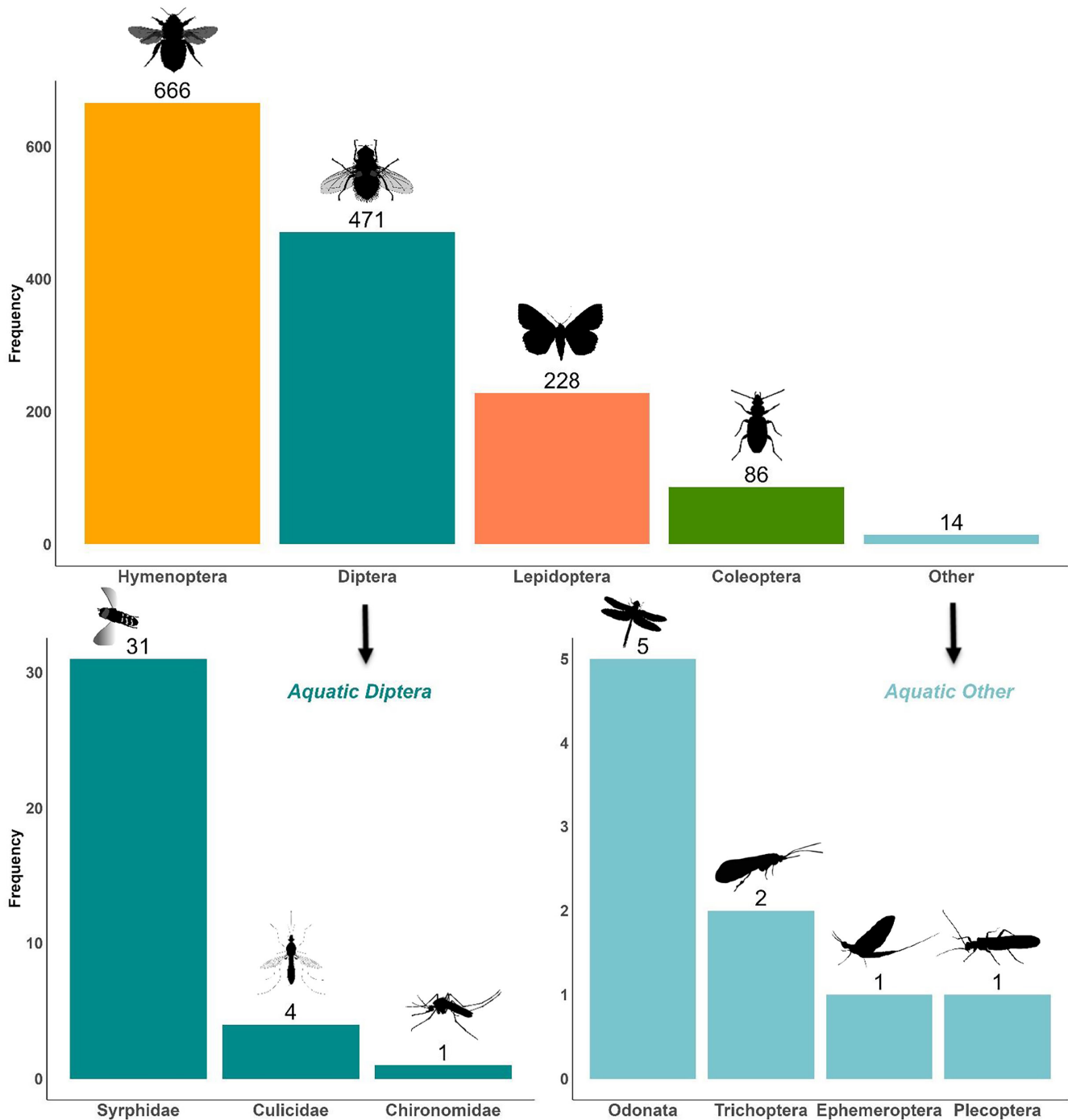


FIGURE 2 | Visitor frequency of hygrophilic and aquatic plants.

12 orders (Dijkstra, Monaghan, and Pauls 2013), so it is highly unlikely that they would not come into contact with flowers in aquatic or riparian environments. This suggests that even if the contact with the flower is accidental, the act of pollination can still occur.

On the other hand, another hypothesis would justify the absence of aquatic insects for the simple reason that they are not considered by researchers. An argument favouring this assumption is that most aquatic insects in the articles are not identified to species or even family level

(Smith-Ramirez et al. 2005; Manning and Cutler 2013). They are also likely to be classified as ‘other’ in studies, or even set aside as minor pollinators (Horth, Campbell, and Bray 2014). Due to the difficulty of identifying many aquatic species, the lack of ecological information on the aquatic status of their larvae (such as Diptera) or the lack of information on their pollination efficiency (Ostrowiecka et al. 2019), it is understandable that aquatic insects have long been sidelined. It is therefore imperative to further investigate to fill this gap, as aquatic insects are probably much more involved in diverse ecosystem functions than previously thought.

