



HAL
open science

Tightly intertwined: Waterscapes prompt urgent reconsideration of aquatic insects and their role in agricultural landscapes

Benjamin Bergerot, Christophe Piscart, J M Roussel

► To cite this version:

Benjamin Bergerot, Christophe Piscart, J M Roussel. Tightly intertwined: Waterscapes prompt urgent reconsideration of aquatic insects and their role in agricultural landscapes. *Science of the Total Environment*, 2025, 966, pp.178728. <10.1016/j.scitotenv.2025.178728>. <hal-04975888>

HAL Id: hal-04975888

<https://hal.science/hal-04975888v1>

Submitted on 10 Apr 2025

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 CC BY-NC 4.0 - Attribution - Non-commercial use - International License

1 Tightly intertwined: waterscapes prompt urgent reconsideration of aquatic
2 insects and their role in agricultural landscapes

3

4

5 Bergerot B.¹, Piscart C. ¹, Roussel JM. ²

6

7 ¹University of Rennes, CNRS, UMR 6553 ECOBIO, Rennes, France

8 ²DECOD (Ecosystem Dynamics and Sustainability), INRAE, Institut Agro, IFREMER, Rennes, France

9

10

11 ***Corresponding author:**

12 * Benjamin Bergerot (benjamin.bergerot@univ-rennes.fr), ORCID: 0000-0003-4313-4925

13 Christophe Piscart (christophe.piscart@univ-rennes.fr), ORCID: 0000-0002-4054-4542

14 Jean-Marc Roussel (jean-marc.rousseau@inrae.fr), ORCID: 0000-0002-6301-3234

15

16

17 **Highlights**

18

19 Landscapes and waterscapes are intertwined rather than superimposed.

20 The meta-ecosystem, based on fluxes between two different adjacent ecosystems, is an attractive
21 concept in landscape ecology for unifying waterscapes and landscapes.

22 Spatial and temporal characterization of water bodies and aquatic fluxes is one of the main keys to
23 bring waterscape and landscape together.

24 A whole field of research is open on aquatic insects – particularly Diptera – to better characterize the
25 aquatic signature of temporary water bodies in agricultural landscapes.

26

27

28

29 **Abstract**

30 In landscape ecology, the waterscape refers to permanent or temporary, running or stagnant surface
31 waters within a terrestrial area. Across ecosystem boundaries, aquatic organisms and nutrients can
32 reach terrestrial ecosystems, as formalised by the meta-ecosystem theory. Recent studies on aquatic
33 insects emerging from temperate streams suggest that the extent of their biomass and fluxes across
34 agricultural landscapes may have been neglected until now. Following a conceptual and empirical
35 approach, we presently discuss how the temporal dynamics of floods coupled with the emergence
36 and aerial fluxes of aquatic insects suggests that the waterscape can largely overlap the landscape.
37 Depending on the season, various species and biomasses of aquatic insects could interact with the
38 receiving terrestrial ecosystems and ultimately support vital ecosystem services and functions such

39 as pollination, soil fertilization, and control of crop pests or facilitation of their natural enemies. In
40 the current context of a global collapse of terrestrial insect populations, we call for an urgent
41 research effort to include the temporal dimension of waterscapes into landscape models to estimate
42 the fluxes of insects emerging from all kinds of aquatic ecosystems and quantify their role in the
43 functioning of terrestrial ecosystems in agricultural landscapes.

44

45

46 **Key-words:** fluxes, aquatic signature, aquatic insects, aquatic subsidies, permanent and temporary
47 water bodies

48

49 **Introduction**

50 Freshwater represents about 2% of the terrestrial land surface but hosts nearly 10% of the
51 Earth's known animal species (Reid et al., 2019). Within the global decline of the biodiversity of
52 vertebrates (Ceballos et al., 2017; Daskalova et al., 2020; Leung et al., 2020) and invertebrates (Potts
53 et al., 2010; Raven and Wagner, 2021; Wagner et al., 2021), freshwaters are no exception (Strayer
54 and Dudgeon, 2010). The threats on freshwater life are multiple (Cazzolla Gatti, 2016), and range
55 from local ones (e.g., over-exploitation, habitat degradation and fragmentation, flow changes and
56 water pollution) to global ones (e.g., biological invasions and land-use changes, eutrophication and
57 acidification, climate change). Freshwater ecosystems in landscape mosaics can create biodiversity
58 hotspots and locally enhance the overall observed biodiversity because they can host species-rich
59 communities. Looking beyond conservation issues, freshwater ecosystems have great economic,
60 cultural, aesthetic and educational values (Dudgeon et al., 2006) and support exclusive services for
61 human societies, agriculture included (Kumar et al., 2024; Li and Tsigaris, 2024; Raitif et al., 2019).
62 However, freshwater and terrestrial ecosystems have specific ways of functioning and requirements,
63 and their dual management remains challenging. In agricultural landscapes, freshwater ecosystems
64 are often viewed at best as water reserves for irrigation or livestock, at worst as cumbersome
65 landscape elements sometimes difficult to keep under control (eutrophication, wasteland). They are
66 part of the landscape mosaics, but they have been surprisingly forgotten in the debate on
67 biodiversity in agricultural landscapes. Freshwater ecosystems are mostly omitted in scenarios for
68 designing multifunctional landscapes, notably when discussing the respective merits of land-sharing
69 (i.e., wildlife-minded farming systems) and land-sparing (i.e., the separation of natural and high-
70 yielding habitats) strategies (Grass et al., 2019), or the role of connectivity and species spillover
71 between mosaic habitats to support ecosystem services in agricultural landscapes (Senapathi et al.,
72 2015).

73 The implementation of ambitious biodiversity management plans for freshwaters requires
74 the recognition of the extensive diversity of aquatic habitats and species, and a systematic
75 assessment of how scientific data can be turned into concrete actions at local (e.g., a pond or a
76 stream section), regional (e.g., a watershed) and global scales (Barouillet et al., 2024; Miller et al.,
77 2024; Valentim et al., 2024). This argues for freshwater ecosystems to be considered as specific
78 constituents of complex landscapes, and for their specificities to be taken into account in a broader
79 management of biodiversity at the territorial scale. But it is also clear that the interactions between
80 aquatic and terrestrial ecosystems are complex and have been poorly investigated (Guenet et al.,
81 2010). Scientific knowledge on aquatic-terrestrial interactions has been hampered by historically
82 separated research fields – aquatic ecology and terrestrial ecology – for decades (Casas-Ruiz et al.,
83 2023; Fausch et al., 2002). However, progress has been made about the waterscape (O’Sullivan et al.,
84 2022) and meta-ecosystem (Gounand et al., 2018) concepts – two recent theoretical frameworks in
85 landscape ecology. The waterscape refers to the surface of water within a terrestrial area as an
86 integral element of the landscape, while the meta-ecosystem focuses on the interdependent
87 functioning between adjacent (aquatic and terrestrial) ecosystems through exchanges of matter and
88 energy. Although they address the same ecosystems, these two concepts have rarely been
89 considered together.

90 Over the last ten years, part of research on aquatic ecosystem-terrestrial ecosystem
91 interactions has focused on aquatic insects in agricultural landscapes, namely the insects with
92 successive aquatic larval and terrestrial imago. After emerging from the water, winged adults can be
93 found as far as hundreds of meters from their original aquatic ecosystems (Muehlbauer et al., 2014;
94 Raitif et al., 2022). As basic knowledge on the fluxes of aquatic insects in terrestrial ecosystems (Raitif
95 et al., 2022) and their physiological and dispersal characteristics (Gerber et al., 2023a, 2022b)
96 increases, distribution models tend to show that their presence in the landscape could have been
97 underestimated (Gerber et al., 2023b). Moreover, their distribution is highly dynamic and depends
98 on seasonal variations in the waterscape and on the life cycle phenology of the insect species. Adult

99 aquatic insects can interact with receiving terrestrial ecosystems, and they are suspected to be
100 involved in some ecosystem services for agriculture (Raitif et al., 2019). But their role in supporting
101 vital functions such as pollination, soil fertilisation, and control of crop pests or facilitation of their
102 natural enemies has not been quantified in agroecosystems to date. As a global perspective on the
103 role of freshwater ecosystems in agricultural landscapes is lacking, referring to the concepts of
104 waterscape and meta-ecosystem could help to refine the multi-functionality of agricultural
105 landscapes, as well as reconsider some key ecosystem services to agriculture associated with aquatic
106 insects.

107

108 **What does “waterscape” represent?**

109 The notion of “waterscape” in scientific literature is much more recent than that of
110 landscape, which has a long historical record in ecology (Turner et al., 2001). One of the earliest
111 mentions dates back to 1978 (Pournelle, 1978). Without defining the term, the word waterscape was
112 used in the development of large-scale water resource management projects in North America and
113 Asia. In 1985, two types of waterscape were described – mountain lakes and running water – as part
114 of a social study on visual landscape preferences (Herzog, 1985). These references to landscape
115 entities were taken up in Hundley's work (Hundley, 1987). He used the term waterscape to describe
116 the perception of nature by California Indians. He described the waterscape in terms of landscape
117 elements such as “*California's rivers flowed uninterrupted into valleys, marshes, bays, and the ocean,*
118 *freshwater marshlands*”. In 1992, Holling also used the term waterscape, referring to the spatial
119 arrangement of a landscape, but without defining it (Holling, 1992). The term appeared in several
120 domains including history, spatial planning and political issues in the late 1990s (Arnold, 1996; Neset,
121 1998; Wilson et al., 1995). It was only in the 2000s that its definition became clearer, notably with
122 the rise of work on urban water management combining architecture and urban planning (Dreiseitl
123 et al., 2001; Meybeck, 2004; Rubin et al., 2003). The waterscape was then defined as “*a water*

124 *infrastructure system as an integral element of architecture and the urbanscape*” (Lim et al., 2002)
125 and “*a perspective that [...] includes the way water travels in time and space and is shaped by culture*
126 *and geography*” (Karpouzoglou and Vij, 2017). Since then, the disciplinary fields relating to the
127 waterscape have diversified, and they concern environmental studies, geography, management of
128 water resources through engineering, political, historical, social or legal aspects (see Appendix A for a
129 complete list of published studies dealing with the notion of waterscape).