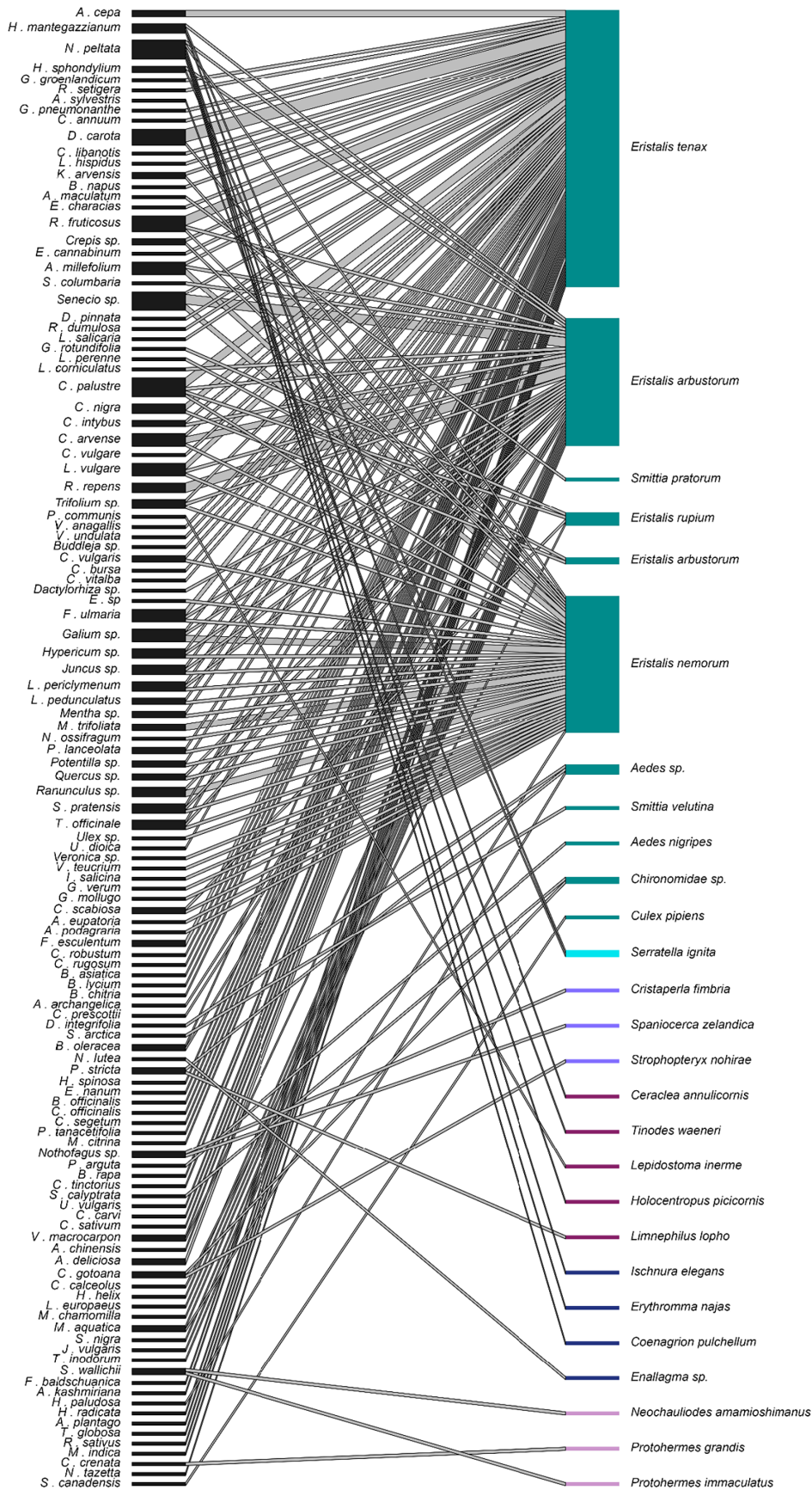


FIGURE 3 | Bipartite network between aquatic insects and visited plants. Left: Plant species. Right: Insect species coloured according to orders (Diptera: Bluish-green; Ephemeroptera: Turquoise; Plecoptera: Lavender; Trichoptera: Purple; Odonata: Blue; Megaloptera: Pink). See Table S2 for the whole plant species names.

TABLE 2 | Aquatic insects carrying pollen and pollen load (mean number of pollen grains) per insect.

References	Insect order	Insect family	Insect species	Pollen load
Free and Williams (1973)	Diptera	Syrphidae	<i>Eristalis arbustorum</i>	261
Levesque and Burger (1982)	Diptera	Syrphidae	<i>Eristalis tenax</i>	278–318
Petanidou et al. (1995)	Diptera	Syrphidae	<i>Eristalis tenax</i>	597
G�omez & Zamora (1999)	Diptera	Syrphidae	<i>Eristalis tenax</i>	136
Diaz and Kite (2002)	Diptera	Chironomidae	<i>Smittia pratorum</i>	5
P�erez-Ba�on et al. (2003)	Diptera	Syrphidae	<i>Eristalis tenax</i>	715
P�erez-Ba�on, Petanidou, and Marcos-Garc�a (2007)	Diptera	Syrphidae	<i>Eristalis tenax</i>	4353
Rader et al. (2009)	Diptera	Syrphidae	<i>Eristalis tenax</i>	106
Sato and Kato (2017)	Plecoptera	Taeniopterygidae	<i>Strophopteryx nohirae</i>	76
Gervais, Chagnon, and Fournier (2018)	Diptera	Syrphidae	<i>Eristalis tenax</i>	313
Gaffney et al. (2018)	Diptera	Syrphidae	<i>Eristalis tenax</i>	10–999
Sugiura and Miyazaki (2021)	Megaloptera	Corydalidae	<i>Neochondriodes amamioshimanus</i>	46
Rashid et al. (2023)	Diptera	Syrphidae	<i>Eristalis tenax</i>	2503

TABLE 3 | Pollen found in the gut contents of eight different families of aquatic insects.

Reference	Insect family	Insect species	Host plant family
Zwick (1990), Germany	Chloroperlidae (Plecoptera)	<i>Siphonoperla</i> sp.	Pinaceae
De Figueroa and S�anchez-Ortega (2000), Spain	Capniidae (Plecoptera)	<i>Capnioneura mitis</i>	
		<i>Leuctra andalusiaca</i>	
		<i>Leuctra fusca</i>	
	Nemouroidae (Plecoptera)	<i>Leuctra iliberis</i>	
		<i>Leuctra inermis</i>	
		<i>Leuctra maroccana</i>	
		<i>Amphinemura triangularis</i>	
		<i>Nemoura cinerea</i>	
		<i>Protonemura alcazaba</i>	
		<i>Protonemura meyeri</i>	
P�erez-Ba�on et al. (2003), Spain	Syrphidae (Diptera)	<i>Eristalis tenax</i>	Fabaceae (<i>Medicago citrina</i>)
Winterbourn (2005), New-Zeland	Notonemouridae (Plecoptera)	<i>Cristaperla fimbria</i>	Fagaceae (<i>Nothofagus</i> sp.)
		<i>Spaniocerca zelandica</i>	
Winterbourn and Pohe (2017), New-Zeland	Eustheniidae (Plecoptera)	<i>Stenoperla maclellani</i>	Podocarpaceae
		<i>Stenoperla prasina</i>	
Sugiura and Miyazaki (2021), Japan	Corydalidae (Megaloptera)	<i>Neochondriodes amamioshimanus</i>	Theaceae (<i>Schima wallichii</i>)

4.2 | Why So Few Aquatic Insects?

4.2.1 | Complex and Multifaceted Ecologies

First of all, few aquatic insects were found in the literature partly because many of them are poorly known and difficult to

identify. For instance, regarding aquatic Diptera, they extend beyond Chironomidae and Culicidae, but compiling a comprehensive list of all species with aquatic larvae is challenging. For example, certain hoverflies include species with aquatic larvae, but many of them require redescription and there is no exhaustive list summarising them, which explains why only a minority

were included in our study (Speight 2011). Additionally, families like the Tabanidae lack sufficient information about their aquatic lifestyle (Bertrand 1954), suggesting that the diversity of aquatic Diptera capable of pollination could be much broader than currently recognised.

The aquatic phases of ETP, Megaloptera and Odonata are much better known than that of Diptera. However, there remains a gap in understanding their ecology during the terrestrial phase. To our knowledge, the first ETP landscape distribution maps were only published in 2023 (Gerber et al. 2023). The fact that these insects are able to play a role in terrestrial environments during their adult stage, participating in the functioning of these ecosystems, is only very recent (Raitif, Plantegenest, and Roussel 2019).