130 The relationship between agriculture and the waterscape is an essential factor in
131 understanding social, economic and political continuity and rupture in the landscape worldwide
132 (Aijaz and Akhter, 2020; Rogers, 2012; Taylor, 2022; Wessels, 2023). In the scientific literature, there
133 are historical and recent examples of the relationships between waterscape, irrigation and
134 agricultural areas. Many wetland fields, reservoirs and canals provide water resources to
135 complement floodplain agriculture and water management. For example, the historical
136 reconstruction of the waterscape in Mount Lebanon during the Ottoman period is rich and varied,
137 providing a better understanding of the evolution of rural communities (McPhillips et al., 2019).
138 Other studies have shown that the Maya created a multi-trophic ecological aquaculture by modifying
139 the waterscape to increase the quantities of food and useful materials, such as fish, turtles,
140 waterfowl and reeds (Palka, 2024). More recently, in the 1990s, the implementation of water
141 reforms in rural African landscapes has shown how influential the waterscape could be for
142 agricultural practices. In particular, privileged farmers have jumped the water queue by moving their
143 agricultural activities upstream where they illegally divert water straight from the river, while
144 downstream, in the smallholder irrigation scheme, farmers resort to rainfed farming (Kemerink-
145 Seyoum et al., 2017).

146 Water as a resource is at the core of the relationship between waterscape and agricultural
147 landscape. Water scarcity in waterscapes poses management challenges (Tallman et al., 2024) and
148 research is needed to guide policy, to reinforce stakeholder engagement and to resolve tensions

149 between water demands (Ricart et al., 2023). In a context of climate change and dwindling water
150 resources, these tensions will also be heightened as many water bodies are temporary (Messenger et
151 al., 2021), in particular in agricultural areas (Borthagaray et al., 2023; Cunillera-Montcusí et al., 2023;
152 Gerber et al., 2022a). However, while historical studies report relationship between the waterscape
153 and regulated water, there is no example on how temporary water bodies have been taken into
154 account in the definition of the waterscape. In Europe, Spain is arguably the country where the water
155 crisis has become most acute in recent years (Swyngedouw, 1999) and where the waterscape is
156 strongly represented by temporary water bodies (Messenger et al., 2021). Although the importance of
157 water in the Iberian Peninsula has received considerable attention, particularly from researchers
158 (Swyngedouw, 1999), studies establishing a link between the waterscape and temporary water
159 bodies are lacking. This may be explained by the hybrid nature of the waterscape, at the interface of
160 water policy, water culture and water engineering, but also of contemporary water geography and
161 ecology as the product of centuries of socio-ecological interaction that have remained largely
162 unexplored.

163 In the meantime, numerous studies have reported a variable flux of energy and variable
164 sediment dynamics processes between river channels and floodplains since the 1950s (Church,
165 2006), underlying the importance of exchanges between aquatic and terrestrial environments. In the
166 1990s, the definition of "subsidies" made it possible to posit the fundamental role of connections
167 between ecosystems (Nakano and Murakami, 2001; Polis et al., 1997; Schindler and Smits, 2017). The
168 term refers to spatiotemporal fluxes of materials (organic or inorganic, particle or solute) from one
169 ecosystem to another, involved in their functioning. The movement of water bodies (e.g., during
170 floods, tides, in aquifers) or aquatic organisms (e.g., their dispersal or transportation by predators)
171 are the chief cause of subsidies of aquatic origin in terrestrial ecosystems (Polis et al., 1997; Schindler
172 and Smits, 2017). These subsidies are identified by their signature (or fingerprints), i.e., "*an emergent
173 property of a set of processes, both biotic or abiotic, acting on a river landscape*" (Gurnell et al.,
174 2016). Aquatic subsidies can be found at the land surface (e.g., vegetation, inorganic material and

175 interactions between them) or subsurface (e.g., alluvial deposits, topography). The dynamic
176 penetration of aquatic subsidies across the landscape is defined as the “envelope”, which
177 corresponds to the signature of the aquatic compartment in the landscapes (Gurnell et al., 2016).
178 Such a definition arouses new questions like “*how large is a river*” (Gurnell et al., 2016), “*how wide is*
179 *a stream*” (Muehlbauer et al., 2014), “*where is the bottom of a watershed*” (Condon et al., 2020) up
180 to the definition of the “*waterscape continuum*” (O’Sullivan et al., 2022). According to O’Sullivan et
181 al. (2022), the waterscape is delineated by surface water, soil moisture, rock moisture, groundwater
182 and all associated fluxes (organic and inorganic, particle and solute), and its definition is close to that
183 of the envelope (Gurnell et al., 2016).

184

185 **A waterscape is much more than just water in a landscape**

186 The meta-ecosystem is a theoretical framework that explicitly addresses energy exchanges
187 between two different ecosystems – e.g., an aquatic one and a terrestrial one – across their
188 boundaries (Gounand et al., 2018; Loreau et al., 2003). This is very close to the definition of subsidies
189 (Nakano and Murakami, 2001; Polis et al., 1997; Schindler and Smits, 2017), but it clearly emphasizes
190 that allochthonous fluxes can ultimately affect the functioning of the receiving ecosystem. Moreover,
191 these fluxes can fade away in the receiving ecosystem as distance from the donor ecosystem
192 increases, and the existence of spatial gradients is also implicit. The meta-ecosystem framework
193 allows formalising energy pathways between ecosystems (Kramer et al., 2023), and it provides a
194 helpful template in the case of freshwater and terrestrial ecosystems to study the influence of the
195 waterscape on the landscape and its spatiotemporal variability (Fig. 1). The allochthonous fluxes
196 considered in the meta-ecosystem approach can be abiotic (e.g., nutrients) or biotic (e.g., living
197 organisms), but they systematically concern ecosystems of different types (e.g., aquatic-terrestrial).
198 This differs from the dispersal of living organisms, which refers to the meta-community concept and

199 characterises their movements between habitats of a same type of ecosystem (e.g., terrestrial-
200 terrestrial, aquatic-aquatic) within the landscape (Clobert et al., 2001; Heino et al., 2015) (Fig. 1A).

201 Fluxes of resources and energy from freshwater ecosystems toward terrestrial ecosystems
202 outline the influence of aquatic environments on landscapes (Gurnell et al., 2016; Muehlbauer et al.,
203 2014). Aquatic subsidies and their effects on the receiving terrestrial ecosystems have been clearly
204 showed by research on salmon-derived nutrients: the growth rates of Sitka spruce (*Picea sitchensis*)
205 increased near salmon spawning streams (Helfield and Naiman, 2001; Naiman et al., 2002).
206 Mammals and birds preying on freshwater fish can also convey aquatic nutrients across the
207 landscape (Gerraty et al., 2024; Shakeri et al., 2018). By identifying the spatial extent of this influence
208 on the landscape, one can characterise the "aquatic envelope" (*sensus* Gurnell et al., 2016), i.e., the
209 encroachment of the aquatic ecosystem into the terrestrial ecosystem along the waterscape.
210 Moreover, the waterscape is usually depicted through its spatial dimension (O'Sullivan et al., 2022),
211 but this is an extreme simplification of reality given the temporal dynamics of the aquatic element
212 and its influence on landscapes (Fig. 1B). The water level variations in permanent water bodies such
213 as ponds, lakes, marshes, streams and rivers, as well as in temporary aquatic habitats like flooded
214 ditches and meadows (Biggs et al., 2017) indicate that the surface of the waterscape can fluctuate
215 along the seasons and bring nutrients and fertile sediment into terrestrial ecosystems. Similarly,
216 aquatic insects emerging from freshwater can disperse beyond the boundaries of the aquatic
217 ecosystem (Gerber et al., 2023b) and interact with the terrestrial ecosystem that receives them
218 (Muehlbauer et al., 2014), thus extending the spatiotemporal aquatic influence – or signature – into
219 the landscape (Fig. 1). The meta-ecosystem provides a dynamic framework to study the functional
220 interactions between aquatic and terrestrial ecosystems, highlighting how the waterscape and the
221 landscape are intimately intertwined in the territories. Gathering data on the temporality of
222 ecological fluxes between different ecosystems is one of the major challenges for research on meta-
223 ecosystems (Kharouba and Wolkovich, 2020).

224 Aquatic-terrestrial interactions can be altered by anthropogenic activities such as water
225 abstraction and diversion, water storage and regulation, climate and land-use changes (Zimmer et al.,
226 2020). They strongly modify the spatial extent of water bodies – whether permanent or temporary
227 ones (Datry et al., 2023; Søndergaard and Jeppesen, 2007) –, alter the spatial and temporal dynamics
228 of waterscapes, and can ultimately hamper the functioning of adjacent terrestrial ecosystems (Little
229 et al., 2022, 2020). For instance, climate warming can shift the lifespan of plants and animals (Morris
230 et al., 2008) and change the behaviour of many animals (Forrest, 2016). Since responses may vary
231 among species and populations, in agricultural landscapes, previously synchronised interdependent
232 key life-cycle stages can be disrupted (Donnelly et al., 2011; Forrest, 2016). Mismatches may occur
233 when the time span of the energy requirement of a consumer does not match with the availability of
234 its prey (Both et al., 2006; Visser and Gienapp, 2019). For example, the nutritional quality of aquatic
235 and terrestrial insect larvae in relation to their fatty acid composition varies seasonally in the
236 landscape (Shiple et al., 2022; Twining et al., 2019). In agricultural ecosystems, aquatic insects such
237 as Ephemeroptera, Plecoptera and Trichoptera are some of the first species to be lost from local food
238 webs following disturbance and exposure to agricultural pesticides (Barmantlo et al., 2021), and their
239 nutritional contributions to consumers cannot be readily offset by conservation of terrestrial systems
240 alone (Shiple et al., 2022). The reproductive success of many agricultural consumers such as birds
241 depends and is positively linked to the availability of aquatic insect prey (Twining et al., 2018, p. 201),
242 with other cascading effects on terrestrial ecosystems that remain largely unknown. With climate
243 change, the maximum biomass of emerging aquatic insects tends to occur earlier in the season and
244 then total production declines, while the biomass of terrestrial insects gradually increases (Shiple et
245 al., 2022), with a suspected decoupling between aquatic subsidies and energy needs in the receiving
246 ecosystem (Berzins et al., 2021). In addition, aquatic insects will emerge over a longer period, dilute
247 in abundance and exhibit less seasonal patterns with smaller fluctuations between months (Nash et
248 al., 2023b) while insect communities may evolve towards an increasing proportion of short-lived
249 insects (e.g. Diptera) in aquatic ecosystems that have become temporary (Datry et al., 2014).

250 Disruption of ecosystem functions seasonally dependent on aquatic insects, such as riparian
251 predation, could occur in this context (Nash et al., 2023a).

252 Water quality is also strongly influenced by the surrounding landscape and affects the
253 aquatic insect communities that emerge from agricultural water bodies (Raitif et al., 2018; Schulz et
254 al., 2015). Emerging insects are mainly negatively correlated with pollution tolerance, suggesting a
255 large-scale loss of this nutritional subsidy for terrestrial environments from altered aquatic
256 ecosystems (Manning and Sullivan, 2021). In recent years, mass emergence of mayflies could be
257 reduced by 50% due to eutrophication, algal blooms, and chemical contaminants including pesticides
258 (Stepanian et al., 2020). If contaminants affect insect emergence, emergence may also result in
259 contaminant transfer to the adjacent agricultural ecosystem. Consequently, the impact of aquatic
260 contaminants on terrestrial ecosystems may be determined by changes in the quantity and quality of
261 adult aquatic insects serving as prey, or contaminants entering terrestrial food webs as part of the
262 diet of terrestrial predators (Bundschuh et al., 2022). Recent findings on rice farming also highlight
263 the potential positive effects of pesticide bans on aquatic macroinvertebrate communities, and
264 hence on improving biodiversity and biological pest control (Pérez-Méndez et al., 2023). Agricultural
265 impacts are not limited to chemical pollution but can also, through the alteration of landscape
266 features, have a strong impact on the spatial distribution of aquatic insects through changes in the
267 composition of aquatic insect communities (Raitif et al., 2022, 2018) or through a reduction in
268 woodland density or an increase in potential incoming solar radiation (Gerber et al., 2023b).

269

270 **Influence of aquatic insects and the waterscape on the landscape**

271 Only few of the publications referring to the waterscape as a structuring element of the
272 landscape (7% of 635 in total, Appendix A deal with aquatic biota), and aquatic insects in particular.
273 However, aquatic insects represent a significant proportion of the aerial flying arthropods in the
274 vicinity of large lakes from which they can emerge in quantities reaching 2,500 kg.ha⁻¹.yr⁻¹ dry

275 biomass (Gratton et al., 2008; Gratton and Vander Zanden, 2009; Salvarina et al., 2017). Along the
276 Upper Mississippi River and the western basin of Lake Erie, a single emergence event can produce
277 87.9 billion mayflies, releasing more than 3 tons of biomass into the airspace within several hours
278 (Stepanian et al., 2020). Insect biomass emergence from lakes generally exceeds that from streams
279 (Bartrons et al., 2013; Williams et al., 2004). Other ecosystems, e.g. estuaries (MacKenzie, 2005;
280 MacKenzie and Kaster, 2004; Williams and Williams, 1998) or wetlands (Vinnersten et al., 2014), can
281 support a high emergence of aquatic insects. Tidal freshwaters such as the James River Estuary,
282 Virginia, USA, produce a mean rate (± 1 SE) of $156 \pm 20 \text{ kg}\cdot\text{ha}^{-2}\cdot\text{yr}^{-1}$ dry biomass (Rogers et al., 2024).
283 In wetlands, emergence can reach $50 \text{ kg}\cdot\text{ha}^{-2}\cdot\text{yr}^{-1}$ with a dominance of Diptera (Whiles and
284 Goldowitz, 2001).

285 In agricultural landscapes in western France, $40 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ dry biomass of aquatic insects
286 emerge from third-order permanent streams on average (Strahler classification), and $12.5 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$
287 of these aquatic insects fall to the ground within 10 meters of the stream edge (Raitif et al., 2022).
288 Although emerging insect biomass is lower than in large lakes, the spatial intertwining of these small
289 streams and other aquatic ecosystems (ponds, ditches) in landscapes is strong. For example, hardly
290 any spot where the probability of the presence of aquatic insects dropped to zero was found in an
291 agricultural landscape including small streams and ponds (Gerber et al., 2023b). This suggests how
292 the waterscape – especially if it includes the dispersal of aquatic insects in its definition – may be
293 tightly intertwined with the landscape. Finally, the majority of studies provide annual rates of
294 emergence, which can hide the phenomena of massive seasonal emergence and the extent of
295 aquatic insect biomass at peak emergence times.

296 A central point regarding the distribution of aquatic insects in the landscape is the influence
297 of aquatic elements acting as a source of production and emergence. Ephemeroptera, Plecoptera,
298 Trichoptera, Odonata and Megaloptera abundances tend to decrease exponentially with distance
299 from the aquatic source (Carlson et al., 2016; Muehlbauer et al., 2014; Raitif et al., 2022) depending

300 on the species (Fig. 2). The flight ability of Ephemeroptera, Plecoptera and Trichoptera species
301 greatly varies, and some of them appear to be able to fly several kilometres from their emergence
302 source (Peredo Arce et al., 2021). However, Diptera are the main source of biomass linked to
303 emerging aquatic insects (Progar and Moldenke, 2009; Salvarina et al., 2017). More than any other
304 group of aquatic flying insects, they are a highly diverse order that can dominate biomass production
305 (Dijkstra et al., 2014). Nearly one-third of all flies (roughly 46,000 species) have some developmental
306 connection with an aquatic environment (Adler and Courtney, 2019), notably Diptera families with
307 aquatic larvae such as Chironomidae, Culicidae and some Syrphidae. Diptera fluxes can exceed the
308 fluxes of other aquatic insect orders, both in biomass and in dispersal distances (Fig. 2), but dispersal
309 data on these taxonomic groups are rarer.

310 Most of aquatic insects (e.g., Ephemeroptera, Plecoptera, Trichoptera, Megaloptera or
311 Odonata) belong to semivoltine or univoltine species that take a year or more to complete their life
312 cycle. They reproduce once a year, and winged adults have a marked seasonal pattern of emergence,
313 mostly in spring in the northern temperate hemisphere. Conversely, Diptera include multivoltine
314 species, and the phenology of their life cycle is less predictable (Salvarina et al., 2017), including
315 several emergence episodes throughout the year (Corbet, 1964; Pinder, 1986). Their larval
316 development depends on environmental conditions (e.g., temperature) and can last a few days to
317 several years for some species (Courtney and Cranston, 2015; Oliver, 1971). It can only take 2 to 3
318 days from egg hatching to imago emergence for some species of Culicidae and Chironomidae well
319 represented in temperate regions (Sarwar, 2020). A consequence of the presence of multivoltine
320 aquatic insect species is that their distribution in landscapes does not necessarily require permanent
321 aquatic ecosystems throughout the year. Some Diptera females need a small surface of temporary
322 water to lay their eggs, and for the resulting imagoes to emerge (Knox et al., 2010). This ability to
323 evolve in environments where water bodies are temporary is also supported by a good capacity of
324 the eggs and the various larval stages to withstand periods of drought (Lancaster et al., 2008;
325 Williams, 1996). This also questions our ability to correctly identify and list the aquatic elements of

326 the waterscape required to understand aquatic-terrestrial interactions in the landscape (Gerber et
327 al., 2022a).

328

329 **How taking into account emerging fluxes of aquatic insects can change the perception of a**
330 **waterscape in a landscape.**

331 When considering permanent and temporary aquatic habitats and the aerial dispersal of various
332 insect species from aquatic to terrestrial ecosystems, the influence of the waterscape on the
333 landscape and their overlap can be much greater. To illustrate this point, we simulated the expansion
334 of the waterscape in an agricultural landscape located in the Loire Valley, France.¹The Loire is the
335 largest river in France (1,012 km), draining a basin of 117,000 km² (Fig. 3. A.), from mountain streams
336 to foothills and large lowland rivers. The total length of the river network is estimated to be 107,000
337 km, and many alluvial plains are regularly flooded in the downstream part of the catchment. An
338 agricultural area of nearly 32,600 hectares with both permanent and temporary water body surfaces
339 (flood zones) has been mapped (Fig. 3. B). Temporary water bodies are found in areas of high
340 flooding probability with a return time of 10 years ([https://www.data.gouv.fr/fr/datasets/zone-](https://www.data.gouv.fr/fr/datasets/zone-inondable-de-la-loire-au-1-25000-issue-du-ppri-30383141)
341 [inondable-de-la-loire-au-1-25000-issue-du-ppri-30383141](https://www.data.gouv.fr/fr/datasets/zone-inondable-de-la-loire-au-1-25000-issue-du-ppri-30383141)). We applied buffers of various sizes from
342 permanent and temporary waterbodies to this map to simulate the spatial coverage of various
343 aquatic insect orders (Fig. 3. C). According to current knowledge on the dispersal abilities of winged
344 adults in agricultural areas for Ephemeroptera, Plecoptera and Trichoptera (Gerber et al., 2023b),
345 and for Chironomidae (Raitif et al., 2022), we estimated the distances at which 10% of the total
346 emerging biomass occur, *i.e.* 6.5 m for Ephemeroptera, 109 m for Plecoptera, 304 m for Trichoptera
347 and 66 m for Chironomids (Fig. 2). Considering the insect fluxes only originating from permanent
348 water bodies (*i.e.*, using a buffer zone around the permanent water bodies), the proportion of
349 waterscape in the landscape became non-negligible, *i.e.*, 13.96%, 21.53% and 40.5% for
350 Ephemeroptera, Plecoptera and Trichoptera, respectively. Considering the insect fluxes from

351 permanent and temporary water bodies (i.e., using a buffer zone around the permanent and
352 temporary water bodies), the proportion of waterscape in the landscape represented 38.56% for
353 Chironomidae. Interestingly, by considering the potential spatial aquatic signature on the basis of the
354 presence of Trichoptera and Diptera such as Chironomidae, the waterscape reached more than 1/3
355 of the landscape. These results illustrate how taking into account aquatic signatures and fluxes
356 associated with permanent and temporary water bodies on the basis of aquatic insects can modify
357 landscape perception.

358

359

360 **Conclusions and perspectives**

361 Freshwater ecosystems are elements of the landscape mosaics. Considered as a whole, they
362 define the waterscape on a territory. The waterscape is dynamic since its spatial extent and
363 imbrication in the landscape evolves according to the seasons, in connection with flood and drought
364 cycles. The production of aquatic insects and their fluxes towards terrestrial ecosystems contribute
365 to broadening the influence of the waterscape on the landscape. In a meta-ecosystem perspective,
366 these aquatic subsidies play a role in the functioning of adjacent terrestrial ecosystems, notably at
367 certain periods of the year. Fluxes of aquatic insects represent freshwater-derived nutrients in
368 terrestrial ecosystems that may ultimately contribute to many ecosystem services such as soil
369 fertilisation or the support of trophic chains (Raitif et al., 2019). Winged aquatic insects are part of
370 the diet of many vertebrates (Sabo and Power, 2002) such as birds and bats (Baxter et al., 2005;
371 Twining et al., 2018), and of terrestrial arthropods such as web-building or wolf spiders (Collier et al.,
372 2002; Kato et al., 2003; Stenroth et al., 2015). They support active natural enemies of crop pests
373 (Henschel et al., 2001). Pollination of terrestrial plants can also be facilitated by aquatic insects
374 visiting flowers (Murail et al., 2024). Yet, the multiple roles of aquatic insects in supporting vital
375 functions in terrestrial ecosystems are poorly known to date and would deserve quantification.