The ecology of Odonata is better known for both aquatic and terrestrial phases (Del-Claro and Guillermo 2019). We reported several Odonata in the course of our survey. Given the plant species where Odonata have been recorded, with very large floating flowers (waterlilies), it is likely that dragonflies and damselflies just perch on flowers as a support, with no particular purpose to visit them. In addition, their impact on pollination is probably more detrimental than beneficial, as they are known to predate valuable pollinators such as bees (Knight et al. 2005). In summary, Odonata appear to be less good candidates for pollination, justifying a more specific interest in ETP, Megaloptera and Diptera in our following discussion.

4.2.2 | A Reduced Spatial Range

The limited flight capabilities of most ETP may slightly explain the lack of consideration for aquatic insects as pollinators. Distribution modelling of ETP performed by Gerber et al. (2023) indicates that distance to water is a strong informative variable in their models, such that the aquatic insect abundance decreases with the distance from the watercourse. Similarly, Carlson et al. (2016) observed that the abundance of Trichoptera decreased exponentially with distance from the stream. Raitif et al. (2022) confirmed that most of the ETP were captured close to the stream, but certain Ephemeroptera and Trichoptera were found at several dozen meters. A recent review by Peredo Arce et al. (2023) however emphasises the great variability in flying abilities among ETP species and that some of them appear to be capable of flying several kilometres from the stream.

Aquatic Diptera are considered to have better dispersal capacities than ETP (e.g., chironomids, Rundle, Bilton, and Fogo 2007) due to their ability to use winds for passive dispersal. Muehlbauer et al. (2014) found few ETP more than a 100 m from the stream, but several Chironomidae up to 20 km. This would be consistent with the fact that our review found much more aquatic Diptera than other aquatic insects visiting flowers.

Since riparian zones are not the first areas considered for pollinator sampling, it is not surprising that ETP are rarely found in many studies. However, our review of aquatic and hygrophilic plants should have shown a high number of ETP

visitors, since the surveys took place logically near watercourses, but this was not the case. It is nevertheless important to note that in the 76 articles mentioning aquatic insect visitations, only 7 of the visited flowering plants were aquatic or semiaquatic, 52 were hygrophilic, while the remaining 43 plants were terrestrial (Table S2). One hypothesis to explain this observation could be that the ability of aquatic insects to move away from the stream and even to visit trees (e.g., *Corylopsis gotoana*) has been underestimated, challenging the assumption of their limited flying abilities. Alternatively, another explanation could be the ability of certain aquatic insects to lay eggs in temporary water reservoirs like puddles (Frouz, Matěna, and Ali 2013; Sohn 2007). These intermittent water sources are often overlooked when assessing the distribution of aquatic insects, potentially leading to an underestimation of their presence in the environment. Indeed, certain species like, *Eristalis tenax* and *E. arbustorum* are able to lay their eggs elsewhere than in watercourses, like in semiaqueous organically rich materials such as manure or compost (Rader et al. 2020), which can partly explain why they were much more frequently reported in the surveys than ETP. In any case, it would be worthwhile to integrate new monitoring efforts of aquatic insects across variable distances from watercourses. This approach would allow a more thorough assessment of their dispersal capabilities, not just at the taxonomic order level but also at the species level. This could help to shed light on their flying abilities, which are currently inadequately understood and poorly documented in the scientific literature.

4.2.3 | A Limited Time Window

A third explanation for the scarcity of aquatic insects in the literature could be the limited emergence time window of the ETP. According to Raitif et al. (2022), Ephemeroptera emerge only in spring and Trichoptera in spring and early summer in North temperate regions. Plecoptera being the largest exclusively aquatic order (Dijkstra, Monaghan, and Pauls 2013), it includes families with diverse ecologies, some of which exhibit a broader temporal range of emergence than the other two ETP taxa, including winter (Lancaster and Downes 2013; Cheney et al. 2019). Similarly, Chironomidae, the most widely distributed family with an estimated 15,000 species worldwide, can emerge throughout the year in temperate regions (Armitage, Cranston, and Pinder 1995). Finally, the *Eristalis* sp. reported in our survey emerge almost all year long except in winter with *E. rupium* predominantly emerging during the summer period (Speight 2011).

Thus, with the exception of Diptera and Plecoptera, aquatic insects generally emerge earlier in the season compared with many pollinators. This timing discrepancy may partly explain their lower representation in surveys, which are usually conducted later in the season to maximise terrestrial insect abundance. This hypothesis is supported by our results, as most of the surveys documenting the floral visitors of aquatic and wetland plants were conducted in the height of summer (June to August in temperate regions), corresponding with the flowering peak of many plant species. This timeframe may be slightly late to coincide with the peak activity of many aquatic insects. Our results however do not clearly show a strong temporal emergence trend towards spring, but the scarce literature offers too few articles to draw general conclusions.

It is nevertheless worth noting that the early emergence of aquatic insects could be very beneficial for agrosystems, as they could pollinate spring cultures such as *Brassica napus* (among other services) during periods when common pollinators are rather absent (Wissinger 1995).

4.3 | Functional Role of Aquatic Insects in Pollination

There is a real lack of scientific knowledge concerning the pollination ability of aquatic insects. Nested rank shows that certain aquatic insects like *Eristalis* sp. are highly generalists and thus able to visit a wide variety of different plant species. This suggests their significant role in the structure and stability of plant–pollinator networks of wetland environments (Martin Gonzalez 2010). However, considering a visit as an act of pollination is under debate (King, Ballantyne, and Willmer 2013). Assessing pollen load is an effective method to distinguish between visitation and pollination, but the information is often lacking for aquatic insects. For example, pollen loads are sometimes only assessed for specific insect taxa, as in the study by Walton et al. (2020) which only recorded pollen from moths, although other insects, including Diptera, were sampled. Hence, there are only a few aquatic insects for which pollen transfer has been documented, and these are almost exclusively Diptera. Although pollen loads vary among flower species because pollen grains vary in size and shape, *Eristalis* sp. appear to carry very large amounts of pollen. Furthermore, it is often stated in the literature that *Eristalis tenax* are incredibly efficient pollinators, even more than certain Hymenoptera, because of their densely covered bodies with finely branched hairs, capable of carrying 16–54 times more pollen than unspecialised flies (Levesque and Burger 1982; Talavera et al. 2001; Gaffney et al. 2018). Moreover, traces of pollen have also been found on some ETP. Some authors have even been able to estimate pollen loads for a Plecoptera and a Megaloptera, which although low, were not insignificant (Sato and Kato 2017; Sugiura and Miyazaki 2021).

In addition, a large gap exists in the scientific literature regarding the precise diet of all imago aquatic insects. However, the ability of aquatic insects (mainly Plecoptera) to ingest pollen raises the question about their true role as pollinators. It should yet be noted that the pollen found in their gut content primarily comes from trees, especially pines. Pines are anemophilous trees that produce pollen in large quantities and disperse it very effectively in the environment (Tauber 1965). This result does therefore not necessarily mean that aquatic insects fly to cones in trees. Either way, the subject deserves further study, as the revelation of a trophic regime that includes pollen and nectar in the same way as recognised pollinators could be very instructive on the role of aquatic insects.

4.4 | Limits of the Review

Some biases are unavoidable and can participate in the low levels of aquatic insects we found in the literature. For example, the omnipresence of *Apis mellifera* in some surveys but not in others influences the diversity of pollinators found, as it is now recognised that the honeybee is known to dominate

plant–pollinator networks (Valido, Rodríguez-Rodríguez, and Jordano 2019) and could eventually compete with aquatic insects for flowering resources (Requier et al. 2024). Also, certain studies aim to be exhaustive, while others focus only on specific species (e.g., the specific visitors of *Hammarbya paludosa*, Tatarenko, Walker, and Dyson 2022), which reduces the diversity of the surveyed visitors. Certain plant species are not considered as hygrophilous despite being common in riparian inventories (e.g., *Rubus fruticosus*, personal observations), which may have reduced our results. In the same way, very common hygrophilous species such as *Veronica beccabunga* are not included in our results because the literature lacks data on their visitors. On the contrary, rarer species such as certain orchids were far more documented, perhaps precisely because their rarity attracts more research interest (e.g., *Epipactis palustris*, Claessens and Kleynen 2016; Gnatiuk et al. 2023). Finally, even considering the high diversity of aquatic insects, Diptera largely dominate these communities, comprising almost half of all aquatic insects. Thus, Diptera are much more likely to be found in surveys, perhaps at the expense of other rarer aquatic orders such as Megaloptera (Dijkstra, Monaghan, and Pauls 2013). It must also be said that if our study was partly focused on continental France, the relationship between insects and plants in humid environments should enhance the interest everywhere, particularly in tropical ecosystems where insects are often understudied (Crespo-Pérez et al. 2020).

Another difficulty is that quite a few articles are focusing on ETP through the prism of pollination ecosystem services, including specific studies carried out in an agricultural context. Many studies consider aquatic insects only at the larval stage (and not adult stage) since their larvae are used as bioindicators to explore the stream water quality (McCafferty 1978; Penrose and Lenat 1982; Lenat 1984; Muenz et al. 2006; Holt et al. 2015). In addition, ETP are also particularly sensitive to pesticides, both indirectly at the larval stage or directly at the adult stage, with species loss estimated at up to 42% in streams (Beketov et al. 2013). This significant impact on their population may also explain their rarity in surveys. In that respect, Plecoptera and Ephemeroptera taxa are considered to be more sensitive to toxic compounds than Trichoptera and far more than Diptera (Wogram and Liess 2001), which aligns with our findings of a higher occurrence of Diptera than ETP in our review.

5 | Conclusion

Pollinators have traditionally been reduced to a small group of insects that deserve to be upgraded in the light of scientific progress. It is clear that many taxa are still neglected in pollination studies, including aquatic insects such as Ephemeroptera, Plecoptera, Trichoptera, Megaloptera and certain Diptera.

Yet, evidence on the presence of pollen on the bodies or in the gut contents of aquatic insects suggest that they may be more involved in pollination than currently documented in the literature. Indeed, if aquatic insects have unequal flight capabilities and time windows, they could play a real role in the pollination ecosystem service, perhaps not by their performance, but by their abundance and diversity; their hitherto neglected benefits could then be far more compelling than previously imagined.

In addition, aquatic insects have already been found on crop plants, for example, Trichoptera on cultivated pear (Ramzan et al. 2016), Diptera on kiwifruit flowers (Broussard et al. 2022; Howlett et al. 2022), carrots (Pérez-Bañón, Petanidou, and Marcos-García 2007; Gaffney et al. 2018) or even colza (Rader et al. 2009). If aquatic insects can effectively pollinate crops, this would open up very interesting avenues in terms of ecosystem services. Conversely, the conservation of aquatic areas could be worthwhile not only from the point of view of aquatic pollinators, but also because hygrophilous plants provide important trophic resources for various guilds of pollinators, as shown in our results.

In the context of such an alarming decline in flying insect biomass, it is important to thoroughly consider the role of all pollinators in our predictive models of pollinator decline, as they may have been underestimated. Our review focused in part on France, but a specific assessment of the role of aquatic insects is essential worldwide, especially as wetlands are under significant threat. A better understanding of the ecosystem services provided by aquatic species could raise the importance of wetland conservation and ensure that these critical habitats receive the protection they need.

Author Contributions

Cassandre Murail: conceptualization, data curation, writing – original draft, formal analysis. **Mathilde Baude:** writing – review and editing, supervision. **Benjamin Bergerot:** writing – review and editing. **Benoit Geslin:** writing – review and editing. **Nicolas Legay:** writing – review and editing. **Irene Villalta:** writing – review and editing, supervision. **Sabine Greulich:** writing – review and editing, supervision.

Acknowledgements

We wish to thank Christophe Piscart who helped us to find references and answered all our questions. We also thank LTSER platforms for both Zones Ateliers Armorique and Loire.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The dataset are available in a public repository at: <https://doi.org/10.5281/zenodo.13935097>.

References

- Aguilar, R., L. Ashworth, L. Galetto, and M. A. Aizen. 2006. "Plant Reproductive Susceptibility to Habitat Fragmentation: Review and Synthesis Through a Meta-Analysis." *Ecology Letters* 9, no. 8: 968–980. <https://doi.org/10.1111/j.1461-0248.2006.00927.x>.
- Albrecht, M., B. Schmid, Y. Hautier, and C. B. Müller. 2012. "Diverse Pollinator Communities Enhance Plant Reproductive Success." *Proceedings of the Royal Society B: Biological Sciences* 279, no. 1748: 4845–4852. <https://doi.org/10.1098/rspb.2012.1621>.
- Armitage, P. D., P. S. Cranston, and L. C. V. Pinder. 1995. *The Chironomidae—Biology and Ecology of Non-biting Midges*. Dordrecht: Springer Netherlands.
- Balfour, N. J., M. C. Castellanos, D. Goulson, A. Philippides, and C. Johnson. 2022. "DoPI: The Database of Pollinator Interactions." *Ecology* 103, no. 11: e3801. <https://doi.org/10.1002/ecy.3801>.