376 Looking beyond the overlooked ecosystem services to agriculture associated with aquatic insects, a
377 global perspective on the role of freshwater ecosystems in the landscape is needed, and we think
378 that the waterscape and meta-ecosystem frameworks could help to refine the multi-functionality of
379 agricultural landscapes. However, only 2 publications mentioning meta-ecosystems and waterscapes
380 have been referenced to date (Heino et al., 2021; Kramer et al., 2023). This does not mean that these
381 fields of research are not related, as they are recently theorized concepts. Studies on meta-
382 ecosystems, the characterisation of ecological fluxes and the associated ecological processes show
383 that in reality landscapes and waterscapes are more intertwined than superimposed. In this sense,
384 meta-ecosystems bring a major contribution to unify the waterscape and landscape concepts.

385 Depending on aquatic insects and their fluxes (e.g., dispersal, use of temporary water
386 bodies), the portion representing the waterscape is far from negligible in the landscape. This is
387 particularly true when considering orders such as Trichoptera and Diptera. While literature is
388 available about Chironomidae, a whole field of research is open about other aquatic Diptera groups,
389 notably to better characterise biomass production from temporary water bodies, their fluxes in
390 landscapes and their ecology. Aquatic insects such as Diptera may be better able to adapt to a
391 changing climate than others (Adler and Courtney, 2019). Quantifying emergence from temporary
392 water bodies could also be used to help understand how the aquatic signature may be influenced by
393 a changing climate.

394 In view of the current global collapse of terrestrial insect populations and climate change
395 threats on perennial waterbodies (Messenger et al., 2021), we call for an urgent research effort to
396 include the temporal dimension of waterscapes into landscape models, to estimate the fluxes of
397 insects emerging from all kinds of aquatic ecosystems, and to quantify their role in agricultural
398 landscapes.

399

400

401 **Acknowledgments**

402 This study was funded by the French National Research Agency (ANR), STRANGE project (ANR-23-
403 CE03-0006).

404

405 **Declaration of interests**

406 The authors declare no conflict of interests.

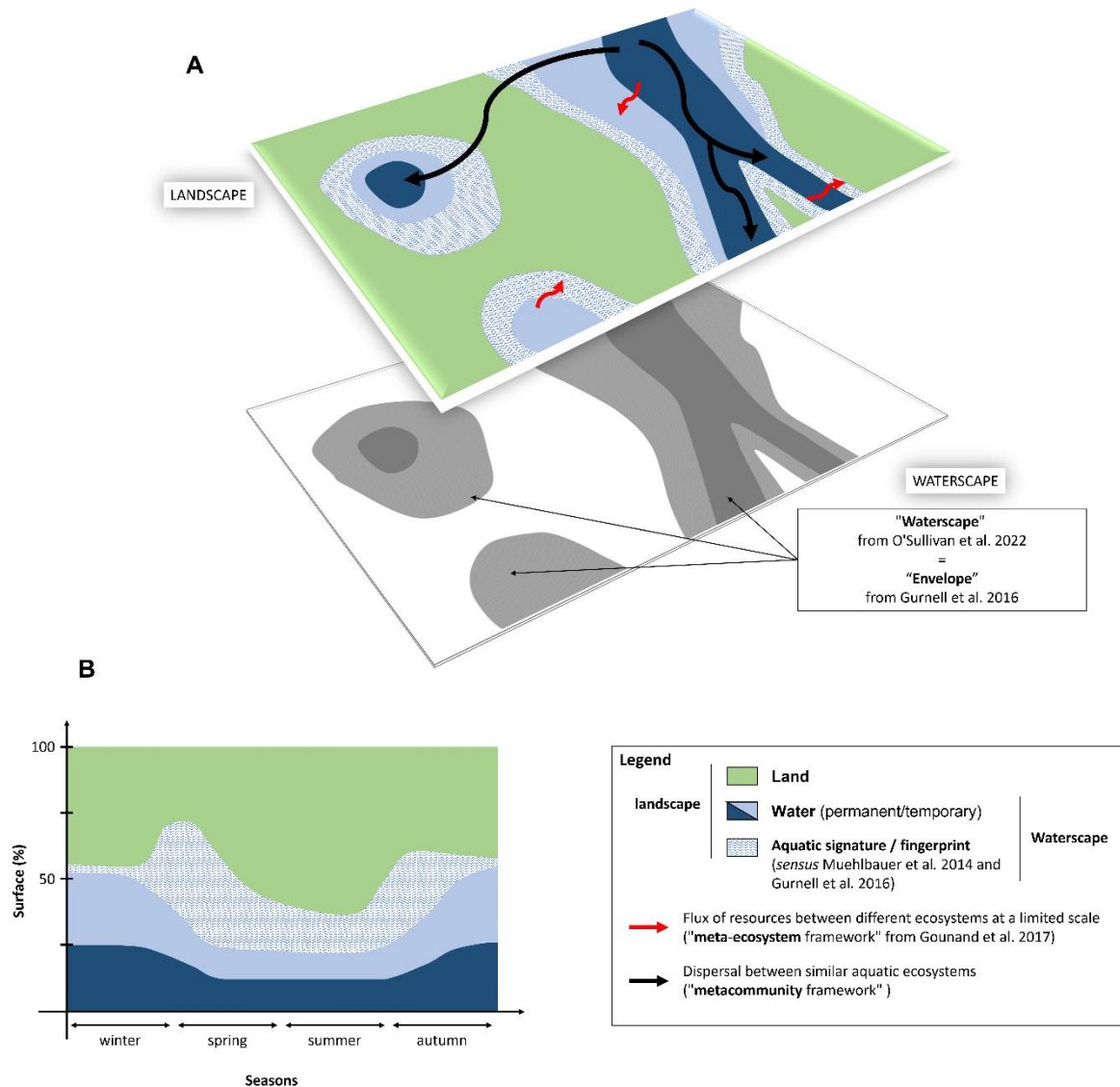
407

408 **CRediT authorship contribution statement**

409 **Bergerot Benjamin:** Writing – original draft, Visualization, Resources, Methodology, Investigation,
410 Data curation, Conceptualization. **Piscart Christophe:** Writing – review & editing, Validation,
411 Conceptualization. **Roussel Jean-Marc:** Writing – review & editing, Validation, Conceptualization.