- Balian, E. V., H. Segers, C. Lévêque, and K. Martens. 2008. "The Freshwater Animal Diversity Assessment: An Overview of the Results." *Hydrobiologia* 595, no. 1: 627–637. <https://doi.org/10.1007/s10750-007-9246-3>.
- Beketov, M. A., B. J. Kefford, R. B. Schäfer, and M. Liess. 2013. "Pesticides Reduce Regional Biodiversity of Stream Invertebrates." *Proceedings of the National Academy of Sciences of the United States of America* 110, no. 27: 11039–11043. <https://doi.org/10.1073/pnas.1305618110>.
- Bertrand, H. 1954. *Les insectes aquatiques d'Europe: Genres: Larves, nymphes, imagos*, Vol. 1. Paris: Lechevalier.
- Bianco, M., J. Cooper, and M. Fournier. 2014. "Honey Bee Population Decline in Michigan: Causes, Consequences, and Responses to Protect the State's Agriculture and Food." *System* 11: 6–20.
- Blackburn, T. A. 2012. "To Bee, or Not to Bee, That Is the Problem: Managing Wild Bee Decline in Canadian Agriculture." Simon Fraser University. <https://summit.sfu.ca/item/12243>.
- Broussard, M. A., B. G. Howlett, L. J. Evans, et al. 2022. "Pollinator Identity and Behavior Affect Pollination in Kiwifruit (*Actinidia chinensis* Planch.)." *PeerJ* 10: e12963. <https://doi.org/10.7717/peerj.12963>.
- Carlson, P. E., B. G. Mckie, L. Sandin, and R. K. Johnson. 2016. "Strong Land-Use Effects on the Dispersal Patterns of Adult Stream Insects: Implications for Transfers of Aquatic Subsidies to Terrestrial Consumers." *Freshwater Biology* 61: 848–861.
- Cheney, K. N., A. H. Roy, R. F. Smith, and R. E. Dewalt. 2019. "Effects of Stream Temperature and Substrate Type on Emergence Patterns of Plecoptera and Trichoptera From Northeastern United States Headwater Streams." *Environmental Entomology* 48, no. 6: 1349–1359. <https://doi.org/10.1093/ee/nvz106>.
- Claessens, J., and J. Kleynen. 2016. "Many Ways to Get Happy: Pollination Modes of European Epipactis Species." *Orchid Digest* 80: 142–150.
- Crespo-Pérez, V., E. Kazakou, D. W. Roubik, and R. E. Cárdenas. 2020. "The Importance of Insects on Land and in Water: A Tropical View." *Current Opinion in Insect Science* 40: 31–38. <https://doi.org/10.1016/j.cois.2020.05.016>.
- De Figueroa, J. M. T., and A. Sánchez-Ortega. 2000. "Imaginal Feeding of Twelve Nemouroidean Stonefly Species (Insecta, Plecoptera)." *Annals of the Entomological Society of America* 93, no. 2: 251–253. [https://doi.org/10.1603/0013-8746\(2000\)093\[0251:IFOTNS\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2000)093[0251:IFOTNS]2.0.CO;2).
- Del-Claro, K., and R. Guillermo (Éds). 2019. *Aquatic Insects: Behavior and Ecology*. Cham: Springer International Publishing.
- Dengler, J., F. Jansen, O. Chusova, et al. 2023. "Ecological Indicator Values for Europe (EIVE) 1.0." *Vegetation Classification and Survey* 4: 7–29. <https://doi.org/10.3897/VCS.98324>.
- Diaz, A., and G. Kite. 2002. "A Comparison of the Pollination Ecology of *Arum maculatum* and *A. italicum* in England." *Watsonia* 24: 171–181.
- Dijkstra, K.-D. B., M. T. Monaghan, and S. U. Pauls. 2013. "Freshwater Biodiversity and Aquatic Insect Diversification." *Annual Review of Entomology* 59: 143–163.
- Dormann, C., J. Frund, N. Bluthgen, and B. Gruber. 2009. "Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks." *Open Journal of Ecology* 2: 7–24. <https://doi.org/10.2174/1874213000902010007>.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, et al. 2006. "Freshwater Biodiversity: Importance, Threats, Status and Conservation Challenges." *Biological Reviews* 81, no. 2: 163–182. <https://doi.org/10.1017/S1464793105006950>.
- Free, J. B., and I. H. Williams. 1973. "The Foraging Behaviour of Honeybees (*Apis mellifera* L.) on Brussels Sprout (*Brassica oleracea* L.). The." *Journal of Applied Ecology* 10, no. 2: 489. <https://doi.org/10.2307/2402297>.

- Frouz, J., J. Matěna, and A. Ali. 2013. "Survival Strategies of Chironomids (Diptera: Chironomidae) Living in Temporary Habitats: A Review." *European Journal of Entomology* 100: 459–465.
- Gaffney, A., B. Bohman, S. R. Quarrell, P. H. Brown, and G. R. Allen. 2018. "Frequent Insect Visitors Are Not Always Pollen Carriers in Hybrid Carrot Pollination." *Insects* 9, no. 2: 61. <https://doi.org/10.3390/insects9020061>.
- Gargominy, O., S. Terceire, C. Régnier, et al. 2022. "TAXREF, référentiel taxonomique pour la France: méthodologie, mise en œuvre et diffusion." Rapport PatriNat (OFB-CNRS-MNHN), Muséum national d'Histoire naturelle, Paris. 47 pp.
- Garibaldi, L. A., L. G. Carvalheiro, S. D. Leonhardt, et al. 2014. "From Research to Action: Enhancing Crop Yield Through Wild Pollinators." *Frontiers in Ecology and the Environment* 12: 439–447.
- Gerber, R., C. Piscart, J.-M. Roussel, et al. 2023. "Landscape Models Can Predict the Distribution of Aquatic Insects Across Agricultural Areas." *Landscape Ecology* 38, no. 11: 2917–2929. <https://doi.org/10.1007/s10980-023-01761-4>.
- Gergs, R., M. Koester, R. S. Schulz, and R. Schulz. 2014. "Potential Alteration of Cross-Ecosystem Resource Subsidies by an Invasive Aquatic Macroinvertebrate: Implications for the Terrestrial Food Web." *Freshwater Biology* 59, no. 12: 2645–2655. <https://doi.org/10.1111/fwb.12463>.
- Gervais, A., M. Chagnon, and V. Fournier. 2018. "Diversity and Pollen Loads of Flower Flies (Diptera: Syrphidae) in Cranberry Crops." *Annals of the Entomological Society of America* 111, no. 6: 326–334. <https://doi.org/10.1093/aesa/say027>.
- Gnatiuk, A. M., M. B. Gaponenko, H. Y. Honchar, and A. M. Gaponenko. 2023. "Diversity of (L.) Crantz () Pollinators and Visitors in Conditions of Kyiv City (Ukraine)." *Hacquetia* 22, no. 2: 247–262. <https://doi.org/10.2478/hacq-2022-0018>.
- Gómez, J. M., and R. Zamora. 1999. "Generalization vs. Specialization in the Pollination System of *Hormathophylla spinosa* (Cruciferae)." *Ecology* 80, no. 3: 796–805. [https://doi.org/10.1890/0012-9658\(1999\)080\[0796:GVSITP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[0796:GVSITP]2.0.CO;2).
- Gratton, C., and M. J. Vander Zanden. 2009. "Flux of Aquatic Insect Productivity to Land: Comparison of Lentic and Lotic Ecosystems." *Ecology* 90, no. 10: 2689–2699. <https://doi.org/10.1890/08-1546.1>.
- Hoffmann, F. 2005. "Biodiversity and Pollination. Flowering Plants and Flower-Visiting Insects in Agricultural and Semi-Natural Landscapes." *Dissertation, University of Groningen*. <http://dissertations.ub.rug.nl/faculties/science/2005/f.hoffmann/>.
- Holt, C. R., D. Pfitzer, C. Scalley, B. A. Caldwell, P. I. Capece, and D. P. Batzer. 2015. "Longitudinal Variation in Macroinvertebrate Assemblages Below a Large-Scale Hydroelectric Dam." *Hydrobiologia* 755, no. 1: 13–26. <https://doi.org/10.1007/s10750-015-2212-6>.
- Horth, L., L. Campbell, and R. Bray. 2014. "Wild Bees Preferentially Visit *Rudbeckia* Flower Heads With Exaggerated Ultraviolet Absorbing Floral Guides." *Biology Open* 3, no. 3: 221–230. <https://doi.org/10.1242/bio.20146445>.
- Howlett, B., M. Davidson, D. Logan, M. Gee, S. Read, and J. Todd. 2022. "Designing semi-natural perennial plantings to support targeted pollinators for kiwifruit orchards." *Acta Horticulturae*: 179–186. <https://doi.org/10.17660/ActaHortic.2022.1332.24>.
- IUCN. 2022. "Over One Third of Hoverflies Threatened with Extinction in Europe – IUCN Red List – Press Release | IUCN." <https://www.iucn.org/press-release/202210/over-one-third-hoverflies-threatened-extinction-europe-iucn-red-list>.
- Julve, P. 1998. "Index Botanique, écologique et Chorologique de la Flore de France." Programme Catminat. <https://www.tela-botanica.org/projets/phytosociologie/porte-documents/>.
- King, C., G. Ballantyne, and P. G. Willmer. 2013. "Why Flower Visitation Is a Poor Proxy for Pollination: Measuring Single-Visit Pollen Deposition, With Implications for Pollination Networks and Conservation." *Methods in Ecology and Evolution* 4, no. 9: 811–818. <https://doi.org/10.1111/2041-210X.12074>.
- Klein, A.-M., B. E. Vaissiere, J. H. Cane, et al. 2007. "Importance of Pollinators in Changing Landscapes for World Crops." *Proceedings. Biological sciences* 274: 303–313.
- Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. "Trophic Cascades Across Ecosystems." *Nature* 437, no. 7060: 880–883. <https://doi.org/10.1038/nature03962>.
- Krenn, H. W., J. D. Plant, and N. U. Szucsich. 2005. "Mouthparts of Flower-Visiting Insects." *Arthropod Structure & Development* 34, no. 1: 1–40. <https://doi.org/10.1016/j.asd.2004.10.002>.
- Lafage, D., E. Bergman, R. L. Eckstein, E. M. Österling, J. P. Sadler, and J. J. Piccolo. 2019. "Local and Landscape Drivers of Aquatic-To-Terrestrial Subsidies in Riparian Ecosystems: A Worldwide Meta-Analysis." *Ecosphere* 10, no. 4: e02697. <https://doi.org/10.1002/ecs2.2697>.
- Lancaster, J., and B. J. Downes. 2013. *Aquatic Entomology*. 1st ed. Oxford: Oxford University Press.
- Lenat, D. R. 1984. "Agriculture and Stream Water Quality: A Biological Evaluation of Erosion Control Practices." *Environmental Management* 8, no. 4: 333–343. <https://doi.org/10.1007/BF01868032>.
- Levesque, C. M., and J. F. Burger. 1982. "Insects (Diptera, Hymenoptera) Associated With *Minuartia groenlandica* (Caryophyllaceae) on Mount Washington, New Hampshire, U.S.A., and Their Possible Role as Pollinators." *Arctic and Alpine Research* 14, no. 2: 117. <https://doi.org/10.2307/1551110>.
- Manning, P., and G. C. Cutler. 2013. "Potential Nocturnal Insect Pollinators of Lowbush Blueberry." *Journal of the Acadian Entomological Society* 3: 1–3.
- Martin Gonzalez, A. M. 2010. "Centrality Measures and the Importance of Generalist Species in Pollination Networks." *Ecological Complexity* 7: 36–43.
- McCafferty, W. P. 1978. "Pre-Management Assessment of Aquatic Macroinvertebrates in a Small, Sedimentary Drainage Area of the Maumee and Lake Erie Basin." *Great Lakes Entomologist* 11, no. 1: 37–43. <https://doi.org/10.22543/0090-0222.1316>.
- Muehlbauer, J. D., S. F. Collins, M. W. Doyle, and K. Tockner. 2014. "How Wide Is a Stream? Spatial Extent of the Potential "Stream Signature" in Terrestrial Food Webs Using Meta-Analysis." *Ecology* 95, no. 1: 44–55. <https://doi.org/10.1890/12-1628.1>.
- Muenz, T. K., S. W. Golladay, G. Vellidis, and L. L. Smith. 2006. "Stream Buffer Effectiveness in an Agriculturally Influenced Area, Southwestern Georgia: Responses of Water Quality, Macroinvertebrates, and Amphibians." *Journal of Environmental Quality* 35, no. 5: 1924–1938. <https://doi.org/10.2134/jeq2005.0456>.
- Ollerton, J., R. Winfree, and S. Tarrant. 2010. "How Many Flowering Plants Are Pollinated by Animals?" *Oikos* 120: 321–326.
- Orford, K. A., P. J. Murray, I. P. Vaughan, and J. Memmott. 2016. "Modest Enhancements to Conventional Grassland Diversity Improve the Provision of Pollination Services." *Journal of Applied Ecology* 53, no. 3: 906–915. <https://doi.org/10.1111/1365-2664.12608>.
- Ostrowiecka, B., I. Tałała, E. Brzosko, et al. 2019. "Pollinators and Visitors of the Generalized Food-Deceptive Orchid *Dactylorhiza majalis* in North-Eastern Poland." *Biologia* 74, no. 10: 1247–1257. <https://doi.org/10.2478/s11756-019-00285-0>.
- Penrose, D. L., and D. R. Lenat. 1982. "Effects of Apple Orchard Runoff on the Aquatic Macrofauna of a Mountain Stream." *Archives of Environmental Contamination and Toxicology* 11, no. 3: 383–388. <https://doi.org/10.1007/BF01055215>.
- Peredo Arce, A., J. Kail, E. Tasser, M. J. Feio, M. Palt, and M. Schletterer. 2023. "The Effect of Riparian Forest on Landscape Connectivity for the