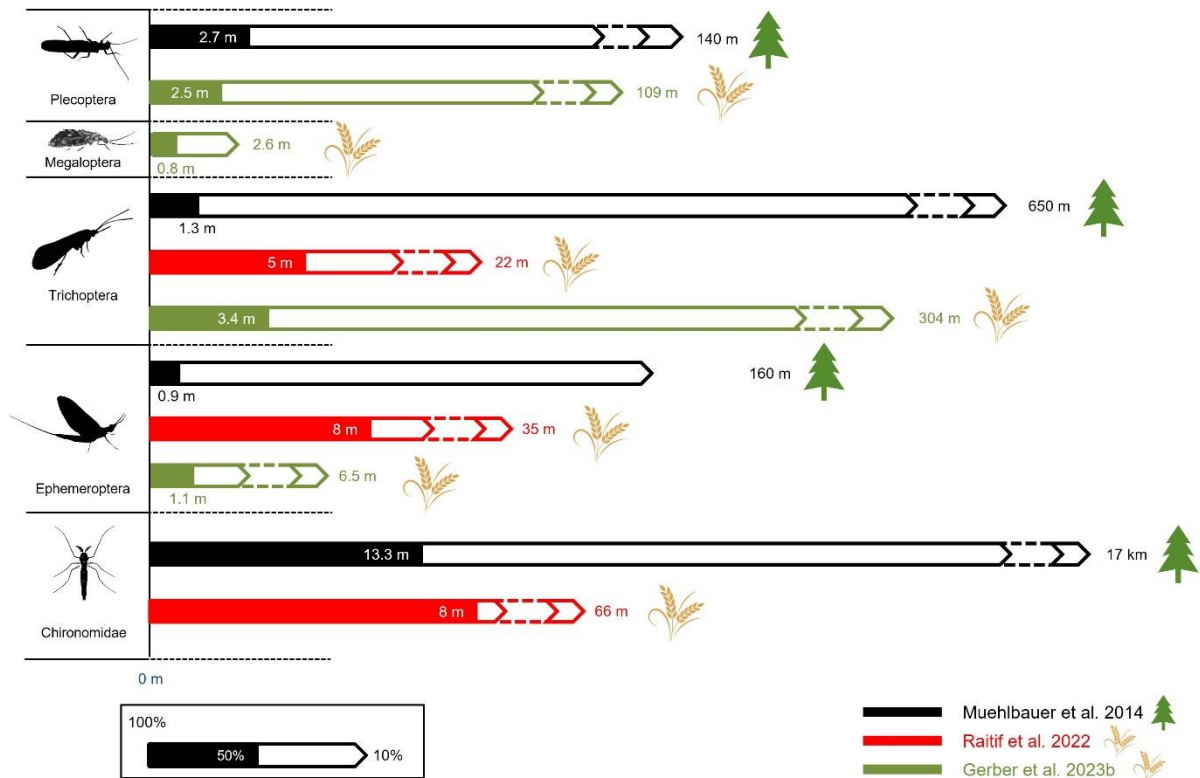
412

413



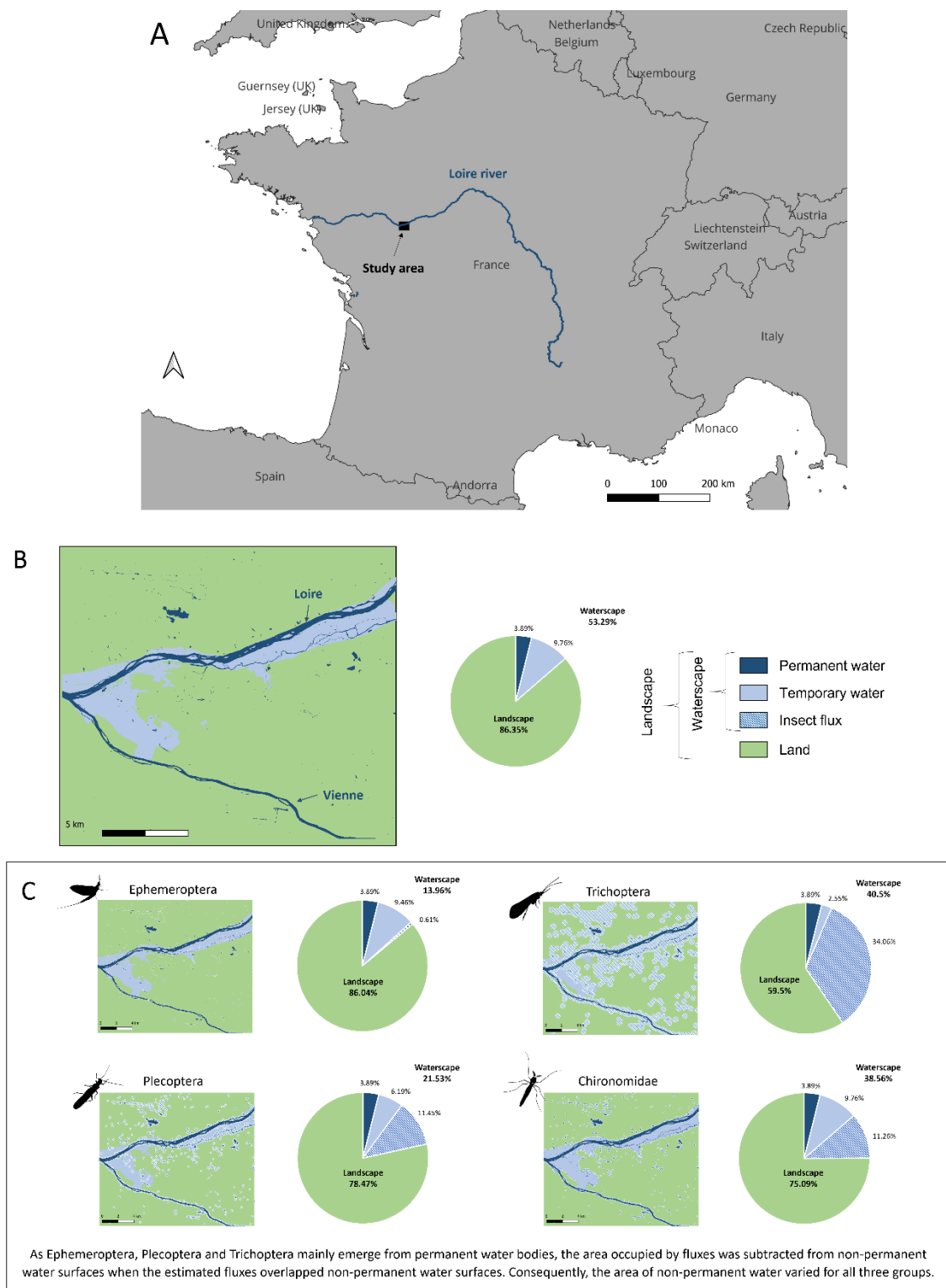
415

416 Fig. 1. A. Schematic spatial representation of a waterscape (grey) within a landscape (colour). Blue
 417 and light blue, permanent (e.g., streams) and temporary (e.g., alluvial plains) aquatic elements,
 418 respectively; hatched blue, extension of the aquatic ecosystems through the emerging aquatic insect
 419 fluxes, or aquatic signatures (Gurnell et al., 2016; Muehlbauer et al., 2014). Arrows, transfer of
 420 aquatic subsidies toward terrestrial ecosystems (red) or dispersal of aquatic organisms among
 421 aquatic ecosystems (black). B. Theoretical temporal evolution of the surface (%) occupied by a
 422 waterscape (i.e., permanent water bodies, temporary water bodies, and aquatic insect signature)
 423 within a landscape in a temperate northern-hemisphere environment.



424

425 Fig. 2. Diagram summarising the distances to which 50% and 10% of the abundances of aquatic
 426 insects of various taxonomic groups have been observed from their emergence sources (i.e., stream).
 427 Black, red and green arrows, distances extracted from the meta-analyses of Muehlbauer et al. (2014)
 428 in forest environments, and Raitif et al. (2022) and Gerber et al. (2023) in agricultural environments,
 429 respectively (Gerber et al., 2023b; Muehlbauer et al., 2014; Raitif et al., 2022). For ease of reading,
 430 the scale representing distances on the horizontal axis is not proportional. Dotted lines on each
 431 arrow, distance breakpoints.



432

433 Fig. 3. A. The Loire River (blue), France. B. An area of nearly 32,600 hectares with both permanent
 434 (dark blue) and temporary (light blue) water body surfaces. C. Maps simulating the spatial coverage
 435 of various aquatic insect orders according to current knowledge on the dispersal abilities of winged

436 adults in agricultural areas for Ephemeroptera, Plecoptera, Trichoptera and Chironomidae (see text
437 for details). The proportion of waterscape (blue) in the landscape (green) are shown in the pie charts.

438

439

440 **References**

441

442 Adler, P.H., Courtney, G.W., 2019. Ecological and societal services of aquatic diptera. *Insects* 10, 70.

443 <https://doi.org/10.3390/insects10030070>

444 Aijaz, A., Akhter, M., 2020. From building dams to fetching water: Scales of politicization in the Indus

445 basin. *Water* 12, 1351. <https://doi.org/10.3390/w12051351>

446 Arnold, T.C., 1996. Theory, history, and the Western waterscape: The market culture thesis. *Journal*

447 *of the Southwest* 38, 215–240.

448 Barmantlo, S.H., Schrama, M., de Snoo, G.R., van Bodegom, P.M., van Nieuwenhuijzen, A., Vijver,

449 M.G., 2021. Experimental evidence for neonicotinoid driven decline in aquatic emerging

450 insects. *Proceedings of the National Academy of Sciences* 118, e2105692118.

451 <https://doi.org/10.1073/pnas.2105692118>

452 Barouillet, C., González-Trujillo, J.D., Geist, J., Gíslason, G.M., Grossart, H.-P., Irvine, K., Jähnig, S.C.,

453 Boon, P.J., 2024. Freshwater conservation: Lost in limnology? *Aquatic Conservation: Marine*

454 *and Freshwater Ecosystems* 34, e4049. <https://doi.org/10.1002/aqc.4049>

455 Bartrons, M., Papeş, M., Diebel, M.W., Gratton, C., Vander Zanden, M.J., 2013. Regional-level inputs

456 of emergent aquatic insects from water to land. *Ecosystems* 16, 1353–1363.

457 <https://doi.org/10.1007/s10021-013-9688-6>

458 Baxter, C.V., Fausch, K.D., Saunders, W.C., 2005. Tangled webs: reciprocal flows of invertebrate prey

459 link streams and riparian zones. *Freshwater Biology* 50, 201–220.

460 <https://doi.org/10.1111/j.1365-2427.2004.01328.x>

461 Berzins, L.L., Mazer, A.K., Morrissey, C.A., Clark, R.G., 2021. Pre-fledging quality and recruitment in an
462 aerial insectivore reflect dynamics of insects, wetlands and climate. *Oecologia* 196, 89–100.
463 <https://doi.org/10.1007/s00442-021-04918-7>

464 Biggs, J., von Fumetti, S., Kelly-Quinn, M., 2017. The importance of small waterbodies for biodiversity
465 and ecosystem services: implications for policy makers. *Hydrobiologia* 793, 3–39.
466 <https://doi.org/10.1007/s10750-016-3007-0>

467 Borthagaray, A.I., Cunillera-Montcusí, D., Bou, J., Biggs, J., Arim, M., 2023. Pondscape or waterscape?
468 The effect on the diversity of dispersal along different freshwater ecosystems. *Hydrobiologia*
469 850, 3211–3223. <https://doi.org/10.1007/s10750-022-05123-0>

470 Both, C., Bouwhuis, S., Lessells, C.M., Visser, M.E., 2006. Climate change and population declines in a
471 long-distance migratory bird. *Nature* 441, 81–83. <https://doi.org/10.1038/nature04539>

472 Bundschuh, M., Pietz, S., Roodt, A.P., Kraus, J.M., 2022. Contaminant fluxes across ecosystems
473 mediated by aquatic insects. *Current Opinion in Insect Science* 50, 100885.
474 <https://doi.org/10.1016/j.cois.2022.100885>

475 Carlson, P.E., McKie, B.G., Sandin, L., Johnson, R.K., 2016. Strong land-use effects on the dispersal
476 patterns of adult stream insects: implications for transfers of aquatic subsidies to terrestrial
477 consumers. *Freshwater Biology* 61, 848–861. <https://doi.org/10.1111/fwb.12745>

478 Casas-Ruiz, J.P., Bodmer, P., Bona, K.A., Butman, D., Couturier, M., Emilson, E.J.S., Finlay, K., Genet,
479 H., Hayes, D., Karlsson, J., Paré, D., Peng, C., Striegl, R., Webb, J., Wei, X., Ziegler, S.E., del
480 Giorgio, P.A., 2023. Integrating terrestrial and aquatic ecosystems to constrain estimates of
481 land-atmosphere carbon exchange. *Nat Commun* 14, 1571. [https://doi.org/10.1038/s41467-](https://doi.org/10.1038/s41467-023-37232-2)
482 [023-37232-2](https://doi.org/10.1038/s41467-023-37232-2)

483 Cazzolla Gatti, R., 2016. Freshwater biodiversity: a review of local and global threats. *International*
484 *Journal of Environmental Studies* 73, 887–904.
485 <https://doi.org/10.1080/00207233.2016.1204133>

486 Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction
487 signaled by vertebrate population losses and declines. *Proceedings of the National Academy*
488 *of Sciences* 114, E6089–E6096. <https://doi.org/10.1073/pnas.1704949114>

489 Church, M., 2006. Bed material transport and the morphology of alluvial river channels. *Annual*
490 *Review of Earth and Planetary Sciences* 34, 325–354.
491 <https://doi.org/10.1146/annurev.earth.33.092203.122721>

492 Clobert, J., Danchin, E., Dhont, A.A., Nichols, J.D., 2001. *Dispersal*, Oxford University Press. ed. Oxford
493 University Press, Oxford.

494 Collier, K.J., Bury, S., Gibbs, M., 2002. A stable isotope study of linkages between stream and
495 terrestrial food webs through spider predation. *Freshwater Biology* 47, 1651–1659.
496 <https://doi.org/10.1046/j.1365-2427.2002.00903.x>

497 Condon, L.E., Markovich, K.H., Kelleher, C.A., McDonnell, J.J., Ferguson, G., McIntosh, J.C., 2020.
498 Where is the bottom of a watershed? *Water Resources Research* 56, e2019WR026010.
499 <https://doi.org/10.1029/2019WR026010>

500 Corbet, P.S., 1964. Temporal patterns of emergence in aquatic insects. *The Canadian Entomologist*
501 96, 264–279. <https://doi.org/10.4039/Ent96264-1>

502 Courtney, G.W., Cranston, P.S., 2015. Order Diptera, in: Thorp, J.H., Rogers, D.C. (Eds.), *Thorp and*
503 *Covich's Freshwater Invertebrates (Fourth Edition)*. Academic Press, Boston, pp. 1043–1058.
504 <https://doi.org/10.1016/B978-0-12-385026-3.00040-1>

505 Cunillera-Montcusí, D., Bou, J., Mehner, T., Brucet, S., Arim, M., Borthagaray, A.I., 2023. The
506 European freshwater landscape and hotspot areas of mass effects and regional connectivity.
507 *Diversity and Distributions* 29, 997–1008. <https://doi.org/10.1111/ddi.13711>

508 Daskalova, G.N., Myers-Smith, I.H., Godlee, J.L., 2020. Rare and common vertebrates span a wide
509 spectrum of population trends. *Nat Commun* 11, 4394. [https://doi.org/10.1038/s41467-020-](https://doi.org/10.1038/s41467-020-17779-0)
510 [17779-0](https://doi.org/10.1038/s41467-020-17779-0)

511 Datry, T., Larned, S.T., Fritz, K.M., Bogan, M.T., Wood, P.J., Meyer, E.I., Santos, A.N., 2014. Broad-
512 scale patterns of invertebrate richness and community composition in temporary rivers:
513 effects of flow intermittence. *Ecography* 37, 94–104. <https://doi.org/10.1111/j.1600->
514 0587.2013.00287.x

515 Datry, T., Truchy, A., Olden, J.D., Busch, M.H., Stubbington, R., Dodds, W.K., Zipper, S., Yu, S.,
516 Messenger, M.L., Tonkin, J.D., Kaiser, K.E., Hammond, J.C., Moody, E.K., Burrows, R.M.,
517 Sarremejane, R., DelVecchia, A.G., Fork, M.L., Little, C.J., Walker, R.H., Walters, A.W., Allen,
518 D., 2023. Causes, responses, and implications of anthropogenic versus natural flow
519 intermittence in river networks. *BioScience* 73, 9–22. <https://doi.org/10.1093/biosci/biac098>

520 Dijkstra, K.-D.B., Monaghan, M.T., Pauls, S.U., 2014. Freshwater biodiversity and aquatic insect
521 diversification. *Annu Rev Entomol* 59, 143–163. <https://doi.org/10.1146/annurev-ento->
522 011613-161958

523 Donnelly, A., Caffarra, A., O’Neill, B.F., 2011. A review of climate-driven mismatches between
524 interdependent phenophases in terrestrial and aquatic ecosystems. *Int J Biometeorol* 55,
525 805–817. <https://doi.org/10.1007/s00484-011-0426-5>

526 Dreiseitl, H., Grau, D., Ludwig, K.H.C. (Eds.), 2001. *Waterscapes: Planning, building and designing with*
527 *water*, 1st edition. ed. Birkhäuser, Basel.

528 Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman,
529 R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater
530 biodiversity: importance, threats, status and conservation challenges. *Biol Rev Camb Philos*
531 *Soc* 81, 163–182. <https://doi.org/10.1017/S1464793105006950>

532 Fausch, K.D., Torgersen, C.E., Baxter, C.V., Li, H.W., 2002. Landscapes to Riverscapes: Bridging the
533 Gap between Research and Conservation of Stream Fishes: A Continuous View of the River is
534 Needed to Understand How Processes Interacting among Scales Set the Context for Stream
535 Fishes and Their Habitat. *BioScience* 52, 483–498. <https://doi.org/10.1641/0006->
536 3568(2002)052[0483:LTRBTG]2.0.CO;2

537 Forrest, J.R., 2016. Complex responses of insect phenology to climate change. *Current Opinion in*
538 *Insect Science, Global change biology * Molecular physiology* 17, 49–54.
539 <https://doi.org/10.1016/j.cois.2016.07.002>

540 Gerber, R., Bergerot, B., Georges, R., Roussel, J.-M., Piscart, C., 2022a. The role of hydrographic
541 mapping in the study of emerging aquatic insects on the landscape scale. *Water* 14, 3019.
542 <https://doi.org/10.3390/w14193019>

543 Gerber, R., Cabon, L., Piscart, C., Roussel, J.-M., Bergerot, B., 2022b. Body stores of emergent aquatic
544 insects are associated with body size, sex, swarming behaviour, and dispersal strategies.
545 *Freshwater Biology* 67, 2161–2175.

546 Gerber, R., Piscart, C., Roussel, J.-M., Bergerot, B., 2023a. Morphology-based classification of the
547 flying capacities of aquatic insects: A first attempt. *Current Zoology* zoad047.
548 <https://doi.org/10.1093/cz/zoad047>

549 Gerber, R., Piscart, C., Roussel, J.-M., Georges, R., Houet, T., Royer, J., Bergerot, B., 2023b. Can
550 landscape models predict the distribution of aquatic insects dispersing across agricultural
551 areas? *Landsc. Ecol.* 38, 2917–2929.

552 Gerraty, F.D., Carroll, T., Williams, S., Isadore, M., 2024. Recovering predators link aquatic and
553 terrestrial ecosystems: River otters subsidize coyotes with carrion. *Ecology and Evolution* 14,
554 e11444. <https://doi.org/10.1002/ece3.11444>

555 Gounand, I., Harvey, E., Little, C.J., Altermatt, F., 2018. Meta-ecosystems 2.0: Rooting the theory into
556 the field. *Trends Ecol Evol* 33, 36–46. <https://doi.org/10.1016/j.tree.2017.10.006>

557 Grass, I., Loos, J., Baensch, S., Batáry, P., Librán-Embid, F., Ficiciyan, A., Klaus, F., Riechers, M., Rosa,
558 J., Tiede, J., Udy, K., Westphal, C., Wurz, A., Tschardtke, T., 2019. Land-sharing/-sparing
559 connectivity landscapes for ecosystem services and biodiversity conservation. *People and*
560 *Nature* 1, 262–272. <https://doi.org/10.1002/pan3.21>

561 Gratton, C., Donaldson, J., Zanden, M.J.V., 2008. Ecosystem linkages between lakes and the
562 surrounding terrestrial landscape in Northeast Iceland. *Ecosystems* 11, 764–774.
563 <https://doi.org/10.1007/s10021-008-9158-8>

564 Gratton, C., Vander Zanden, M.J., 2009. Flux of Aquatic Insect Productivity to Land: Comparison of
565 Lentic and Lotic Ecosystems. *Ecology* 90, 2689–2699. <https://doi.org/10.1890/08-1546.1>

566 Guenet, B., Danger, M., Abbadie, L., Lacroix, G., 2010. Priming effect: bridging the gap between
567 terrestrial and aquatic ecology. *Ecology* 91, 2850–2861. <https://doi.org/10.1890/09-1968.1>

568 Gurnell, M., Bertoldi, W., Tockner, K., Wharton, G., Zolezzi, G., 2016. How large is a river?
569 Conceptualizing river landscape signatures and envelopes in four dimensions. Wiley
570 *Interdisciplinary Reviews: Water* n/a-n/a. <https://doi.org/10.1002/wat2.1143>

571 Heino, J., Alahuhta, J., Bini, L.M., Cai, Y., Heiskanen, A.-S., Hellsten, S., Kortelainen, P., Kotamäki, N.,
572 Tolonen, K.T., Vihervaara, P., Vilmi, A., Angeler, D.G., 2021. Lakes in the era of global change:
573 moving beyond single-lake thinking in maintaining biodiversity and ecosystem services.
574 *Biological Reviews* 96, 89–106. <https://doi.org/10.1111/brv.12647>

575 Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S., Bini, L.M., 2015. Metacommunity
576 organisation, spatial extent and dispersal in aquatic systems: patterns, processes and
577 prospects. *Freshw Biol* 60, 845–869. <https://doi.org/10.1111/fwb.12533>

578 Helfield, J.M., Naiman, R.J., 2001. Effects of salmon-derived nitrogen on riparian forest growth and
579 implications for stream productivity. *Ecology* 82, 2403–2409. [https://doi.org/10.1890/0012-9658\(2001\)082\[2403:EOSDNO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[2403:EOSDNO]2.0.CO;2)

581 Henschel, J.R., Mahsberg, D., Stumpf, H., 2001. Allochthonous aquatic insects increase predation and
582 decrease herbivory in river shore food webs. *Oikos* 93, 429–438.
583 <https://doi.org/10.1034/j.1600-0706.2001.930308.x>

584 Herzog, T.R., 1985. A cognitive analysis of preference for waterscapes. *Journal of Environmental*
585 *Psychology* 5, 225–241. [https://doi.org/10.1016/S0272-4944\(85\)80024-4](https://doi.org/10.1016/S0272-4944(85)80024-4)

586 Holling, C.S., 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological*
587 *Monographs* 62, 447–502. <https://doi.org/10.2307/2937313>

588 Hundley, N., 1987. California's original waterscape: Harmony & manipulation. *California History* 66,
589 2–11. <https://doi.org/10.2307/25158424>

590 Karpouzoglou, T., Vij, S., 2017. Waterscape: A perspective for understanding the contested
591 geography of water. *WIREs Water* 4, e1210. <https://doi.org/10.1002/wat2.1210>

592 Kato, C., Iwata, T., Nakano, S., Kishi, D., 2003. Dynamics of aquatic insect flux affects distribution of
593 riparian web-building spiders. *Oikos* 103, 113–120. [https://doi.org/10.1034/j.1600-](https://doi.org/10.1034/j.1600-0706.2003.12477.x)
594 [0706.2003.12477.x](https://doi.org/10.1034/j.1600-0706.2003.12477.x)

595 Kemerink-Seyoum, J.S., Chinguno, N.L.T., Seyoum, S.D., Ahlers, R., Bolding, J.A., Zaag, P. van der,
596 2017. Jumping the water queue: changing waterscapes under water reform processes in
597 rural Zimbabwe. *Water SA* 43, 423–432. <https://doi.org/10.4314/wsa.v43i3.07>

598 Kharouba, H.M., Wolkovich, E.M., 2020. Disconnects between ecological theory and data in
599 phenological mismatch research. *Nat. Clim. Chang.* 10, 406–415.
600 <https://doi.org/10.1038/s41558-020-0752-x>

601 Knox, T.B., Nguyen, Y.T., Vu, N.S., Kay, B.H., Ryan, P.A., 2010. Quantitative relationships between
602 immature and emergent adult *Aedes aegypti* (Diptera: Culicidae) populations in water
603 storage container habitats. *Journal of Medical Entomology* 47, 748–758.
604 <https://doi.org/10.1093/jmedent/47.5.748>

605 Kramer, L., Troost, T.A., Janssen, A.B.G., Brederveld, R.J., van Gerven, L.P.A., van Wijk, D., Mooij,
606 W.M., Teurlinx, S., 2023. Connecting lakes: Modeling flows and interactions of organisms
607 and matter throughout the waterscape. *Environmental Modelling & Software* 167, 105765.
608 <https://doi.org/10.1016/j.envsoft.2023.105765>

609 Kumar, R., Singh, C.K., Kamesh, Misra, S., Singh, B.P., Bhardwaj, A.K., Chandra, K.K., 2024. Chapter 16
610 - Water biodiversity: ecosystem services, threats, and conservation, in: Singh, K., Ribeiro,

611 M.C., Calicioglu, Ö. (Eds.), *Biodiversity and Bioeconomy*. Elsevier, pp. 347–380.
612 <https://doi.org/10.1016/B978-0-323-95482-2.00016-X>

613 Lancaster, J., Briers, R.A., Macadam, C., Danks, H., Bradley, T., Johansson, F., Kohler, S., Boulton, A.,
614 Death, R., Lytle, D., Diehl, S., Downes, B.J., Marden, J., Harrison, S., Hughes, J., Ribera, I.,
615 2008. *Aquatic insects: Challenges to populations*. Proceedings of the Royal Entomological
616 Society's 24th Symposium. CABI Publishing, Wallingford, Oxfordshire ; Cambridge, MA.