- EPT Community Across European Regions.” *Hydrobiologia*. <https://doi.org/10.1007/s10750-023-05353-w>.
- P rez-Ba n n, C., A. Juan, T. Petanidou, M. A. Marcos-Garc a, and M. B. Crespo. 2003. “The Reproductive Ecology of *Medicago citrina* (Font Quer) Greuter (Leguminosae): A Bee-Pollinated Plant in Mediterranean Islands Where Bees Are Absent.” *Plant Systematics and Evolution* 241, no. 1: 29–46. <https://doi.org/10.1007/s00606-003-0004-3>.
- P rez-Ba n n, C., T. Petanidou, and M.  . Marcos-Garc a. 2007. “Pollination in Small Islands by Occasional Visitors: The Case of *Daucus carota* subsp. *Commutatus* (Apiaceae) in the Columbretes Archipelago, Spain.” *Plant Ecology* 192, no. 1: 133–151. <https://doi.org/10.1007/s11258-006-9233-1>.
- Petanidou, T., J. C. M. Den Nijs, J. G. B. Oostermeijer, and A. C. Ellis-Adam. 1995. “Pollination Ecology and Patch-Dependent Reproductive Success of the Rare Perennial *Gentiana pneumonanthe* L.” *New Phytologist* 129, no. 1: 155–163. <https://doi.org/10.1111/j.1469-8137.1995.tb03019.x>.
- Rader, R., I. Bartomeus, L. A. Garibaldi, et al. 2015. “Non-Bee Insects Are Important Contributors to Global Crop Pollination.” *Proceedings of the National Academy of Sciences of the United States of America* 113: 146–151.
- Rader, R., S. A. Cunningham, B. G. Howlett, and D. W. Inouye. 2020. “Non-Bee Insects as Visitors and Pollinators of Crops: Biology, Ecology, and Management.” *Annual Review of Entomology* 65, no. 1: 391–407. <https://doi.org/10.1146/annurev-ento-011019-025055>.
- Rader, R., B. G. Howlett, S. A. Cunningham, et al. 2009. “Alternative Pollinator Taxa Are Equally Efficient but Not as Effective as the Honeybee in a Mass Flowering Crop.” *Journal of Applied Ecology* 46, no. 5: 1080–1087. <https://doi.org/10.1111/j.1365-2664.2009.01700.x>.
- Raitif, J., M. Plantegenest, and J.-M. Roussel. 2019. “From Stream to Land: Ecosystem Services Provided by Stream Insects to Agriculture.” *Ecosystems & Environment* 270–271: 32–40.
- Raitif, J., J.-M. Roussel, M. Olmos, et al. 2022. “Assessing Spatial Deposition of Aquatic Subsidies by Insects Emerging From Agricultural Streams.” *Science of the Total Environment* 837: 155686. <https://doi.org/10.1016/j.scitotenv.2022.155686>.
- Ramzan, S., M. A. Paray, S. H. Parrey, M. Yaqoob, and R. Khurshid. 2016. “Species Richness and Abundance of Insect Pollinators on Pear Blossoms in Kashmir Himalayans.” *Journal of Eco-Friendly Agriculture* 12: 1–9.
- Rashid, S., K. Rashid, B. A. Wani, A. H. Ganie, I. A. Nawchoo, and A. A. Khuroo. 2023. “Reproductive Biology of Actaea Kashmiriana, an Endemic Medicinal Plant Species From the Himalaya: Implications for Conservation and Sustainable Utilisation.” *Journal of Applied Research on Medicinal and Aromatic Plants* 34: 100461. <https://doi.org/10.1016/j.jarmp.2023.100461>.
- Reid, A. J., A. K. Carlson, I. F. Creed, et al. 2019. “Emerging Threats and Persistent Conservation Challenges for Freshwater Biodiversity.” *Biological Reviews of the Cambridge Philosophical Society* 94, no. 3: 849–873. <https://doi.org/10.1111/brv.12480>.
- Requier, F., M. Abdelli, M. Baude, et al. 2024. “Neglecting Non-Bee Pollinators May Lead to Substantial Underestimation of Competition Risk Among Pollinators.” *Current Research in Insect Science* 6: 100093. <https://doi.org/10.1016/j.cris.2024.100093>.
- Requier, F., N. P rez-M endez, G. K. S. Andersson, E. Blareau, I. Merle, and L. A. Garibaldi. 2023. “Bee and Non-Bee Pollinator Importance for Local Food Security.” *Trends in Ecology & Evolution* 38, no. 2: 196–205. <https://doi.org/10.1016/j.tree.2022.10.006>.
- Rundle, S. D., D. T. Bilton, and A. Fogo. 2007. “By Wind, Wings or Water: Body Size, Dispersal and Range Size in Aquatic Invertebrates.” In *Body Size: The Structure and Function of Aquatic Ecosystems*. *Ecological Reviews*, edited by A. G. Hildrew, D. G. Raffaelli, and R. Edmonds-Brown, 186–209. Cambridge: Cambridge University Press.
- Sato, A. A. W., and M. Kato. 2017. “Pollination System of *Corylopsis gotoana* (Hamamelidaceae) and Its Stonefly (Plecoptera) Co-Pollinator.” *Plant Species Biology* 32, no. 4: 440–447. <https://doi.org/10.1111/1442-1984.12178>.
- Schurr, L., B. Geslin, L. Affre, et al. 2021. “Landscape and Local Drivers Affecting Flying Insects Along Fennel Crops (*Foeniculum vulgare*, Apiaceae) and Implications for Its Yield.” *Insects* 12, no. 5: 404. <https://doi.org/10.3390/insects12050404>.
- Seibold, S., M. M. Gossner, N. K. Simons, et al. 2019. “Arthropod Decline in Grasslands and Forests Is Associated With Landscape-Level Drivers.” *Nature* 574, no. 7780: 671–674. <https://doi.org/10.1038/s41586-019-1684-3>.
- Smith, T. J., and M. E. Saunders. 2016. “Honey Bees: The Queens of Mass Media, Despite Minority Rule Among Insect Pollinators.” *Insect Conservation and Diversity* 9, no. 5: 384–390. <https://doi.org/10.1111/icad.12178>.
- Smith-Ram rez, C., P. Martinez, M. Nu ez, C. Gonz lez, and J. J. Armesto. 2005. “Diversity, Flower Visitation Frequency and Generalism of Pollinators in Temperate Rain Forests of Chilo  Island, Chile.” *Botanical Journal of the Linnean Society* 147, no. 4: 399–416. <https://doi.org/10.1111/j.1095-8339.2005.00388.x>.
- Sohn, S. R. 2007. “Seasonal Prevalence of the *Culex pipiens* Group (Diptera: Culicidae) Larvae Occurring in a Puddle in the Basement of an Apartment Building.” *Entomological Research* 37, no. 2: 95–99. <https://doi.org/10.1111/j.1748-5967.2007.00059.x>.
- Speight, M. C. D. 2011. “Species Accounts of European Syrphidae (Diptera), Glasgow 2011.” In *Syrph the Net, the Database of European Syrphidae*, Vol. 65, edited by M. C. D. Speight, E. Castella, J. P. Sarthou, and C. Monteil, 285. Dublin: Syrph the Net Publications.
- Stenroth, K., L. E. Polvi, E. F ltstr m, and M. Jonsson. 2015. “Land-Use Effects on Terrestrial Consumers Through Changed Size Structure of Aquatic Insects.” *Freshwater Biology* 60, no. 1: 136–149. <https://doi.org/10.1111/fwb.12476>.
- Stewart, R., G. Andersson, C. Br nmark, et al. 2016. “Ecosystem Services Across the Aquatic-Terrestrial Boundary: Linking Ponds to Pollination.” *Basic and Applied Ecology* 18: 13–20. <https://doi.org/10.1016/j.baae.2016.09.006>.
- Sugiura, N., and S. Miyazaki. 2021. “Discovery of Flower-Visiting Fishflies: Adult *Neochauliodes amamioshimanus* (Megaloptera: Corydalidae) Nocturnally Forages on *Schima wallichii* ssp. *Noronhae* Trees.” *Entomological Science* 24, no. 2: 152–156. <https://doi.org/10.1111/ens.12463>.
- Talavera, S., F. Bastida, P. L. Ortiz, and M. Arista. 2001. “Pollinator Attendance and Reproductive Success in *Cistus libanotis* L. (Cistaceae).” *International Journal of Plant Sciences* 162, no. 2: 343–352. <https://doi.org/10.1086/319573>.
- Tatarenko, I., K. Walker, and M. Dyson. 2022. “Biological Flora of Britain and Ireland: *Fritillaria meleagris*.” *Journal of Ecology* 110, no. 7: 1704–1726. <https://doi.org/10.1111/1365-2745.13886>.
- Tauber, H. 1965. “Differential Pollen Dispersion and the Interpretation of Pollen Diagrams. With a Contribution to the Interpretation of the Elm Fall.” *Danmarks Geologiske Unders gelse II. R kke* 89: 1–69.
- Tich y, L., I. Axmanov , J. Dengler, et al. 2023. “Ellenberg-Type Indicator Values for European Vascular Plant Species.” *Journal of Vegetation Science* 34, no. 1: e13168. <https://doi.org/10.1111/jvs.13168>.
- Triponez, Y., N. Arrigo, A. Esp ndola, and N. Alvarez. 2015. “Decoupled Post-Glacial History in Mutualistic Plant–Insect Interactions: Insights From the Yellow Loosestrife (*Lysimachia vulgaris*) and Its Associated Oil-Collecting Bees (*Macropis europaea* and *M. fulvipes*).” *Journal of Biogeography* 42, no. 4: 630–640. <https://doi.org/10.1111/jbi.12456>.
- Valido, A., M. C. Rodr guez-Rodr guez, and P. Jordano. 2019. “Honeybees Disrupt the Structure and Functionality of Plant–Pollinator