617 Leung, B., Hargreaves, A.L., Greenberg, D.A., McGill, B., Dornelas, M., Freeman, R., 2020. Clustered
618 versus catastrophic global vertebrate declines. *Nature* 588, 267–271.
619 <https://doi.org/10.1038/s41586-020-2920-6>

620 Li, X., Tsigaris, P., 2024. The global value of freshwater lakes. *Ecology Letters* 27, e14388.
621 <https://doi.org/10.1111/ele.14388>

622 Lim, J., Jern, N.W., Chew, K.L., Kallianpur, V., 2002. A model for decentralised grey wastewater
623 treatment system in Singapore public housing. *Water Science and Technology* 46, 63–69.
624 <https://doi.org/10.2166/wst.2002.0206>

625 Little, C.J., Rizzuto, M., Luhring, T.M., Monk, J.D., Nowicki, R., Paseka, R.E., Stegen, J., Symons, C.C.,
626 Taub, F.B., Yen, J., 2020. Filling the information gap in meta-ecosystem ecology. *EcoEvoRxiv*.

627 Little, C.J., Rizzuto, M., Luhring, T.M., Monk, J.D., Nowicki, R.J., Paseka, R.E., Stegen, J.C., Symons,
628 C.C., Taub, F.B., Yen, J.D.L., 2022. Movement with meaning: Integrating information into
629 meta-ecology. *Oikos* 2022, e08892. <https://doi.org/10.1111/oik.08892>

630 Loreau, M., Mouquet, N., Holt, R.D., 2003. Meta-ecosystems: A theoretical framework for a spatial
631 ecosystem ecology. *Ecology Letters* 6, 673–679. [https://doi.org/10.1046/j.1461-](https://doi.org/10.1046/j.1461-0248.2003.00483.x)
632 [0248.2003.00483.x](https://doi.org/10.1046/j.1461-0248.2003.00483.x)

633 MacKenzie, R., 2005. Spatial and temporal patterns in insect emergence from a Southern Maine salt
634 marsh. *amid* 153, 257–269. [https://doi.org/10.1674/0003-](https://doi.org/10.1674/0003-0031(2005)153[0257:SATPII]2.0.CO;2)
635 [0031\(2005\)153\[0257:SATPII\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2005)153[0257:SATPII]2.0.CO;2)

636 MacKenzie, R.A., Kaster, J.L., 2004. Temporal and spatial patterns of insect emergence from a Lake
637 Michigan coastal wetland. *Wetlands* 24, 688–700. [https://doi.org/10.1672/0277-](https://doi.org/10.1672/0277-5212(2004)024[0688:TASPOI]2.0.CO;2)
638 [5212\(2004\)024\[0688:TASPOI\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2004)024[0688:TASPOI]2.0.CO;2)

639 Manning, D.W.P., Sullivan, S.M.P., 2021. Conservation across aquatic-terrestrial boundaries: Linking
640 continental-scale water quality to emergent aquatic insects and declining aerial insectivorous
641 birds. *Front. Ecol. Evol.* 9. <https://doi.org/10.3389/fevo.2021.633160>

642 McPhillips, S., Meier, A., Slim, S., Bradbury, J., 2019. The Jawz Valley. Reconstructing an Ottoman
643 ‘waterscape’ in Mount Lebanon. *Levant* 51, 201–218.
644 <https://doi.org/10.1080/00758914.2020.1845478>

645 Messenger, M.L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., Tockner, K.,
646 Trautmann, T., Watt, C., Datry, T., 2021. Global prevalence of non-perennial rivers and
647 streams. *Nature* 594, 391–397. <https://doi.org/10.1038/s41586-021-03565-5>

648 Meybeck, M., 2004. The global change of continental aquatic systems: Dominant impacts of human
649 activities. *Water Science and Technology* 49, 73–83. <https://doi.org/10.2166/wst.2004.0420>

650 Miller, S.A., Faunce, K.E., Barber, L.B., Fleck, J.A., Burns, D.W., Jasmann, J.R., Hladik, M.L., 2024.
651 Factors contributing to pesticide contamination in riverine systems: The role of wastewater
652 and landscape sources. *Science of The Total Environment* 954, 174939.
653 <https://doi.org/10.1016/j.scitotenv.2024.174939>

654 Morris, W.F., Pfister, C.A., Tuljapurkar, S., Haridas, C.V., Boggs, C.L., Boyce, M.S., Bruna, E.M., Church,
655 D.R., Coulson, T., Doak, D.F., Forsyth, S., Gaillard, J.-M., Horvitz, C.C., Kalisz, S., Kendall, B.E.,
656 Knight, T.M., Lee, C.T., Menges, E.S., 2008. Longevity can buffer plant and animal populations
657 against changing climatic variability. *Ecology* 89, 19–25. <https://doi.org/10.1890/07-0774.1>

658 Muehlbauer, J.D., Collins, S.F., Doyle, M.W., Tockner, K., 2014. How wide is a stream? Spatial extent
659 of the potential “stream signature” in terrestrial food webs using meta-analysis. *Ecology* 95,
660 44–55. <https://doi.org/10.1890/12-1628.1>

661 Murail, C., Baude, M., Bergerot, B., Geslin, B., Legay, N., Villalta, I., Greulich, S., 2024. From stream to
662 bloom: Exploring the potential role of aquatic insects for oollination in wetland
663 environments. *J. Appl. Entomol.* 0, 1–14. <https://doi.org/10.1111/jen.13359>

664 Naiman, R.J., Bilby, R.E., Schindler, D.E., Helfield, J.M., 2002. Pacific salmon, nutrients, and the
665 dynamics of freshwater and riparian ecosystems. *Ecosystems* 5, 399–417.
666 <https://doi.org/10.1007/s10021-001-0083-3>

667 Nakano, S., Murakami, M., 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial
668 and aquatic food webs. *Proceedings of the National Academy of Sciences* 98, 166–170.
669 <https://doi.org/10.1073/pnas.98.1.166>

670 Nash, L.N., Kratina, P., Recalde, F.C., Jones, J.I., Izzo, T., Romero, G.Q., 2023a. Tropical and temperate
671 differences in the trophic structure and aquatic prey use of riparian predators. *Ecology*
672 *Letters* 26, 2122–2134. <https://doi.org/10.1111/ele.14322>

673 Nash, L.N., Zorzetti, L.W., Antiqueira, P.A.P., Carbone, C., Romero, G.Q., Kratina, P., 2023b. Latitudinal
674 patterns of aquatic insect emergence driven by climate. *Global Ecology and Biogeography* 32,
675 1323–1335. <https://doi.org/10.1111/geb.13700>

676 Neset, A., 1998. Rowing in eden: Waterscapes in 19th century American art and literature. *American*
677 *Studies in Scandinavia* 30, 1–16. <https://doi.org/10.22439/asca.v30i1.1114>

678 Oliver, D.R., 1971. Life history of the Chironomidae. *Annual Review of Entomology* 16, 211–230.
679 <https://doi.org/10.1146/annurev.en.16.010171.001235>

680 O’Sullivan, A.M., Devito, K.J., D’Orangeville, L., Curry, R.A., 2022. The waterscape continuum concept:
681 Rethinking boundaries in ecosystems. *WIREs Water* 9, e1598.
682 <https://doi.org/10.1002/wat2.1598>

683 Palka, J.W., 2024. Ancestral Maya domesticated waterscapes, ecological aquaculture, and integrated
684 subsistence. *Ancient Mesoamerica* 35, 208–236.
685 <https://doi.org/10.1017/S0956536122000402>

686 Peredo Arce, A., Hörrén, T., Schletterer, M., Kail, J., 2021. How far can EPTs fly? A comparison of
687 empirical flying distances of riverine invertebrates and existing dispersal metrics. *Ecological*
688 *Indicators* 125, 107465. <https://doi.org/10.1016/j.ecolind.2021.107465>

689 Pérez-Méndez, N., Martínez-Eixarch, M., Llevat, R., Mateu, D., Marrero, H.J., Cid, N., Catala-Forner,
690 M., 2023. Enhanced diversity of aquatic macroinvertebrate predators and biological pest
691 control but reduced crop establishment in organic rice farming. *Agriculture, Ecosystems &*
692 *Environment* 357, 108691. <https://doi.org/10.1016/j.agee.2023.108691>

693 Pinder, L.C.V., 1986. Biology of freshwater Chironomidae. *Annual Review of Entomology* 31, 1–23.
694 <https://doi.org/10.1146/annurev.en.31.010186.000245>

695 Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web
696 ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and*
697 *Systematics* 28, 289–316. <https://doi.org/10.1146/annurev.ecolsys.28.1.289>

698 Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global
699 pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25, 345–353.
700 <https://doi.org/10.1016/j.tree.2010.01.007>

701 Pournelle, J., 1978. Redrawing the world’s waterscapes: “the next generation may see projects so
702 vast as to compete with nature.” *The UNESCO Courier* 2, 23–24.

703 Progar, R., Moldenke, A.R., 2009. Aquatic insect emergence from headwater streams flowing through
704 regeneration and mature forests in Western Oregon. *Journal of Freshwater Ecology* 24, 53–
705 66. <https://doi.org/10.1080/02705060.2009.9664265>

706 Raitif, J., Plantegenest, M., Agator, O., Piscart, C., Roussel, J.-M., 2018. Seasonal and spatial variations
707 of stream insect emergence in an intensive agricultural landscape. *Sci. Total Environ.* 644,
708 594–601. <https://doi.org/10.1016/j.scitotenv.2018.07.021>

709 Raitif, J., Plantegenest, M., Roussel, J.-M., 2019. From stream to land: Ecosystem services provided by
710 stream insects to agriculture. *Agriculture, Ecosystems & Environment* 270–271, 32–40.
711 <https://doi.org/10.1016/j.agee.2018.10.013>

712 Raitif, J., Roussel, J.-M., Olmos, M., Piscart, C., Plantegenest, M., 2022. Assessing spatial deposition of
713 aquatic subsidies by insects emerging from agricultural streams. *Sci. Total Environ.* 837,
714 155686. <https://doi.org/10.1016/j.scitotenv.2022.155686>

715 Raven, P.H., Wagner, D.L., 2021. Agricultural intensification and climate change are rapidly
716 decreasing insect biodiversity. *Proceedings of the National Academy of Sciences* 118,
717 e2002548117. <https://doi.org/10.1073/pnas.2002548117>

718 Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., MacCormack,
719 T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., Taylor, W.W., Tockner, K., Vermaire, J.C., Dudgeon,
720 D., Cooke, S.J., 2019. Emerging threats and persistent conservation challenges for freshwater
721 biodiversity. *Biological Reviews* 94, 849–873. <https://doi.org/10.1111/brv.12480>

722 Ricart, S., Villar, R., Hernández-Hernández, M., Rico-Amorós, A.M., Olcina-Cantos, J., Baños, C., 2023.
723 Reinforcing the Hydrosocial Cycle to foster water governance and stakeholders'
724 interdependence in urban agroecosystems: a local test in Benidorm, Spain. *Front. Agron.* 5.
725 <https://doi.org/10.3389/fagro.2023.1057211>

726 Rogers, A., 2012. The transformation of urban waterscapes : documenting waterscape manipulation
727 as an aspect of urban development in the Roman period. *Revue belge de Philologie et*
728 *d'Histoire* 90, 165–190. <https://doi.org/10.3406/rbph.2012.8394>

729 Rogers, S.L., Bulluck, L.P., Bukaveckas, P.A., 2024. Substantial pulses of aquatic insects emerge from
730 tidal freshwaters along the James River Estuary, Virginia, USA. *Freshwater Science* 43, 65–82.
731 <https://doi.org/10.1086/729306>

732 Rubin, E.J., Shaffer, C.A., Ramakrishnan, N., Watson, L.T., Dymond, R., Kibler, D., Dietz, R., Chanut, J.,
733 Lohani, V., Bosch, D., Speir, C., 2003. From landscapes to waterscapes: A PSE for landuse
734 change analysis. *Eng. Comp.* 19, 9–25. <https://doi.org/10.1007/s00366-002-0245-8>

735 Sabo, J., Power, M., 2002. River-watershed exchange: Effects of riverine subsidies on riparian lizards
736 and their terrestrial prey. *Ecology* 83, 1860–1869. <https://doi.org/10.2307/3071770>

737 Salvarina, I., Gravier, D., Rothhaupt, K.-O., 2017. Seasonal insect emergence from three different
738 temperate lakes. *Limnologica* 62, 47–56. <https://doi.org/10.1016/j.limno.2016.10.004>

739 Sarwar, M. (Ed.), 2020. Life cycle and development of Diptera. Intechopen.

740 Schindler, D.E., Smits, A.P., 2017. Subsidies of aquatic resources in terrestrial ecosystems. *Ecosystems*
741 20, 78–93. <https://doi.org/10.1007/s10021-016-0050-7>

742 Schulz, R., Bundschuh, M., Gergs, R., Brühl, C.A., Diehl, D., Entling, M.H., Fahse, L., Frör, O., Jungkunst,
743 H.F., Lorke, A., Schäfer, R.B., Schaumann, G.E., Schwenk, K., 2015. Review on environmental
744 alterations propagating from aquatic to terrestrial ecosystems. *Science of The Total*
745 *Environment* 538, 246–261. <https://doi.org/10.1016/j.scitotenv.2015.08.038>

746 Senapathi, D., Biesmeijer, J.C., Breeze, T.D., Kleijn, D., Potts, S.G., Carvalheiro, L.G., 2015. Pollinator
747 conservation - the difference between managing for pollination services and preserving
748 pollinator diversity. *Current Opinion in Insect Science, Neuroscience * Special Section: Insect*
749 *conservation* 12, 93–101. <https://doi.org/10.1016/j.cois.2015.11.002>

750 Shakeri, Y.N., White, K.S., Levi, T., 2018. Salmon-supported bears, seed dispersal, and extensive
751 resource subsidies to granivores. *Ecosphere* 9, e02297. <https://doi.org/10.1002/ecs2.2297>

752 Shipley, J.R., Twining, C.W., Mathieu-Resuge, M., Parmar, T.P., Kainz, M., Martin-Creuzburg, D.,
753 Weber, C., Winkler, D.W., Graham, C.H., Matthews, B., 2022. Climate change shifts the timing
754 of nutritional flux from aquatic insects. *Current Biology* 32, 1342-1349.e3.
755 <https://doi.org/10.1016/j.cub.2022.01.057>

756 Søndergaard, M., Jeppesen, E., 2007. Anthropogenic impacts on lake and stream ecosystems, and
757 approaches to restoration. *Journal of Applied Ecology* 44, 1089–1094.
758 <https://doi.org/10.1111/j.1365-2664.2007.01426.x>

759 Stenroth, K., Polvi, L.E., Fältström, E., Jonsson, M., 2015. Land-use effects on terrestrial consumers
760 through changed size structure of aquatic insects. *Freshwater Biology* 60, 136–149.
761 <https://doi.org/10.1111/fwb.12476>

762 Stepanian, P.M., Entekin, S.A., Wainwright, C.E., Mirkovic, D., Tank, J.L., Kelly, J.F., 2020. Declines in
763 an abundant aquatic insect, the burrowing mayfly, across major North American waterways.
764 Proceedings of the National Academy of Sciences 117, 2987–2992.
765 <https://doi.org/10.1073/pnas.1913598117>

766 Strayer, D.L., Dudgeon, D., 2010. Freshwater biodiversity conservation: recent progress and future
767 challenges. *jnbs* 29, 344–358. <https://doi.org/10.1899/08-171.1>

768 Swyngedouw, E., 1999. Modernity and hybridity: Nature, regeneracionismo, and the production of
769 the Spanish waterscape, 1890–1930. *Annals of the Association of American Geographers* 89,
770 443–465. <https://doi.org/10.1111/0004-5608.00157>

771 Tallman, P.S., Piland, N.C., Villarmarzo, M., Victoria-Lacy, L., Valdés-Velásquez, A., 2024. Waterscapes
772 meet socio-ecological models: A relational framework to examine water insecurity and
773 human health and well-being. *People and Nature* 6, 1036–1047.
774 <https://doi.org/10.1002/pan3.10635>

775 Taylor, J., 2022. Waterscapes of power in Bangladesh: The politics and anthropology of contested
776 access in large-scale irrigation modernisation. *The Australian Journal of Anthropology* 33, 47–
777 73. <https://doi.org/10.1111/taja.12419>

778 Turner, M.G., Gardner, R.H., O’Neill, R.V., 2001. *Landscape ecology in theory and practice: pattern
779 and process*, 2001st edition. ed. Springer, New York.

780 Twining, C.W., Brenna, J.T., Lawrence, P., Winkler, D.W., Flecker, A.S., Hairston Jr., N.G., 2019.
781 Aquatic and terrestrial resources are not nutritionally reciprocal for consumers. *Functional
782 Ecology* 33, 2042–2052. <https://doi.org/10.1111/1365-2435.13401>

783 Twining, C.W., Shipley, J.R., Winkler, D.W., 2018. Aquatic insects rich in omega-3 fatty acids drive
784 breeding success in a widespread bird. *Ecology Letters* 21, 1812–1820.
785 <https://doi.org/10.1111/ele.13156>

786 Valentim, H.I.L., Feio, M.J., Almeida, S.F.P., 2024. Fluvial protected areas as a strategy to preserve
787 riverine ecosystems—a review. *Biodivers Conserv* 33, 439–462.
788 <https://doi.org/10.1007/s10531-023-02774-w>

789 Vinnersten, T.Z.P., Östman, Ö., Schäfer, M.L., Lundström, J.O., 2014. Insect emergence in relation to
790 floods in wet meadows and swamps in the River Dalälven floodplain. *Bulletin of*
791 *Entomological Research* 104, 453–461. <https://doi.org/10.1017/S0007485314000078>

792 Visser, M.E., Gienapp, P., 2019. Evolutionary and demographic consequences of phenological
793 mismatches. *Nat Ecol Evol* 3, 879–885. <https://doi.org/10.1038/s41559-019-0880-8>

794 Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R., Stopak, D., 2021. Insect decline in the
795 Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences*
796 118, e2023989118. <https://doi.org/10.1073/pnas.2023989118>

797 Wessels, M.T., 2023. What’s in a name? Politicising wastewater reuse in irrigated agriculture. *Water*
798 *Alternatives* 16, 563–580.

799 Whiles, M.R., Goldowitz, B.S., 2001. Hydrologic Influences on Insect Emergence Production from
800 Central Platte River Wetlands. *Ecological Applications* 11, 1829–1842.
801 [https://doi.org/10.1890/1051-0761\(2001\)011\[1829:HIOIEP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[1829:HIOIEP]2.0.CO;2)

802 Williams, D.D., 1996. Environmental constraints in temporary fresh waters and their consequences
803 for the insect fauna. *Journal of the North American Benthological Society* 15, 634–650.
804 <https://doi.org/10.2307/1467813>

805 Williams, D.D., Williams, N.E., 1998. Aquatic insects in an estuarine environment: densities,
806 distribution and salinity tolerance. *Freshwater Biology* 39, 411–421.
807 <https://doi.org/10.1046/j.1365-2427.1998.00285.x>

808 Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P., Sear, D., 2004. Comparative
809 biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern
810 England. *Biological Conservation* 115, 329–341. [https://doi.org/10.1016/S0006-](https://doi.org/10.1016/S0006-3207(03)00153-8)
811 [3207\(03\)00153-8](https://doi.org/10.1016/S0006-3207(03)00153-8)

812 Wilson, M.I., Robertson, L.D., Daly, M., Walton, S.A., 1995. Effects of visual cues on assessment of
813 water quality. *Journal of Environmental Psychology* 15, 53–63. [https://doi.org/10.1016/0272-](https://doi.org/10.1016/0272-4944(95)90014-4)
814 [4944\(95\)90014-4](https://doi.org/10.1016/0272-4944(95)90014-4)

815 Zimmer, M.A., Kaiser, K.E., Blaszcak, J.R., Zipper, S.C., Hammond, J.C., Fritz, K.M., Costigan, K.H.,
816 Hosen, J., Godsey, S.E., Allen, G.H., Kampf, S., Burrows, R.M., Krabbenhoft, C.A., Dodds, W.,
817 Hale, R., Olden, J.D., Shanafield, M., DelVecchia, A.G., Ward, A.S., Mims, M.C., Datry, T.,
818 Bogan, M.T., Boersma, K.S., Busch, M.H., Jones, C.N., Burgin, A.J., Allen, D.C., 2020. Zero or
819 not? Causes and consequences of zero-flow stream gage readings. *WIREs Water* 7, e1436.
820 <https://doi.org/10.1002/wat2.1436>

821

822