- Networks.” *Scientific Reports* 9, no. 1: 4711. <https://doi.org/10.1038/s41598-019-41271-5>.
- Vallenduuk, H. J., and H. M. J. Cuppen. 2004. “The Aquatic Living Caterpillars (Lepidoptera: Pyraloidea: Crambidae) of Central Europe. A Key to the Larvae and Autecology.” *Lauterbornia* 49: 1–17.
- van Klink, R., D. E. Bowler, K. B. Gongalsky, M. Shen, S. R. Swengel, and J. M. Chase. 2024. “Disproportionate Declines of Formerly Abundant Species Underlie Insect Loss.” *Nature* 628, no. 8007: 359–364. <https://doi.org/10.1038/s41586-023-06861-4>.
- Walton, R. E., C. D. Sayer, H. Bennion, and J. C. Axmacher. 2020. “Nocturnal Pollinators Strongly Contribute to Pollen Transport of Wild Flowers in an Agricultural Landscape.” *Biology Letters* 16, no. 5: 20190877. <https://doi.org/10.1098/rsbl.2019.0877>.
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. New York, NY: Springer-Verlag New York. <https://ggplot2.tidyverse.org>.
- Williams, P., M. Whitfield, J. Biggs, et al. 2003. “Comparative Biodiversity of Rivers, Streams, Ditches and Ponds in an Agricultural Landscape in Southern England.” *Biological Conservation* 115: 329–341.
- Winterbourn, M. J. 2005. “Dispersal, Feeding and Parasitism of Adult Stoneflies (Plecoptera) at a New Zealand Forest Stream.” *Aquatic Insects* 27, no. 3: 155–166. <https://doi.org/10.1080/01650420500062840>.
- Winterbourn, M. J., and S. R. Pohe. 2017. “Feeding and Parasitism of Adult *Stenoperla* spp. (Plecoptera: Eustheniidae) in New Zealand.” *Austral Entomology* 56, no. 2: 191–197. <https://doi.org/10.1111/aen.12222>.
- Wissinger, S. A. 1995. “Cyclic Colonization in Predictably Ephemeral Habitats: A Template for Biological Control in Annual Crop Systems.” *Biological Control* 10: 4–15.
- Wogram, J., and M. Liess. 2001. “Rank Ordering of Macroinvertebrate Species Sensitivity to Toxic Compounds by Comparison With That of *Daphnia Magna*.” *Bulletin of Environmental Contamination and Toxicology* 67, no. 3: 360–367. <https://doi.org/10.1007/s001280133>.
- Zhang, X., L. Zhang, Y. Wang, et al. 2022. “Pollinators and Urban Riparian Vegetation: Important Contributors to Urban Diversity Conservation.” *Environmental Sciences Europe* 34, no. 1: 78. <https://doi.org/10.1186/s12302-022-00661-9>.
- Zwick, P. 1990. “Emergence, Maturation and Upstream Oviposition Flights of Plecoptera From the Breitenbach, With Notes on the Adult Phase as a Possible Control of Stream Insect Populations.” *Hydrobiologia* 194, no. 3: 207–223. <https://doi.org/10.1007/BF00007121>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.